Falling Out of Time: Enhanced Memory for Scenes Presented at Behaviorally Irrelevant Points in Time in Posttraumatic Stress Disorder (PTSD)

Einat Levy-Gigi1,2, Szabolcs Kéri2,3*

1 Rutgers University, Center for Molecular and Behavioral Neuroscience, Newark, New Jersey, United States of America, 2 National Psychiatry Center, Budapest, Hungary, 3 University of Szeged, Faculty of Medicine, Department of Physiology, Szeged, Hungary

Abstract
Spontaneous encoding of the visual environment depends on the behavioral relevance of the task performed simultaneously. If participants identify target letters or auditory tones while viewing a series of briefly presented natural and urban scenes, they demonstrate effective scene recognition only when a target, but not a behaviorally irrelevant distractor, appears together with the scene. Here, we show that individuals with posttraumatic stress disorder (PTSD), who witnessed the red sludge disaster in Hungary, show the opposite pattern of performance: enhanced recognition of scenes presented together with distractors and deficient recognition of scenes presented with targets. The recognition of trauma-related and neutral scenes was not different in individuals with PTSD. We found a positive correlation between memory for scenes presented with auditory distractors and re-experiencing symptoms (memory intrusions and flashbacks). These results suggest that abnormal encoding of visual scenes at behaviorally irrelevant events might be associated with intrusive experiences by disrupting the flow of time.

Introduction
Posttraumatic stress disorder (PTSD) may develop after exposure to psychological trauma that threatens basic security and exceeds coping abilities [1]. PTSD symptoms include intrusive mental contents (unwanted memories, flashbacks, and nightmares), avoidance of thoughts and cues related to trauma, emotional numbing, and increased vigilance. Although memory is usually impaired in PTSD, the coexistence of avoidance and intrusions highlights the Janus-face of these symptoms. There are deficits in voluntary control (e.g., inability to recall basic details of events) and enhancement of spontaneous memories (unintended re-experiencing) [2–8].

Brewin [9] defined three aspects of memory that predict progression of PTSD and may have a causal role in the development of symptoms: integration of trauma with identity, disorganized contextual memories, and sensation-based memories/flashbacks. Disorders of contextualization refer to a lesseened ability of patients to recall coherent and integrated narratives of trauma-related autobiographical memories. Instead, patients often experience intrusive and emotion-laden fragments of traumatic events (flashbacks), which are vivid, stereotyped, and sensual images [9]. Despite a growing amount of evidence suggesting that memory dysfunctions are critical in PTSD, basic mechanisms of visual memory for complex information and its modulation by behavioral context are unknown.

Humans have a tremendous capacity to perceive visual scenes but recognition memory for them is often weak [10–15]. However, if investigators use a rapid serial visual presentation paradigm and expose scenes at behaviorally relevant points in time (i.e., together with a target stimulus), recognition memory is better relative to trials when scenes appear at behaviorally irrelevant points in time (i.e., together with distractors) [16]. Greater attention allocation may explain this enhanced memory, which facilitates not only the processing of the behaviorally relevant target, but also its background, the scene [17]. In the current study, we used this paradigm to investigate scene perception and memory (Figure 1).

We studied whether individuals with PTSD are able to use behaviorally relevant events (detecting target letters and auditory tones) to increase recognition memory for background scenes. We predicted that individuals with PTSD exhibit a reduced capacity to develop memory traces for target letters/tones and background scenes at behaviorally relevant points in time because of their dysfunction of attentional control [18]. We also tested whether individuals with PTSD are able to create memory representations of trauma-related scenes in a rapid serial presentation paradigm. We hypothesized that attention is enhanced for trauma-related scenes relative to neutral scenes in PTSD. Therefore, the prediction was that individuals with PTSD show better recognition performance for trauma-related scenes as compared to controls.

Materials and Methods
Participants
Forty individuals with PTSD, including seven late-onset cases when symptoms appeared more than six months after the
traumatic event, and 40 control volunteers without PTSD participated in the study. On October 4, 2010, a damn of a sludge reservoir owned by an aluminum company had ruptured, and a mixture of toxic red sludge inundated the settlements of Kolontár, Devecser, and Somlóvásárhely. It was Hungary’s largest ecological disaster (http://redsludge.bm.hu/). Individuals with PTSD and controls lived in the red sludge-affected area and personally witnessed the disaster. Volunteers were recruited via local psychiatric units, general practitioners, and self-help organizations. Exclusion criteria included history of other psychiatric and neurological disorders, including former PTSD related to other traumatic events and psychoactive substance misuse. All participants were offered the option to be referred to treatment regardless of their involvement in the study. Participants did not receive monetary compensation. The assessment approximately took two hours.

We conducted the assessments prior to therapy. Therefore, participants did not receive medications or psychotherapy at the time of testing. We administered the Structured Clinical Interview for DSM-IV axis I disorders (SCID-CV) [19], the Trauma and Life Events Self-report Inventory (TLESI) [20], the Clinician-Administered PTSD Scale (CAPS) [21], the Hamilton Depression Rating Scale (HAM-D) [22], and the Wechsler Abbreviated Scale of Intelligence (WASI) [23]. The scales were administered by trained clinicians who were not aware of the data obtained from the experiments. Table 1 depicts the demographic and clinical characteristics.

Ethics statement
The study was approved by the institutional ethics committee (University of Szeged, No. 2697/2010) and was done in accordance with the Declaration of Helsinki. After full description of the study, all participants gave written informed consent.

Stimuli
We used a VP2765-LED-27” monitor for stimulus presentation (ViewSonic, Walnut, CA; refresh rate: 60 Hz; resolution: 1920×1080 pixel; viewing distance: 50 cm; output luminance: 65 cd/m²). Stimuli were photographs (size: 28 degrees of visual angle) from the LabelMe Natural and Urban Scenes database [24] (http://cvcl.mit.edu/database.htm) and a previously used stimulus set [14]. We also made 250 photographs of the red sludge disaster, which served as trauma-related stimuli. All stimuli were adjusted to meet the properties of the LabelMe database [24]. Ten trauma-exposed individuals rated each stimulus for emotional valence and trauma-related features on a five-level Likert scale (1 – emotionally neutral, trauma unrelated; 5 – emotionally laden, trauma-related). In the neutral condition, we included only scenes with a score of 1 point, whereas in the trauma-related condition we used scenes that received 4–5 points.

Procedure
We tested participants on three different tasks (described below as Experiments 1–3). The order of the tasks was counterbalanced across participants. The experiments were separated by breaks in order to avoid fatigue.

Experiment 1: Neutral scenes with visual target. We used the modified method of Lin et al. [16]. Each trial included a rapid serial presentation stream of 16 scenes (exposure time: 133 msec/scene, inter-stimulus interval: 367 msec). This presentation rate is slow enough to avoid attentional blink [16]. A gray square (size: 1 degree of visual angle) appeared in the center of some scenes.
Table 1. Demographic and clinical characteristics of the participants.

|                          | PTSD (n = 40, 11 male, 29 female) | Controls (n = 40; 11 male, 29 female) |
|--------------------------|-----------------------------------|--------------------------------------|
| Age (years)              | 41.3 (7.6)                        | 41.9 (8.7)                           |
| Education (years)        | 10.9 (5.4)                        | 11.1 (6.1)                           |
| IQ                       | 102.1 (11.5)                      | 103.0 (12.0)                        |
| TLSI*                    | 5.1 (2.1)                         | 3.1 (1.9)                            |
| HAM-D**                  | 15.0 (6.0)                        | 8.4 (3.4)                            |
| Duration of symptoms (months) | 4.3 (1.8)                      | -                                    |
| CAPS                     | -                                 | -                                    |
| Re-experiencing          | 19.4 (7.0)                        | -                                    |
| Hyperarousal             | 31.0 (6.5)                        | -                                    |
| Avoidance                | 23.7 (6.7)                        | -                                    |

Data are mean (standard deviation). TLSI - Trauma and Life Events Self-report Inventory (mean number of traumatic and adverse life events), HAM-D - Hamilton Depression Rating Scale, CAPS - Clinician-Administered PTSD Scale.

* t(78) = -4.39, p < 0.001; ** t(78) = -6.10, p < 0.001.

The square contained white target or black distractor letters (type: Calibri; font size: 20) (Figure 1). Target and distractor letters appeared in the center of two-two non-consecutive scenes out of the total 16 scenes. The remaining 12 scenes contained neither target nor distractor letters. Participants were requested to remember target letters and to ignore distractor letters. Following each trial, we first asked the participants to type the target and the distractor letter. After the letter recall phase, two test scenes (“A” and “B”) were exposed for 3000 msec. One of these scenes was from the sequence (serial position: 6–14), whereas the other scene was new. We asked the participants to choose which of the scenes appeared in the sequence by pressing key “A” or “B” on the computer keyboard (Figure 1). The test stimulus could be a scene without a letter, with a target letter, or with a distractor letter in the sequence. We applied 300 intermixed trials (10 blocks of 30 trials) separated by breaks. Before the test, we administered a training session of 30 trials for each participant, but they were not familiarized with the test scenes.

**Experiment 2: Neutral scenes with auditory target.** Stimulus presentation was similar to that described in Experiment 1 with the exception that each scene was paired with a brief auditory tone (duration: 50 msec). No letters were presented. The frequency of baseline tones was 260 Hz (40 dB). Baseline tones were paired with 12 out of the 16 scenes. Target tones were presented together with two non-consecutive scenes. The frequency of the target tones was either 130 Hz (low pitch) or 520 Hz (high pitch). Two scenes appeared together with distractor tones, which were louder than the baseline tones (60 dB). Participants were asked to ignore the distractor tones. Following the trial, the task was to discriminate the pitch of the target tones as either lower or higher than the baseline tones. Participants responded by pressing two different keys (“A” for high, “B” for low) on the computer keyboard. After the tone discrimination, there was a scene recognition task as described in Experiment 1. The number of trials was the same as in Experiment 1.

**Experiment 3: Neutral vs. trauma-related scenes.** We presented sequences of scenes and tested recognition performance as described in Experiment 1. We did not use letters or tones. Two of the 16 scenes were trauma-related, whereas 14 stimuli were neutral. There were 200 intermixed trials (10 blocks of 20 trials; 100 trials testing the recognition of trauma-related scenes and 100 trials for neutral scenes).

Data analysis

We performed data analysis using STATISTICA 9 software (StatSoft Inc., Tulsa). The primary dependent measure was scene recognition performance (percentage of correct judgments). The normal distribution of the data was evaluated with Kolmogorov-Smirnov tests, whereas the homogeneity of variance was explored with Levene's tests. We used repeated measures analyses of variance (ANOVAs) to examine the difference between individuals with PTSD and controls in the case of different stimuli. We applied Scheffe’s tests for post hoc comparisons. Demographic data and test performances not included in ANOVAs (letter recall and tone discrimination) were compared with two-tailed t tests. Pearson’s product moment correlation coefficients described the relationship between test performances and clinical scores. The level of statistical significance was alpha <0.05.

Results

**Experiment 1**

The results from the three experiments are summarized in Table 2. Figure 2 depicts recall performances for target and distractor letters. There were no statistically significant differences between individuals with PTSD and controls in the case of target and distractor letters (t test, p > 0.5). Participants exhibited a lower level of recall for distractor letters than for target letters (controls: t(78) = 22.10, p < 0.0001; PTSD: t(78) = 22.15, p < 0.0001) (Figure 2).

Figure 3 depicts scene recognition performance from Experiment 1. We conducted a two-way ANOVA with group (PTSD vs. controls) as the between-subjects factor and stimulus type (no-letter, distractor letter, target letter) as the within-subjects factor. There was no significant main effect of group (p > 0.5), whereas the effect of stimulus type was significant (F(2,156) = 66.54, p < 0.001, η² = 0.46). There was a significant interaction between group and stimulus type (F(2,156) = 88.26, p < 0.001, η² = 0.53).

Scheffé’s tests conducted on the two-way interaction indicated similar performances in the PTSD and control group for scenes with no letters (p > 0.5). Individuals with PTSD and controls did not differ from chance level in recognition performance (t test, p > 0.2). In the case of scenes with distractor letters, individuals with PTSD achieved a higher recognition performance as compared to controls (p < 0.001), whereas in the case of scenes with target letters, the opposite results were found, that is, controls...
displayed a higher level of recognition compared to individuals with PTSD ($p<0.001$) (Figure 3).

**Experiment 2**

Pitch discrimination performance was similar in controls (96.2%, CI: 94.9–97.5) and individuals with PTSD (95.8%, CI: 94.4–97.2) ($t$ test, $p>0.5$). The ANOVA design was the same as used in Experiment 1. Figure 4 depicts the results. The main effect of group (control vs. PTSD) was not significant ($p>0.1$), whereas the effect of stimulus type (scenes with baseline, target, and distractor tones) was significant ($F(2,156)=39.04$, $p<0.001$, $\eta^2=0.33$). Critically, the interaction between group and stimulus type was also significant ($F(2,156)=36.17$, $p<0.001$, $\eta^2=0.32$).

Scheffé’s tests revealed that the two groups did not differ in the case of baseline tones ($p>0.5$). However, in the case of distractor tones, individuals with PTSD outperformed controls ($p<0.01$), and in the case of target tones, controls outperformed the PTSD group ($p<0.001$) (Figure 4). In controls, scene recognition performance did not differ from the chance level (50%) for baseline tones ($t$ test, $p>0.1$).

### Table 2. Behavioral results.

|                          | Controls (n = 40) | PTSD (n = 40) |
|--------------------------|-------------------|---------------|
|                          | Mean 95% CI       | Mean 95% CI   |
| Target letter identification | 95.4 94.1        | 95.8 94.5      |
| Distractor letter identification | 60.3 57.3        | 61.3 58.4      |
| Scenes with no letters | 50.6 49.4         | 50.7 49.4      |
| Scenes with target letters* | 68.2 66.1        | 54.5 52.1      |
| Scenes with distractor letters* | 50.5 49.4        | 61.1 58.4      |
| Scenes with baseline tones | 50.5 49.0         | 49.4 47.5      |
| Scenes with target tones* | 63.2 61.1         | 53.7 51.4      |
| Scenes with distractor tones* | 51.4 49.7         | 58.3 55.6      |
| Trauma-related scenes | - -               | 51.5 48.9      |
| Neutral scenes with no letters or tones | - -               | 52.9 50.0      |

Mean letter identification and scene recognition performances (% correct) and 95% confidence intervals (CI) in controls and individuals with posttraumatic stress disorder (PTSD).

*Significant differences, Scheffé’s tests.

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Figure 2. Recall performance for target and distractor letters in individuals with PTSD and controls. Error bars indicate 95% confidence intervals. The performance was significantly lower for distractors relative to targets (*$p<0.001$, $t$ test), but the two groups did not differ. doi:10.1371/journal.pone.0042502.g002
Experiment 3

In the PTSD group, there was no significant difference between the recognition of neutral and trauma-related scenes (t test, p > 0.4) (Figure 5).

Gender differences and correlation with clinical symptoms

We found no differences between male and female participants in all three experiments (p > 0.2). There were no significant correlations between CAPS avoidance, hyperarousal, and HAM-D scores and scene recognition performances in all three experiments (−0.2 < r < 0.2, p > 0.1). A significant correlation was
found between CAPS re-experiencing scores and scene recognition performance when distractor tones were applied in Experiment 2 ($r = 0.41$, $p < 0.05$) (Figure 6), indicating that more severe re-experiencing symptoms were associated with a better recognition of scenes presented at irrelevant points in time.

**Discussion**

Contrary to our hypothesis, individuals with PTSD showed intact performance on letter identification and tone discrimination tasks, suggesting that they were able to allocate attentional resources to target stimuli. In accordance with previous findings [16,17], healthy controls showed a higher level of recognition in the case of background scenes presented with target stimuli.
According to Swallow and Jiang [17], focused spatial attention on a target stimulus has a global impact on memory formation and facilitates the encoding of temporally coincident scenes [17]. It is not likely that arousal elicited by perceptual novelty can explain this effect [25], because recognition memory for the stimuli presented before or after the target was at chance [16].

Individuals with PTSD displayed impaired recognition of scenes presented with targets, suggesting a weakened effect of focused attention on the background. However, we found the opposite pattern of performance for distractors. Despite the fact that distractor omission was similarly successful in PTSD and controls (lower recall performance for distractors relative to targets), it did not lead to decreased encoding of temporally coincident scenes in the PTSD group. In the case of both visual and auditory distractors, individuals with PTSD outperformed controls in scene recognition. These findings suggest that individuals with PTSD do not have impairments in focal spatial attention per se, and they exhibit enhanced encoding of background information at behaviorally irrelevant points in time relative to that at behaviorally relevant events.

In the case of auditory distractors, scene recognition performance was associated with more severe re-experiencing symptoms in PTSD, including intrusive memories and flashback experiences. This relationship between scene memory and re-experiencing symptoms in the case of auditory distractors, but not in the case of visual distractors, is puzzling. A possible explanation is that auditory distractors elicited more attention than visual distractors, or audiovisual integration (sounds paired with scenes) more closely resembles real life scenarios than letters in front of scenes.

We found no evidence for greater encoding of trauma-related scenes relative to neutral images in PTSD. These results suggest that enhanced memory is not confined to trauma-related or emotionally arousing information [26]. Past studies have shown that, during rapid serial visual presentation, individuals with PTSD symptoms process trauma-related stimuli more rapidly and efficiently (i.e., “consuming less attentional resources”) [27], and these stimuli elicit enhanced frontotemporal and amygdala activation [28]. However, it does not necessarily mean enhanced conscious recognition. Our results might suggest that enhanced encoding of irrelevant peripheral information can be associated with overactive memory representations in PTSD. As an involuntary process, it may be one of the mechanisms in the development of intrusive memories and images [29,30].

In the model of Brewin et al. [29], there are two types of memory representations. Contextual memory is abstract, verbal, extends to an attentional window as a part of prior knowledge. Sensation-based memory is situationally accessible, extends to the entire visual field, and supports immediate action [29]. Overactivity in the amygdala, linked to emotional arousal and fear in PTSD, may boost the activation of sensory cortical areas [31–33], which results in intrusive images. We described a possible mechanism for the emergence of sensation-based intrusive memories, which is based on the abnormal encoding of context at behaviorally irrelevant points in time. Contrary to the model of arousal-driven cortical activation and memory modulation [31–33], abnormal encoding of context (background scenes) is independent of trauma-related negative emotional contents when the symptoms of PTSD are present. Future studies are warranted to examine the relationship among abnormal encoding at behaviorally irrelevant events, stress, trauma exposure, and individual vulnerability. It is interesting, for example, whether participants in the control group could develop late-onset PTSD as well. In addition, future research should address whether this is a vulnerability factor (trait marker) or just present in individuals with current PTSD (state marker) and will disappear with effective treatment.

Why is visual information processing relevant to PTSD? Two pioneering studies demonstrated either increased [34] or decreased [35] activation in visual areas during the provocation of traumatic memories. Lanius et al. [36] found that, compared with controls, individuals with PTSD in a dissociative state showed more activation in the occipital lobe, which also displayed greater functional connectivity with other cortical areas [37]. Critically, visual activation in PTSD seems to be modulated by the level of information processing. Hendler et al. [38] found that responses to combat images evoked more activation in the visual cortex in people with PTSD than in non-PTSD controls, only when masked images were below recognition threshold. However, recognition threshold did not affect amygdala activation [38]. Although we did not use images below the detection threshold, short duration and rapid serial presentation are similar to the approach of Hendler et al. [38]. Evidence also suggests structural alterations of the visual cortex in PTSD [39–41]. These findings are particularly important in light of recent data, indicating that greater re-experiencing scores in PTSD correlated with reduced volume in the middle temporal and inferior occipital cortices [40].

Although several studies explored neuronal activity during rapid serial visual presentation [e.g., 42–44], the mechanism of enhanced scene encoding at target events is unknown. According to the theory of attentional boost effect [17], there may be greater activation not only in the attentional spotlight but also in peripheral locations at behaviorally relevant points in time [16]. When participants suppress distractors, this peripheral enhancement may be inhibited. We suggest that both peripheral enhancement, associated with focal attention to targets, and peripheral-inhibition, associated with focal suppression of distractors are deficient in PTSD. Future studies will explore these assumptions and their relationship with attentional alterations in the case of trauma-related and emotional cues [e.g., 45–49], and the possible implications of these findings for the cognitive models of PTSD [9,29,45,49,50].

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Author Contributions

Conceived and designed the experiments: ELG SK. Performed the experiments: ELG SK. Analyzed the data: ELG SK. Contributed reagents/materials/analysis tools: SK. Wrote the paper: ELG SK.

References

1. American Psychiatric Association (2000) Diagnostic and Statistical Manual of Mental Disorders. Revised 4th ed. Washington, DC: American Psychiatric Association.

2. Brenner JD, Krystal JH, Southwick SM, Charney DS (1995) Functional neuroanatomical correlates of the effects of stress on memory. J Trauma Stress 8: 527–533.

3. van der Kolk BA, Fiser R (1995) Dissociation and the fragmentary nature of traumatic memories: overview and exploratory study. J Trauma Stress 8: 505–525.

4. Harvey AG, Bryant R (1999) A qualitative investigation of the organization of traumatic memories. Br J Clin Psychol 38: 401–405.

5. Elders A, Clark D (2000) A cognitive model of posttraumatic stress disorder. Behav Res Ther 38: 319–345.
6. Halligan SL, Michael T, Clark DM, Elders A (2003) Posttraumatic stress disorder following assault: the role of cognitive processing, trauma memory, and appraisals. J Consult Clin Psychol 71: 419–431.

7. Brewin CR (2007) Autobiographical memory for trauma: update on four controversies. Memory 15: 227–248.

8. Evans C, Elders A, Mezey G, Clark DM (2007) Intrusive memories in perpetrators of violent crime: emotions and cognitions. J Consult Clin Psychol 75: 134–144.

9. Brewin CR (2011) The nature and significance of memory disturbance in posttraumatic stress disorder. Annu Rev Clin Psychol 7: 203–227.

10. Potter MC (1975) Meaning in visual search. Science 187: 965–966.

11. Stone BR (1993) Very short-term conceptual memory. Mem Cognit 21: 156–161.

12. Schyns PG, Oliva A (1994) From blobs to boundary edges: Evidence for time representation of the spatial envelope. Int J Comp Vis M 42: 145–175.

13. Thorpe S, Fize D, Marlot C (1996) Speed of processing in the human visual system. Nature 381: 520–522.

14. Durlach IN, Green DD, Pelli DG (1980) On the presence of two stages in visual processing. J Opt Soc Am 70: 1421–1425.

15. Greene MR, Oliva A (2009) The briefest of glances: the time course of natural scene understanding. Psychol Sci 20: 464–472.

16. Lin JY, Pye AD, Murray SO, Boynton GM (2010) Enhanced memory for scenes presented at behaviorally relevant points in time. PLoS Biol 8: e1000337.

17. Swallow KM, Jiang YV (2010) The Attentional Boost Effect: Transient increases in attention to one task enhance performance in a second task. Cognition 115: 118–132.

18. Leskin LP, White PM (2007) Attentional networks reveal executive function deficits in posttraumatic stress disorder. Neuropsychology 21: 275–284.

19. First MB, Spitzer RL, Gibbons RM, Williams JB (1996) Structured Clinical Interview for DSM-IV Axis I Disorders, Clinician Version (SCID-CV). Washington, DC: American Psychiatric Press.

20. Hovens JE, Bramsen I, van der Ploeg HM, Reuling IE (2000) Test-retest reliability of the trauma and life events self-report inventory. Psychol Rep 87: 730–752.

21. Blake DD, Weathers FW, Nacmuk G, Klauminzer G, Charney DS, Keane TM (1990) A clinician rating scale for assessing current and lifetime PTSD: the CAPS-1. Behav Therapeut 13: 167–188.

22. Hamilton M (1960) A rating scale for depression. J Neurol Neurosurg Psychiatry 23: 56–62.

23. Wechsler D (1999) Wechsler Abbreviated Scale of Intelligence. New York, NY: The Psychological Corporation, Harcourt Brace & Company.

24. Durlach IN, Green DD, Pelli DG (1980) On the presence of two stages in visual processing. J Opt Soc Am 70: 1421–1425.

25. Foa EB, Kozak MJ (1986) Emotional processing of fear: Exposure to corrective feedback. J Consult Clin Psychol 54: 689–699.

26. Wechsler D (1999) Wechsler Abbreviated Scale of Intelligence. New York, NY: The Psychological Corporation, Harcourt Brace & Company.

27. Amir N, Taylor CT, Bomyea JA, Badour CL (2009) Temporal allocation of attention to one task enhance performance in a second task. Cognition 115: 1080–1085.

28. Elbert T, Schauer M, Ruf M, Weierstall R, Neuner F, Rockstroh B, Junghofer M (2011) The tortured brain: Imaging neural representations of traumatic stress. Neuroimage 56: 1265–1274.

29. Brewin CR, Gregory JD, Lipton M, Burgess N (2010) Intrusive images in psychological disorders: characteristics, neural mechanisms, and treatment implications. Psychol Rev 117: 210–232.

30. Conway MA (1994) Flashbulb Memories. Hillsdale, Erlbaum.

31. Joanicov T, Resler KJ (2010) How the neurocircuity and genetics of fear inhibition may inform our understanding of PTSD. Am J Psychiatry 167: 648–662.

32. Cunnignham VA, Bresch T (2012) Motivational salience. Amygdala tuning from traits, needs, values, and goals. Curr Dir Psychol Sci 21: 54–59.

33. Pessoa L (2010) Emotion and cognition and the amygdala: from “what is it?” to “what’s to be done?” Neuropeychology 48: 3416–3429.

34. Rauch SL, van der Kolk BA, Fader RE, Alpert NM, Orr SP, et al. (1996) A symptom provocation study of posttraumatic stress disorder using positron emission tomography and script-driven imagery. Arch Gen Psychiatry 53: 380–387.

35. Brenner JD, Narayan M, Staub LH, Southwick SM, Mcclagan T (1999) Neural correlates of memories of childhood sexual abuse in women with and without posttraumatic stress disorder. Am J Psychiatry 156: 1787–1795.

36. Landis RA, Williamson PG, Bokman K, Densmore M, Gupta M, et al. (2002) Brain activation during script-driven imagery induced dissociative responses in PTSD: a functional magnetic resonance imaging investigation. Biol Psychiatry 52: 305–311.

37. Landis RA, Williamson PG, Bokman K, Neufeld RW (2004) The nature of traumatic memories: a 4-T FMRI functional connectivity analysis. Am J Psychiatry 161: 36–44.

38. Hensler T, Rotshtein P, Yeshurum Y, Weizmann T, Kuhn I, Ben-Bashat D (2003) Sensing the invisible: differential sensitivity of visual cortex and amygdala to traumatic context. Neuroimage 19: 587–600.

39. Fenemra-Navestine C, Stein MB, Kennedy CM, Archibald SL, Jernigan TL (2002) Brain morphometry in females victims of intimate partner violence with and without posttraumatic stress disorder. Biol Psychiatry 52: 1089–1101.

40. Kros MC, Whalley MG, Rugg MD, Brewin CR (2011) Association between flashbacks and structural brain abnormalities in posttraumatic stress disorder. Eur Psychiatry 26: 525–531.

41. Chao LL, Lenzci M, Neylan TC (2012) Effects of post-traumatic stress disorder on occipital lobe function and structure. Neuroreport 23: 412–419.

42. Keysers C, Xiao DK, Foltiak P, Perrett DI (2001) The speed of sight. J Cogn Neurosci 13: 90–101.

43. De Baene W, Premereur E, Vogels R (2007) Properties of shape tuning of maraque inferior temporal neurons examined using rapid serial visual presentation. J Neurophysiol 97: 2900–2916.

44. Jacoby O, Visser TA, Hart BC, Cuninngham R, Mattingley JB (2011) No evidence for early modulaiton of evoked responses in primary visual cortex to irrelevant probe stimuli presented during the attentional blink. PLoS ONE 6: e24255.

45. Buckley TC, Blanchard EB, Neil WT (2000) Information processing and PTSD: a review of the empirical literature. Clin Psychol Rev 20: 1041–1063.

46. Karl A, Malta LS, Matzcker A (2006) Meta-analytic review of event-related potential studies in post-traumatic stress disorder. Biol Psychiatry 71: 123–147.

47. Adanauer H, Pino¨sch S, Catani C, Gola H, Keil J (2010) Early processing of threat cues in posttraumatic stress disorder-evidence for a cortical vigilance-avoidance reaction. Biol Psychiatry 68: 451–459.

48. Bevers CG, Lee HJ, Wells TT, Ellis AJ, Telch MJ (2011) Association between predeployment gaze bias for emotion stimuli with later symptoms of PTSD and depression in soldiers deployed in Iraq. Am J Psychiatry 168: 735–741.

49. For EB, Kozak MJ (1996) Emotional processing of fear: Exposure to corrective information. Psychol Bull 106: 20–35.

50. Dalgleish T (2004) Cognitive approaches to posttraumatic stress disorder: the evolution of multirepresentational theorizing. Psychol Bull 130: 228–260.