Neurobiology of Learning and Memory 116 (2014) 96–104

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

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

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ARTICLE INFO

Article history:
Received 17 April 2014
Revised 12 September 2014
Accepted 15 September 2014
Available online 26 September 2014

Keywords:
Explicit memory
Implicit memory
Psychophysiology
Posttraumatic Stress Disorder
Contextual fear
Gist-based memory

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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http://dx.doi.org/10.1016/j.nlm.2014.09.004
1074-7427/

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.

tual-dependent memory effect is maximized with the passage of time (i.e., a week).

2.1. Materials and methods

2.1.1. Subjects

Forty-six healthy college students from the University of Barcelona were recruited for the experiment, and randomly assigned to the immediate group ($N = 24$; 19 female, $M = 23.00$ years, $SD = 4.85$), or to the delayed group ($N = 22$; 21 female, $M = 20.86$ years, $SD = 2.77$). All had normal or corrected-to-normal vision and reported no history of medical, neurological or psychiatric disorders. None of the subjects had previous knowledge of the DRM task. All subjects signed informed consent, approved by the Institute of Biomedical Research of Bellvitge Ethics Committee.

2.1.2. Procedures

2.1.2.1. Encoding phase. Encoding phase included two contextual conditions: fearful and neutral context. The fearful context was created by adapting a fear-potentiating paradigm in which a robust fearful state was evoked by the anticipation of electric shocks (Grillon, Ameli, Woods, Merikangas, & Davis, 1991; Riba et al., 2001). Thus, the encoding of word lists could take place either under contexts of anticipated electric shocks (i.e., fearful context) or not (neutral), which were indicated by colored clocks at the beginning of each trial (Fig. 1). Subjects were told which clock colors indicated which contextual conditions. The clock colors were randomly assigned across subjects and the clock remained on the screen throughout the 45 s trial. In the fearful context, the shocks were unpredictable (Grillon, 2008). Before encoding began, subjects were delivered a familiarization shock at the moment of their choosing, and were told that a shock could be delivered during any of the fear trials in an increasing intensity. In fact, only two shocks were delivered during encoding, in increasing intensity, and always during the last 15 s of the trial when the word list presentation was over. This way, expectancy of shock was maintained throughout all the fear trials, and although the shocks were always during the third and fifth fear trials, the wordlists presented during these trials were randomly selected and counterbalanced. Also, whether encoding started with a fearful or a neutral context was also counterbalanced across subjects. During each trial, the subject listened to a word list, which started 5 s after the clock appeared on the screen, and lasted 15 s. Contextual conditions alternated, seven lists being randomly assigned to each condition in a counterbalanced fashion between subjects. The order of the alternation was randomized across participants. Between trials, subjects rated their level of fear from one to ten in an analogical scale and waited for the next trial to begin. The next trial did not begin until 30–60 s had gone by and not before any rapid variations in SCR or peaks due to subjects' movements had disappeared (Bach, Flandin, Friston, & Dolan, 2010).

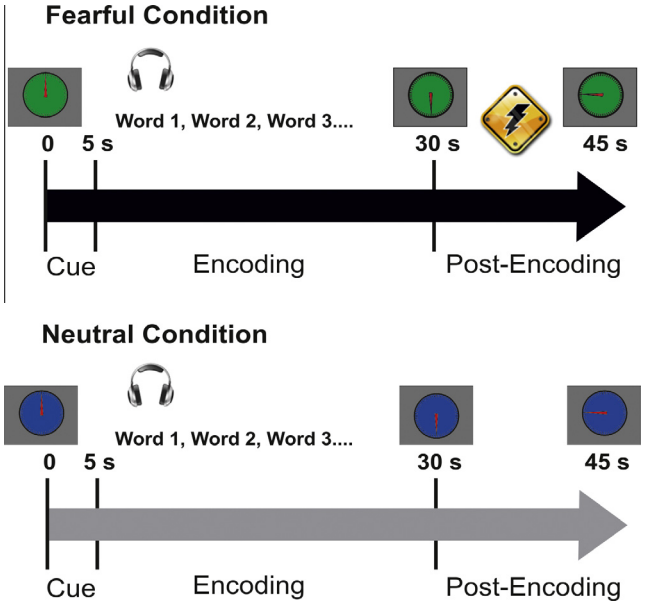

Fig. 1. Overview of encoding phase of experiment 1 and 2. Word-lists were randomly assigned to each experimental condition: fearful (above) or neutral (below) context, and counterbalanced between subjects. Note that the lightning bolt represents the shock. The analogical timer served as the starting signal and remained on the screen throughout the 45 s trial. The headphones refer to the presentation of the word lists. Between trials, subjects were given the time they needed (30–60 s) to rate their subjective level of fear on an analogical scale and regain their position. Only the first 30 s of the encoding trials were used to calculate zSCR means during encoding.

2.1.2.2. Recognition phase. Subjects were randomly assigned to respond to an immediate recognition memory test (30 min after encoding; $N = 24$), or returned the next week (range 6–8 days, $N = 22$) for the same test. Subjects were told before encoding that they would be subsequently tested for the word-lists, but were not given instructions about how they would be tested until immediately before the test. During the test, words were shown on the screen for 2 s in pseudorandom order (words from the same list were separated with a spacing of 13 other different words in between). For each list there were six test items: three items had been presented during the study phase (the 2nd, 8th and 13th word of each list), two were unrelated words, and one was the critical gist-based lure word with a strong semantic relation to the list. As in the original DRM task (Roediger & McDermott, 1995), subjects were not aware that gist-based lures were included in the test. 'Old/New' discrimination was required after the presentation of each word by pressing a button on the mouse accordingly. If they chose 'New' they were then asked whether they were 'Sure' or 'Not-Sure'. 'Old' choice was followed by a Remember/Know judgment (Tulving, 1985). Subjects were instructed to choose, by mouse click, 'Remember' ('Recuerdo', in Spanish (Fuentemilla et al., 2009) when they experienced a conscious recollection with contextual details (i.e., order in list, temporal context, perceptual details or associated thoughts or feelings), whereas they were instructed to choose 'Know' ('Saber', in Spanish (Fuentemilla et al., 2009) when they felt that the word had been previously presented but without a clear memory of its context.

2.1.3. Stimuli and physiological responses

2.1.3.1. Stimuli. We used 14 DRM semantically related word lists in Spanish (see Supplementary material), selected from previous studies (Alonso, Fernandez, Díez, & Beato, 2004; Fuentemilla et al., 2009; Roediger & McDermott, 1995), which were presented via headphones (Spanish native female voice). The lists had a mean valence of 5.29 and a mean arousal of 3.48 according to a Self-Assessment Manikin questionnaire from 1 to 9.

Three single electric shocks were delivered through an electrode attached with a Velcro strap to participant's dominant inner wrist, maximum intensity of 15 mA, duration of 50 ms, the familiarization shock at 30 V, the first encoding-shock at 40 V and the second at 50 V. A Grass Medical Instruments stimulator (Grass S48 Square Pulse Stimulator) charged by a stabilized current was used with a Photoelectric Stimulus Isolation Unit (Model PSIU6). Shocks were described by subjects as very uncomfortable, but not painful.

2.1.3.2. Physiological responses. Skin conductance was recorded during the whole session using Brain Amps amplifiers. SCR was

assessed using two Ag–AgCl electrodes, with a 32 channel BrainVision amplifier (BrainAmp ExG) and a GSR module. The electrodes were attached to the first and second fingers of the non-dominant hand. SCR waveforms were analyzed offline.

2.1.4. Data analysis

2.1.4.1. Behavioral data analysis. We performed the statistical analyses on behavioral data using the *d′* transformation, i.e., subtracting the *z* score that corresponded to the false-alarm rate (i.e., 'Old' responses to unrelated distractors not actually presented) from the *z* score that corresponded to the hit rate for either verbatim (measured by the subjects' responses to words that actually did appear during encoding) or gist-based memories (measured by the subjects' responses to unstudied critical words) (Stanislaw & Todorov, 1999). For both types of items, *d′* was calculated and repeated measures ANOVAs with condition (fearful, neutral) × group (immediate test, 2 week delayed test) × item type (verbatim item, gist-based item) was performed. Separate ANOVAs or *T*-tests were performed to decompose any possible interactions. Alpha was set at .05. A condition (fearful, neutral) × group (immediate test, delayed test) repeated measures ANOVA was used to evaluate mean subjective ratings of fear. To estimate effect sizes we used partial eta-squared and Cohen's *d* as appropriate.

2.1.4.2. SCR data analysis. Single-trial changes in SCR were assessed by subtracting mean SCR activity during the 1000 ms previous to the clock cue from mean SCR value during the encoding trial (from 0 to 30 s). The last 15 s of data were not included in this analysis as we were interested only in processes occurring during encoding. Individual mean SCR (*z*) was averaged for each contextual condition and normalized for individual differences by subtracting each individual's mean amplitude and dividing by the individual's standard deviation. A condition (fearful, neutral) × group (immediate test, delayed test) repeated measures ANOVA was used to evaluate mean SCR. To examine whether the *z*SCR difference between conditions was constant throughout the 14 encoding lists, we ran an ANOVA of the mean difference in *z*SCR between conditions for each pair of lists in order of presentation.

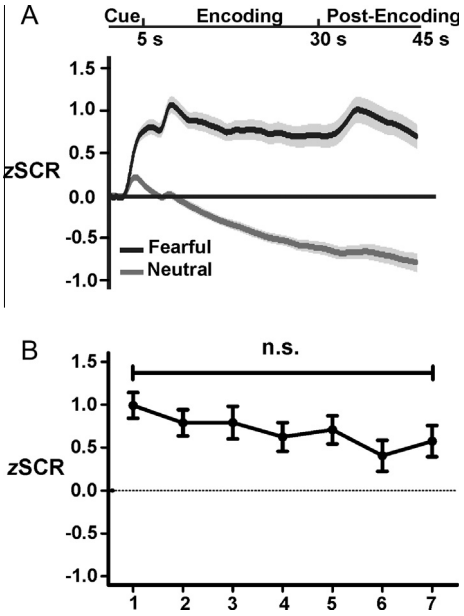

Fig. 2. (A) Mean Skin Conductance Response (*z*SCR) as a function of encoding condition across all subjects pooled together for immediate and delay conditions after cue presentation in Experiment 1. For this figure we excluded the two fearful trials with shock and included the entire 45 s of the trial to specifically illustrate the difference due to anticipation of shock only during the entire trial. Shaded colors indicate standard error of the mean. (B) List by list *z*SCR difference (fearful versus neutral) during encoding. Each point is the mean difference between the respective pair of encoding trials in corresponding order. Error bars indicate standard errors of the mean.

2.2. Results

2.2.1. Psychophysiological (SCR) and subjective indices of fear

In order to verify whether our paradigm produced reliable indices of fear states for the fearful condition, we examined SCR during encoding and subjective ratings provided after each trial by the subjects. Fig. 2A displays the SCR magnitude of each contextual condition. We found a main effect of fearful condition ($F_{1,44} = 92.66$, $p < .001$, $\eta_p^2 = .68$), mean zSCR ($M = .62$, $SD = .57$) was greater during the encoding of words in anticipation of an electric shock than in anticipation of no electric shock ($M = -.23$, $SD = .28$), (Fig. 2A). The analysis of the mean difference between conditions for each pair of lists confirmed that the effect of contextual fear was stable throughout the experiment ($F_{6,40} = 1.45$, $p = .221$, $\eta_p^2 = .04$, ns) (Fig. 2B). In addition, for subjective fear ratings we found a main effect of fearful condition ($F_{1,44} = 78.97$, $p < .001$, $\eta_p^2 = .64$). Mean subjective fear ratings were greater after fearful contexts ($M = 5.40$, $SD = 2.03$) than after neutral contexts ($M = 3.04$, $SD = 1.80$).

2.2.2. Explicit memory: verbatim and gist-based recognition memory

We found a three level interaction ($F_{1,44} = 7.23$, $p = .010$, $\eta_p^2 = .14$) and a item type∗group interaction ($F_{1,44} = 7.60$, $p = .008$, $\eta_p^2 = .15$). The ANOVA for verbatim items showed a main effect of fearful condition (Fig. 3A) ($F_{1,44} = 16.13$, $p < .001$, $\eta_p^2 = .27$) and a main effect of delay ($F_{1,44} = 6.28$, $p = .016$, $\eta_p^2 = .13$) (see Table 1 and 2). However, we found a significant interaction (condition × group, $F_{1,44} = 5.25$, $p = .027$, $\eta_p^2 = .11$). Post-hoc repeated measures *t*-tests further

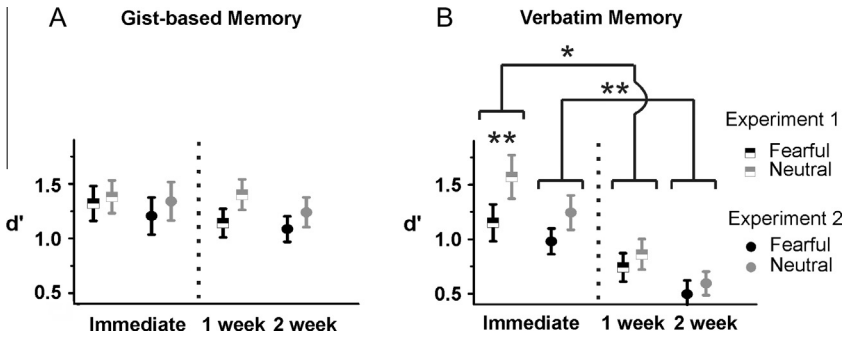

Fig. 3. Recognition memory performance (*d′*) for gist-based memories (A) and verbatim memories (B) items in Experiment 1 and 2, as a function of delay condition. We calculated a verbatim recognition score for words presented during the encoding phase, and a gist-based recognition score for critical "lure" words. Error bars indicate standard errors of the mean. Asterisks represent $p < .05$. Double asterisks (∗∗) represent $p < .01$.

confirmed that the decrease in verbatim memory due to contextual fear appeared in the immediate recognition test ($t_{23} = -3.73$, $p = .001$, Cohen's $d = .57$) but not after a week ($t_{21} = -1.89$, $p = .072$, Cohen's $d = .053$, ns), possibly explained by the low behavioral accuracy at 1 week for words encoded in both fearful and neutral contexts. There was neither a decrease in subjects' recognition of gist-based lure items due to delay nor due to a condition × group interaction (all effects were $p > .20$) (Fig. 3B). The ANOVA for gist-based items did not show a significant effect of fearful context on the overall proportion of gist-based memories ($F_{1,44} = 3.48$, $p = .069$, $\eta_p^2 = .073$, ns).

In sum, we found that fearful contexts produced a dissociation of the verbatim versus the gist-based explicit episodic memory representations. Thus, whilst verbatim memory representations were compromised when event information was encoded under contextual fear, gist-based memories were unaffected when compared to similar information encoded under neutral contexts. However, and against our initial hypothesis, the fearful context-dependent effect on verbatim memories was not observed when testing was delayed a week.

Table 2
A summary of ANOVA results.

Encoding		Experiment 1 $F(1,44)$	Experiment 2 $F(1,38)$
	zSCR fearful context	92.66**	68.27**
	zSCR delay	<0.01	0.11
	zSCR fearful context × Delay	0.15	0.09
	Subjective ratings fearful context	78.97**	76.92**
	Subjective ratings delay	0.07	0.70
	zSCR fearful context × Delay	0.23	2.19
	Effect of list on zSCR fear-neutral	$F_{6,40} = 1.45$	$F_{6,34} = 2.20$
Recognition memory test			
Verbatim	Fearful context	16.13**	4.06, $p = .051$
	Delay	6.28*	12.66**
	Fearful context × Delay	5.25*	1.13
Gist	Fearful context	3.48	1.53
	Delay	0.17	0.38
	Fearful context × Delay	1.17	0.01

F-values of main effects and interactions from the ANOVAs comparing Experiment 1 and 2.
** Significance level of $p < .01$.
* Significance level $p < .05$.

3. Experiment 2

In Experiment 2 we made two additional variations to the previous design with the aim to test the hypothesis that implicit and explicit memory traces of fearful episodes remain distinguishable with the passage of time. Firstly, we extended the delay period to investigate verbatim and gist-based memory traces after longer periods of time, given more time for differentially selective memory processing. Thus, doubling the time interval between encoding and test should allow for more time for both forgetting and consolidation to take place, which have been shown to be highly selective processes (Born & Wilhelm, 2012). This selective processing and reorganization of memory representations could arguably lead to differential changes in the structure of verbatim/gist memory traces. Secondly, we recorded SCR at test as a measure of the implicit memory trace. 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 (Baioui, Ambach, Walter, & Vaitl, 2012; Raio et al., 2012).

3.1. Materials and methods

3.1.1. Subjects

Recruitment was conducted as in Experiment 1, except that there were nineteen participants randomly assigned to the immediate group (14 female, $M = 21.74$ years, $SD = 3.35$), and twenty-one to the delayed group (12 female, $M = 22.52$ years, $SD = 3.63$).

3.1.2. Procedure

Experiment 2 followed the same procedure of Experiment 1 except as noted here.

In order to measure the implicit memory response associated to the words a subsample of the test items (the first verbatim item, the gist-based lure and an unrelated word for each list) were presented again and randomly after the recognition test (~10 min). In this subsequent test, the shock-electrodes were strapped to subjects' wrists and each word appeared on the screen during 2 s. Words were separated by a random interval ranging from 8 to 9 s, thus avoiding overlap between item-specific SCR (Boucsein, 1992). We further asked the subjects to recall, if possible, the context in which each word was respectively presented in. Thus, they were reminded of the structure of the encoding phase and instructed to indicate, when the word disappeared from the screen, whether the item was presented either during fearful context (i.e., during a trial with the corresponding clock color and possibility of shock) or a neutral trial, or was not presented during the encoding phase.

3.1.3. Stimuli and physiological responses

Stimuli (i.e., 14 word lists and electric shock characteristics) were the same as in Experiment 1 and SCR and subjective ratings were acquired with similar parameters as in Experiment 1.

3.1.4. Data analysis

Analysis for behavioral and SCR data were conducted as in Experiment 1. In addition, single-trial changes in SCR during retrieval (for the subsample of words represented with longer intervals, after the initial test) were assessed also by subtracting mean SCR activity during the 1000 ms previous to the word presentation from mean SCR value during word presentation, calculated as the mean SCR during the 1000 ms window centered on the peak SCR at 1000 ms after the appearance of the word. SCR during retrieval were normalized for individual differences, and average trial amplitudes were pooled together for each group and condition (Mas-Herrero, Zatorre, Rodriguez-Fornells, & Marco-Pallarés, 2014). Repeated measures ANOVAs with condition (fearful, neutral) × group (immediate test, 2 week delayed test) × item type (verbatim item, gist-based item) was performed on SCR during retrieval and d' values for explicit encoding context memory responses. Separate ANOVAs or *T*-tests were performed to decompose any possible interactions. Bonferroni corrected one-sampled *t*-tests were performed to examine whether subjects were able to explicitly retrieve correctly above chance (i.e., $d' = 0$) the encoding context (fearful or neutral) for the subsample of words represented after the initial test.

3.2. Results

3.2.1. Psychophysiological (SCR) and subjective indices of fear

Congruent with Experiment 1 findings, we found a main effect of fearful condition ($F_{1,38} = 68.27$, $p < .001$, $\eta_p^2 = .64$) for mean zSCR during encoding, mean zSCR throughout encoding was higher under fearful ($M = -.01$, $SD = .91$) than under neutral contexts ($M = -1.01$, $SD = .49$). In addition, and replicating Experiment 1 findings, zSCR differences between encoding conditions did not vary throughout the experiment ($F_{6,34} = 2.20$, $p = .074$, $\eta_p^2 = .053$,

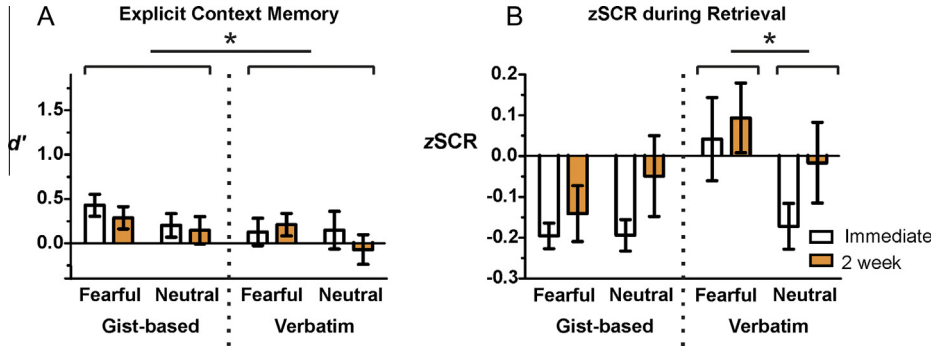

Fig. 4. (A) Context memory awareness (d') for verbatim items in Experiment 2, in function of delay condition. (B) Skin Conductance Response (zSCR) during retrieval in Experiment 2. Error bars indicate standard errors of the mean. Asterisks represent $p < .05$. Note that the difference indicated in Fig. 4A is marginal ($p = .051$).

ns).We found a main effect of fearful condition for subjective fear ratings ($F_{1,38} = 76.92$, $p < .001$, $\eta_p^2 = .67$), which were significantly greater after trials in a fearful context ($M = 4.66$, $SD = 2.21$) than after neutral context trials ($M = 1.83$, $SD = 1.40$).

3.2.2. Explicit memory: verbatim and gist-based recognition memory

The ANOVA showed an item type∗group interaction ($F_{1,38} = 10.43$, $p = .003$, $\eta_p^2 = .22$) and a main effect of fear ($F_{1,38} = 4.93$, $p = .032$, $\eta_p^2 = .12$) (see Table 1 and 2). The three level interaction and the condition∗item type interaction both resulted non-significant ($p > .49$). The ANOVA for verbatim items showed a marginal effect of fearful condition ($F_{1,38} = 4.06$, $p = .051$, $\eta_p^2 = .10$) on the memory accuracy for verbatim items, and a main effect of delay group ($F_{1,38} = 12.66$, $p = .001$, $\eta_p^2 = .25$) (Fig. 3B). The interaction was not significant (condition × group, $F_{1,38} = 1.13$, $p = .294$, $\eta_p^2 = .03$, ns). Replicating data from Experiment 1, the ANOVA for gist-based items showed that memory for gist-based information between groups or conditions was not significantly different (all effects were $p > .20$) (Fig. 3A).

3.2.3. Behavioral data and SCR for context memory

To directly test subjects' explicit ability to identify the encoding context in which verbatim items were embedded in we ran a repeated measures ANOVA with condition (within: fearful, neutral) x group (between: immediate, delayed) x item type (within: verbatim, gist-based) on the d' values of the explicit encoding context memory responses. We found a trend, albeit not significant, effect of item type ($F_{1,38} = 3.97$, $p = .054$, $\eta_p^2 = .10$), otherwise no significant effects were found (all $p > .09$). Explicit encoding context memory was marginally higher ($t_{39} = 2.01$, $p = .051$) for lure items ($M = 0.26$; $SD = .48$) compared to true items ($M = 0.10$; $SD = .56$). Given that low accuracy was observed (Fig. 4A), we performed post-hoc one-sampled t-tests to test whether subjects were able to retrieve correctly (above chance) the item-context association for presented words. We found they were only able to correctly retrieve encoding context for gist-based items associated to words encoded in fearful contexts. d' for gist-based items associated to fearful contexts was significantly different from 0 both for the immediate group ($t_{18} = 3.43$, $p = .003$, Cohen's $d = 1.62$), and the delay group ($t_{21} = 2.30$, $p = .032$, Cohen's $d = 1.00$), although for the delay group significance does not pass the Bonferroni correction. No other d' values were significantly above chance (all $p > 0.10$). These results suggest subjects only encoded a gist-based representation for the encoding context of the trials. This is in line with the DRT's concept of a dissociated gist-based contextual representation which might contain explicit memory for the theme of the list associated to emotional content, but apparently dissociated from implicit responses to the words, as seen through SCR.

Despite subjects' inability to consciously access item-context associations, we investigated whether such item-context memory trace was reflected implicitly. Thus, we contrasted zSCR for when subjects were presented with words learned in a fearful context and in a neutral context, independently of their subjective response. The ANOVA revealed a main effect of item type ($F_{1,38} = 7.36$, $p = .010$, $\eta_p^2 = .16$), characterized by an interaction (condition × item type, $F_{1,38} = 4.26$, $p = .046$, $\eta_p^2 = .10$). We then ran two separate ANOVAs, one for each item type. For verbatim items, we found a main effect of fear ($F_{1,38} = 4.18$, $p = .048$, $\eta_p^2 = .10$). Whereas for gist-based items we found no difference due to fearful context or interactions with condition (all $p > .55$)). For both item types, we found no effect of delay group or interactions with group (all $p > .09$).

4. Discussion

We used a contextual fear paradigm in humans to test the prediction from a recent theoretical account of PTSD (Brewin, 2001) that the encoding of a fearful event induces dissociated explicit and implicit memory representations. These findings indicate that the implicit, but not the explicit, memory trace of a fearful context of an episode can be detected through SCR at long-term and is dissociated from the gist-based memory. We found no clear evidence of accurate explicit memory traces for the fearful or neutral contexts during encoding, either 30 min or 2 weeks afterwards.

Our results highlight the dissociation between explicit and implicit memory systems (Schacter, 1987) and support the idea that contextual fear differentially affects both memory systems in a way that possibly interferes with their dynamics at long term. Subjects were not able to explicitly access the specific memory for the fearful context the words were presented in when tested, although they showed long-term implicit 'recognition' through SCR for words presented in a fearful context. Although our data do not permit ruling out the possibility of conscious emotion associated to the implicit 'recognition' through SCR, the fact that subjects were unable to report verbally the emotional context in which the word was presented speaks against this possibility (Schacter, 1987). Similarly, implicit recognition through SCR in the absence or dissociated from explicit verbal recognition has been demonstrated in a variety of recognition experiments (Baioui et al., 2012; Knight, Nguyen, & Bandettini, 2003; Tranel & Damasio, 1985). Such experiments suggest the emotional network supports implicit recognition observable through SCR even when such information is inaccessible explicitly. Interestingly, how explicit and implicit memory systems differentially process fearful events and interact in fear expression may be critical in understanding the nature of psychopathology related to traumatic events (Brewin, 2014).

More generally, if increased SCR can accurately reflect implicit memory content, then SCR may also allow distinguishing verbatim from gist-based memories (Baioui et al., 2012; Brainerd & Reyna, 2002). According to this view, the SCR in our paradigm may simply reflect direct involuntary input from implicit memory associations for lower-level perceptions, dissociated from gist-based memory (Brainerd & Reyna, 2002). Whether this type of implicit memory can be interpreted as an implicit type of episodic memory or is possibly related to long-term perceptual memory (Brewin, 2014), awaits further investigation.

Long-term contextual fear learning involves the amygdala, the hippocampus and the prefrontal cortex (Lonsdorf, Haaker, & Kalisch, 2014). The amygdala is a central part of the fear memory circuit (Maren, 2005). It automatically searches for signals of threat in the environment (Ohman, 2005) and supports the association between fear response and external stimuli (Joseph, 2003). Contextual fear learning additionally involves the hippocampus (Bouton et al., 2006), which supports context discrimination and the processing of contextual stimuli (Frankland, Cestari, Filipkowski, McDonald, & Silva, 1998). The prefrontal cortex allows further flexibility by supporting the regulation and inhibition of fear (Lee & Choi, 2012) as well as the anticipation of different types of possible risks (Bechara, Tranel, Damasio, & Damasio, 1996; Guyer et al., 2008). The implicit fear traces we detected may correspond to emotion-based biasing signals (Damasio, 1996; Dunn, Dalgleish, & Lawrence, 2006) that respond specifically to verbatim memories encoded within the fearful context, through an automatic reactivation of fear associations in the amygdala (Maren, 2005). Similarly, implicit emotion-based recognition without awareness has been detected through SCR in other paradigms. Classical fear conditioning has been shown to elicit SCR to subliminal stimuli (Morris et al., 1998), prosapagnosics have been shown to be capable of implicit emotion-based recognition through SCR (Tranel & Damasio, 1985), and implicit emotion-based learning associated to anticipatory SCR activity has been shown in the Iowa Gambling Task (Bechara, Damasio, Tranel, & Damasio, 1997). In our experiments, that we did not find implicit SCR fear traces for the gist-based memories is interesting because it suggests a different involvement in fear learning between verbatim explicit memory and gist-based explicit memory (Reyna & Brainerd, 1998). Gist-based explicit memory is well supported by prefrontal areas whereas verbatim explicit memory depends on the involvement of the medial temporal lobe regions, and especially the hippocampus (Alonso et al., 2004; Kim & Cabeza, 2007). The absence of implicit fear traces for gist-based memories thus suggests a differential contribution of the prefrontal cortex compared to the hippocampus in contextual fear learning and a lack of specific associations between prefrontal based gist memories and amygdala based fear associations (Ohman, 2005).

Our results provide experimental evidence supporting predictions based on the DRT model (Brewin et al., 2010), a clinical-based model of PTSD and other anxiety related disorders. In this model, fearful memories are held to be formed by at least two dissociable memory traces: an involuntary sensorial-affective (implicit) representation and a verbal contextualized (explicit) representation. Our results showed how aspects of memory that are likely to play a causal role in PTSD (Brewin, 2011), such as an enhanced tendency to memory generalization and strong sensorial-affective involuntary responses, may be induced by implementing a DRM task and SCR recording within a contextual fear paradigm in a controlled laboratory setting. If such memory aspects are easily inducible through contextual fear, this suggests that these aspects may not be caused by PTSD, although further evidence is needed to understand what causal role they may play in the development and maintenance of PTSD (Brewin, 2011). Also, considering that gist-based processing is the basis for the formation of false memories, an interesting possible implication is that false gist-based memory production may prove to be adaptive in preventing anxiety disorders.

According to the DRT, if a traumatic sensorial-affective representation is not coupled to an adequately contextualized representation, anxiety disorders are likely to develop (Brewin et al., 2010). Similarly, learning theory posits that contextual representations play a crucial role in fear extinction in animals and humans (Bouton et al., 2006). It follows then that long-term implicit fear memories, such as we detected through SCR, are the source of clinical anxiety symptoms. The failure to recover from the effects of trauma (Yehuda & LeDoux, 2007) may be due to the unregulated activation of such long-term implicit fear memories in the absence of an adequate contextualization process (Brewin, 2011), leading to a failure of fear extinction (Lommen, Engelhard, Sijbrandij, van den Hout, & Hermans, 2013). The repetition and intensification of the involuntary reactivation of fearful memories (Giezen, 2005), due to the absence of a contextual control of fear extinction (Maren, Phan, & Liberzon, 2013), may underlie clinical symptoms such as flashbacks and nightmares (Brewin et al., 2010). The involuntary reactivation of fearful memories when coupled with random association and generalization to novel cues (Kaouane et al., 2012; Oyarzún & Packard, 2012), may explain how PTSD develops, sometimes after long periods of time such as in delayed-onset PTSD (Andrews, Brewin, Philpott, & Stewart, 2007). Treatments for clinical anxiety, typically involving the reduction of the fear response through repeated exposures, although effective (Mabey & van Servellen, 2014), are often a short-lived success and followed by relapse (Vervliet et al., 2013). Such treatments generally attempt to induce the process of fear extinction, through which a contextual memory that suppresses and controls the fearful memory is formed (Maren et al., 2013). Relapse can be simply explained through a persistence and reactivation of the fearful memory coupled with insufficient contextual control. Depending on which role contextual representations play, the return of fear is designated in a variety of different ways, namely renewal, spontaneous recovery, or reinstatement (Vervliet et al., 2013). However, direct evidence of the nature of such fear-related traces that are at the base of persistent clinical anxiety is scarce.

The current results indicated that long-term implicit fearful traces detected through SCR are dissociated from gist-based memories and inaccessible explicitly, although these long-term implicit fear traces are closely associated to specific verbatim memories. These results give support to the idea that studying SCR of patients presented with specific perceptual stimuli, while testing for gist-based and verbatim explicit memories, may help in identifying the exact conditions that produce successful long-term reduction of the fear response (Vervliet et al., 2013). Our data suggests that such aspects of memory can be elicited by even moderate levels of fear, and measured through SCR, thereby providing the possibility to model, at the laboratory level, the starting conditions and the long term course of fearful memories. Thus, the dynamics and interactions of the implicit and explicit components of fearful memories can be specified empirically, and the predictions then tested in a clinical setting, promoting thereby the emergence of translational treatment strategies for pathological fearful memories. Although the DRT is a plausible and productive framework, more evidence is needed to better understand how the nature of memory representations in the brain relates to aspects of memory which we conceptualize as explicit, implicit, detailed and abstract memories.

There are however several aspects of the results and design that should be discussed. We reasoned the discrepancy in the results of the analysis of explicit memory between Experiment 1 and Experiment 2 could be partly explained by a lesser degree of memory accuracy for true items in fearful and neutral context at the immediate test in Experiment 2. However, we think this does not directly

affect the claims of the study. Firstly, because they concern the explicit and implicit contextual memory, and secondly, because in both experiments we found that explicit memory for words was highest when tested immediately after encoding. Concerning the explicit memory responses for the different item types, we did not find conclusive evidence of fearful contexts augmenting the formation of explicit gist-based memories, however our data cannot rule out that this may indeed occur under different conditions and our results do suggest that fearful contexts decrease explicit verbatim memories, which ultimately can be derived as an increased tendency of the participants to rely on their gist memory. Concerning the possible effect of modality (Smith & Hunt, 1998), several studies (Gallo, McDermott, Percer, & Roediger, 2001; Kellogg, 2001; Pierce & Gallo, 2005, 2011) have shown a modality effect on DRM false memory. Visual presentation at study tends to reduce false memories. Visual presentation tends to make words more distinctive than auditory presentation, and this difference facilitates subsequent memory discrimination. One of our main purposes was to test how gist-based memory was modulated by the effects of a fear-conditioning paradigm. Therefore, our design incorporated a modality presentation mismatch between study and test to guarantee, as much as possible, a minimum amount of gist-based memories. Concerning the validity of the encoding contexts, although our data does not allow ruling out the possibility of subtle long-term tonal differences that might exist between the neutral condition and a theoretical relaxed baseline condition without any stimuli, we think our rational for characterizing the conditions as we did is nonetheless justified, considering the differences we found in both SCR and subjective fear ratings.

The present findings may have implications towards the understanding of how the processing of fearful memories sometimes leads to normally contextualized fear memories and in other cases to pathological trauma and anxiety disorders such as PTSD (Brewin, 2011). If, as our results suggest, even moderate levels of fear produce memory disturbances hypothesized to cause and maintain PTSD, whether PTSD develops or not after a possibly traumatic event might then critically depend on the adequate contextualization of the fearful memory that serves to inhibit the otherwise pathological overemotional responses associated to PTSD (Maren et al., 2013).

Financial disclosure

The authors report no biomedical financial interests or potential conflicts of interest.

Acknowledgements

This research has been supported by Grants from the Spanish Government (PSI2010-15024 to L.F. and PSI2008-03901/PSIC to A.R.F), the Catalan Government (Generalitat de Catalunya, 2009 SGR 93) and the Brazilian National Research Council (CNPq) to L.M.S. L.F. is a fellow of the Ramon y Cajal program.

We thank David Cucurell for advice and technical assistance.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2014.09.004.

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