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Intracranial EEG Correlates of Implicit Relational Inference Within the Hippocampus

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ABSTRACT: Drawing inferences from past experiences enables adaptive behavior in future situations. Inference has been shown to depend on hippocampal processes. Usually, inference is considered a deliberate and effortful mental act which happens during retrieval, and requires the focus of our awareness. Recent fMRI studies hint at the possibility that some forms of hippocampus-dependent inference can also occur during encoding and possibly also outside of awareness. Here, we sought to further explore the feasibility of hippocampal implicit inference, and specifically address the temporal evolution of implicit inference using intracranial EEG. Presurgical epilepsy patients with hippocampal depth electrodes viewed a sequence of word pairs, and judged the semantic fit between two words in each pair. Some of the word pairs entailed a common word (e.g., "winter–red," "red–cat") such that an indirect relation was established in following word pairs (e.g., "winter–cat"). The behavioral results suggested that drawing inference implicitly from past experience is feasible because indirect relations seemed to foster "fit" judgments while the absence of indirect relations fostered "do not fit" judgments, even though the participants were unaware of the indirect relations. A event-related potential (ERP) difference emerging 400 ms post-stimulus was evident in the hippocampus during encoding, suggesting that indirect relations were already established automatically during encoding of the overlapping word pairs. Further ERP differences emerged later post-stimulus (1,500 ms), were modulated by the participants' responses and were evident during encoding and test. Furthermore, response-locked ERP effects were evident at test. These ERP effects could hence be a correlate of the interaction of implicit memory with decision-making. Together, the data map out a time-course in which the hippocampus automatically integrates memories from discrete but related episodes to implicitly influence future decision making. © **2015 Wiley Periodicals, Inc.**

KEY WORDS: **memory; declarative; non-declarative; ERP; awareness**

INTRODUCTION

Making accurate predictions in novel situations is vital for flexible, adaptive behavior. Accurate predictions are often based on inference on how components of a novel situation relate to one another. Such inference hence requires "connecting the dots" of multiple, discrete memories of previous encounters with these components in different contexts. For example, one watches a boy playing soccer with a woman (components A and B), and then later sees the same boy at the grocery-store with a man (components B and C). When meeting the man and the women together (A–C), one can draw inferences about their relationship even when one has never seen the two together before: they are probably married and have a boy.

Extensive evidence points to the hippocampus as the key structure that accomplishes flexible retrieval of relational memories enabling such inferences (Dusek and Eichenbaum, 1997; Heckers et al., 2004; Preston et al., 2004; Smith and Squire, 2005; Shohamy and Wagner, 2008). Relational memory representations and flexibility of retrieval are features thought to be exclusive to episodic memory (Eichenbaum, 2004), the memory for personally experienced events in time and place (Tulving, 2002). According to a standard view of human long-term memory (Squire, 1992), episodic memory is a form of declarative memory, which relies on the hippocampus and is believed to operate only under conscious instances of encoding and retrieval (Clark and Squire, 1998; Smith and Squire, 2005). Recently, this notion that flexible hippocampus-dependent memories require conscious encoding and retrieval has been questioned by findings of inference under implicit retrieval (Greene et al., 2006; Greene, 2007; Leo and Greene, 2008), and subliminal encoding conditions (Reber and Henke, 2012; Reber et al., 2012; Henke et al., 2013). These results rather support notions which question

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the use of consciousness as defining feature of memory systems (Reder et al., 2009; Henke, 2010; Hannula and Greene, 2012).

Investigating whether inference is possible outside of awareness has been somewhat complicated by the fact that inference can be achieved in several ways (Greene, 2007; Frank et al., 2008). It seems undisputed that "inference-like" (Leo and Greene, 2008) behavior can be achieved without hippocampal contribution and awareness through simple and rigid reward-learning (Van Elzakker et al., 2003; Frank et al., 2006). Here, some inference-tasks can partly be solved by strategies which do not require memory representations that are relational. For "true," relational, and hippocampus-dependent inference, the relevant processes may occur during encoding or during retrieval. The encoding-based account (Shohamy and Wagner, 2008; Wimmer and Shohamy, 2012) holds that episodes sharing common components (e.g., AB, BC) are integrated into an extended memory representation (A-B-C) already at the time of encoding. The encounter of an overlapping episode (BC) during encoding was found to be associated with a coupling of activity in the hippocampus and the midbrain that may promote the mnemonic integration of the current (BC) with the previous experience (AB; Shohamy and Wagner, 2008). Later, an indirect relation between novel combinations of memory components (e.g., AC) can be recognized without further effort and maybe also outside of awareness (Wimmer and Shohamy, 2012) because the indirect relation has already been established. On the other hand, the retrieval-based account (Smith and Squire, 2005; DeVito et al., 2010) suggests that the two overlapping episodes (AB, BC) are encoded separately and stored as distinct memory representations in the hippocampus. At the encounter of AC, two separate memory representations (AB and BC) are retrieved and their components are flexibly restructured (AB, BC—A-B-C) such that the indirect relation (A-C) can be recognized (Smith and Squire, 2005; DeVito et al., 2010).

Electrophysiological data of relational memory and inference is scarce but holds the potential to inform the debate. EEG studies have reported that relational memory effects can be detected on a positive component peaking around 300 ms post-stimulus at retrieval (P320; Hannula et al., 2006) and at encoding of overlapping associations (P3b; Bonnefond et al., 2014). These findings relate to a line of research suggesting implicit hippocampus-dependent relational memory on grounds of eye-movement measures indicative of memory (Ryan et al., 2000; Hannula et al., 2007; Hannula and Ranganath, 2009; Ryals et al., 2015). A functional interrelation between these scalp P300 components and field potentials measured from within the hippocampus has been suggested as field potentials within the hippocampus reveal an early negativity peaking between 300 and 400 ms post-stimulus that is sensitive to similar experimental manipulations as the scalp P300 (Halgren et al., 1980; McCarthy et al., 1989; Ludowig et al., 2010). Additionally, a sustained positivity from 500 ms up to 2,000 ms has been shown to be more pronounced for subsequently remembered versus forgotten items in single item declarative memory tasks at encoding (Fernández et al., 1999, 2002). However, whether and how these intracranial components from within the hippocampus are sensitive to relational memory and inference remains open.

The current work is set out to investigate the time-course of relational inference outside of awareness. We asked whether inference occurs during encoding, retrieval, or both. A further vital question concerns the latency of the earliest neural effects indicative of relational inference within the hippocampus. Both of these questions can be addressed with intracranial EEG from within the hippocampus. Effects as early as P300 support that some processing stages of relational inference may occur in an automatic and therefore implicit fashion. On the basis of the previous work (e.g., Shohamy and Wagner, 2008; Reber et al., 2012), we hypothesized effects of relational inference to emerge in the hippocampus also during encoding, and potentially also at early time-points post-stimulus (Halgren et al., 1980; McCarthy et al., 1989; Hannula et al., 2006). Intracranial EEG enables not only to discern processing stages associated with the stimulus onset (stimulus-locked analyses) but also with the behavioral response (response-locked analyses) and hence could provide new insights on how relational memory in the hippocampus interacts with inference and decision making at later stages of processing.

In past experiments, we used subliminal procedures to test implicit inference (Reber and Henke, 2012; Reber et al., 2012; Henke et al., 2013). While intracranial recordings offer a unique view on neural processes within the hippocampus, they are also acquired in a context in which effects of memories of subliminal stimulus presentations seem extremely challenging to obtain. We therefore decided to refrain from using subliminal procedures in the current study and present encoding and retrieval stimuli supraliminally throughout the experiment. As a consequence, awareness of relational inference was assessed in post-experiment interviews.

METHODS

Participants

Eleven patients suffering from pharmacoresistant temporal lobe epilepsy participated in the study. The patients were implanted with depth electrodes in their medial temporal lobes (Van Roost, et al., 1998) to determine seizure onset zones for potential epilepsy surgery. Two patients had bilateral epileptic foci and were thus excluded from analysis. The remaining nine patients (three women) had a mean age of $M = 34.0$ yrs (SD = 9.3 yrs). Eight of the included patients were implanted with depth electrodes in the hippocampus bilaterally. In these cases, only electrodes from the contralesional side (three left, five right hemispheric) were analyzed. One patient had only one electrode in the right hippocampus, but the epileptic focus was found to be extrahippocampal, namely in the right insula.

TABLE 1.

Demographics and Results From Neuropsychological Tests for Each Patient as well as Means and Standard Deviations (SD) of the Whole Sample

Patient	Sex	Age	BDI	Attention	Figural memory	Verbal memory	IQ
1	f	25	0	3	3	2	101
2	m	35	3	2	2	1	97
3	f	32	1	4	1	2	85
4	m	32	1	1	3	1	90
5	m	38	0	3	0	0	111
6	m	25	1	3	2	2	127
7	m	52	3	3	3	1	113
8	m	24	2	0	3	2	100
9	f	43	1	2	1	1	103
Mean		34.00	1.33	2.33	2.00	1.33	103.00
SD		9.30	1.12	1.22	1.12	0.71	12.66

Scores on cognitive tests (attention, figural, and verbal memory) are ratings on a five-tiered scale ranging from 0 (severe impairment) to 4 (above average). BDI: Becks Depression Inventory, values range from 0 (severe depression) to 3 (no depression); IQ: intelligence quotient (normative sample mean = 100, SD = 15; Wechsler Adult Intelligence Scale). Further details on the attention and memory tests are given in the main text under Neuropsychological Assessment.

The study was approved by the local ethics committee, and participants gave written and informed consent.

Neuropsychological Assessment

The neuropsychological analysis focused on IQ, attention and material-specific memory functions. IQ was assessed by a short version of the WAIS-R which estimates the full scale IQ regression including six subtests: picture completion, block design, vocabulary, similarities, digit span, and arithmetics (Schwarzkopf -Streit, 2000). For the assessment of attention, we derived three scores, namely (1) performance on a letter cancellation test (Brickenkamp, 2002), (2) speed of perception and (3) interference inhibition (Lehrl and Fischer, 1997). Three scores (learning, memory, recognition) were obtained from the Verbaler Lern- und Merkfähigkeitstest (VLMT; Lux, et al., 1999; Helmstaedter et al., 2001), a modified German version of the Rey Auditory Verbal Learning Test (RAVLT; Rey, 1964) and the most frequently used verbal memory test in German speaking epilepsy centers (Witt and Helmstaedter, 2009). Three scores (total learning, supraspan, recognition) were obtained using the revised version of the Diagnosticum für Cerebralschädigung (DCS-R; Helmstaedter et al., 1991; Lamberti and Weidlich, 1999). Furthermore, depression was assessed using a German version of Becks Depression Inventory, first edition (BDI, Hautzinger et al., 1994).

For the analysis of the data and in order to reduce the amount of information from different test parameters per domain, the parameters of the different cognitive domains (i.e., attention, verbal memory and figural memory) were combined and rated on a five-tiered scale per domain (0 = severe impairment, i.e., at least two test scores >2 standard deviations (SD) below the mean of the normative sample (always taking age into consideration); 1 = impairment, i.e. at least two test scores >1 SD below the mean of the normative sample; 2 = borderline, i.e. one test score >1 SD below the mean of the normative sample; 3 = unimpaired, i.e. no test scores >1 standard deviations (SD) below the mean of the normative sample; 4 = above average, at least two test scores >1 SD above the mean score of the normative sample) based on the underlying psychometric test results (Clusmann, et al., 2002; Helmstaedter and Witt, 2012). The difference between two neighboring categories resembles approximately one standard deviation of the mean standardized score across all underlying test parameters (Clusmann et al., 2002). In case of the BDI, the reported scores range from 0 to 3 and reflect the cutoffs usually used together with the BDI (3: 0–9 points, minimal depression; 2: 10—18 points, mild depression; 1: 19–29 points, moderate depression; 0: 30–63 points, severe depression). An overview of patients' characteristics and performance on neuropsychological tests is given in Table 1.

Neuropsychological assessment revealed that the patients on average scored within the normal range on intelligence and attention but were impaired in the memory domain (Table 1). Furthermore, patients were more depressed than people in the calibration sample.

Behavioral Task

The experiment entailed 10 runs, each subdivided in three phases: encoding phase I, encoding phase II, and a test phase (Fig. 1). In the experimental condition, word pairs in encoding phase I (e.g., winter–red, AB) and encoding phase II (e.g., red–cat, BC) were related through a common word (red, B). These overlapping word pairs established an indirect relation between two words in a test pair (e.g., winter–cat, AC). In the control condition, word pairs in encoding phase I (e.g., bag–horse, AB) and encoding phase II (e.g., grass–key,

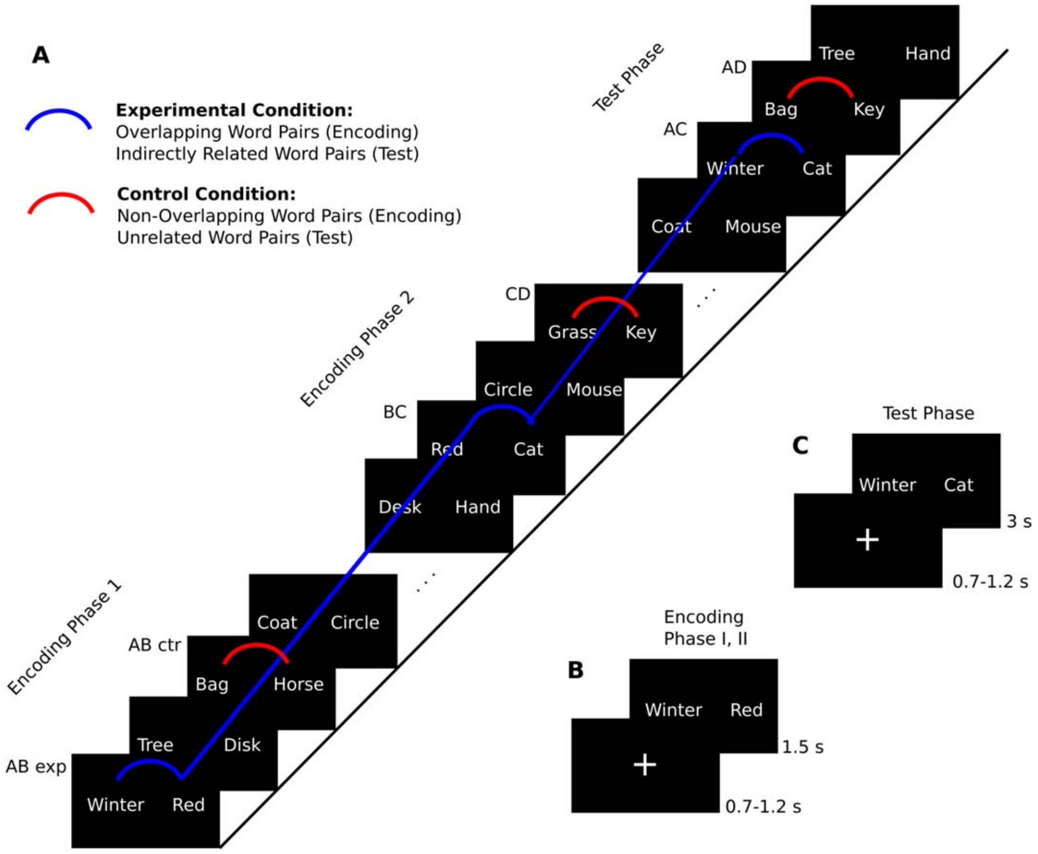

FIGURE 1. A. The sequence of word pairs in one (of ten) runs is depicted. One run entailed two encoding phases, and a test phase. Word pairs in the experimental condition were linked through a common word during encoding, which established an indirect relation at test (blue). Word pairs in the control condition (red) did not contain a common word during encoding. The sequence of events is depicted from the bottom left to top right. B. One trial during encoding entailed a presentation of a fixation cross with random duration (0.7–1.2 s) followed by a presentation of a word pair for 1.5 s. C. One Trial in the test-phase entailed a presentation of a fixation cross (0.7–1.2 s) followed by a presentation of a word pair for 3 s. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

CD) did not contain a common word. Therefore, the corresponding test pairs (e.g., bag–key, AD) were unrelated. One run entailed 42 unique word pairs (7 in each condition and phase). Word pairs in encoding phase I and II were presented for 1.5 s each, followed by an inter-stimulus-interval of a random duration (0.7–1.2 s) in which a fixation cross was presented. Word pairs in the following test phase were presented for 3 s, followed again by a fixation cross of variable duration (0.7–1.2 s). The reason for the difference in presentation times of word pairs during encoding and test is the following. We intended to be able to capture both encoding and retrieval based inference and also to take into account that they may co-occur. Retrieval-based inference has been described as not automatic and may therefore require more time. By extending the trial duration at test we intended to exclude the possibility that retrieval based inference—if at play—would be unsuccessful or would not occur at all due to too short trials at test. The participants' task was to judge the semantic fit between two words in a pair in all phases of the experiment. Responses were registered from word pair onset up to onset of the next word pair. In trials in which the participant did not provide a response within the predefined SOA, the paradigm was paused and the next trial followed only after a response was made. The participants were neither told that they are about to engage in a memory experiment, nor that there are overlapping and indirectly related word pairs.

Two counterbalanced lists of stimuli were created and were varied between participants. Because of dropouts (see above), six patients received list A, and three patients received list B. The two lists were counterbalanced by the following: The overlapping words in the first list were replaced by new words (list A: winter–red, red–cat → list B: winter–red, tulip–cat). The corresponding test pairs (list A/B: winter–cat) were therefore identical in both lists, but either did or did not carry an indirect relation. Accordingly, an overlap was introduced in non-overlapping pairs from the first list (list A: sushi–beard, tulip–dust → list B: sushi–beard, beard–dust), such that the corresponding retrieval pair (list A/B: sushi–dust) either was indirectly related or not.

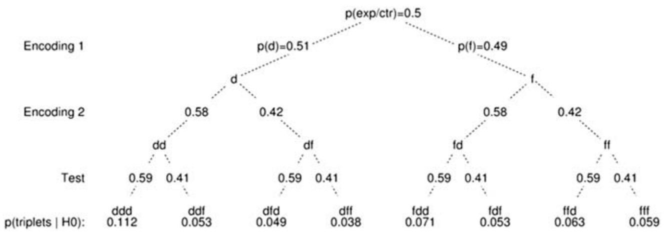

FIGURE 2. The probability tree denotes the average "fit" (f) and "do not fit" (d) rates for each phase of the experiment together with the resulting H0 triplet proportions.

At the end of the experimental session, participants were interviewed on whether they noticed indirect relations in word pairs. This interview entailed following three questions. (1) "Did you notice anything special about the experiment in general?" (2) "Did you notice anything special about the words in the experiment?" (3) "Did you notice anything special about the arrangement of the words in pairs?".

Analysis of Behavioral Data

We were interested in whether indirect relations established during encoding could influence the participants' semantic judgments on indirectly related vs. unrelated pairs at test. To address this question, one has to consider that indirect relations are but one potential determinant of the outcome of semantic judgments. A further determinant might be the judgments made on corresponding word-pairs during encoding phases I and II. Thus, we classified corresponding triplets of word pairs from encoding phase I, II and the test phase according to the "fit" and "'do not fit" judgments they received. For example, a participant gave a "fit" answer (f) to "winter–red" (AB), a "do not fit" answer (d) to "red–cat" (BC), and a "fit" answer (f) to "winter-cat" (AC). Such an outcome was classified as an "fdf" triplet. The frequencies by which the triplets occurred in each patient are expressed as proportions with respect to all triplets presented to a patient.

Next, we computed triplet proportions that would be expected if no effect of relational memory and inference were at play (H0). These H0 proportions are calculated by taking rates of responding with either a "fit" or "do not fit" answer into account, which may vary between participants and phases of the experiment, but are collapsed over experimental and control condition. Rates of responding with either a "fit" answer P(f) or a "do not fit" answer P(d) were obtained for each subject at encoding phases I and II (e1, e2) and at test (t). H0 triplet proportions were then computed separately for each subject by taking the probability of an experimental versus control trial, i.e., 0.5, and multiplying it with the product of the respective response rates, e.g., $p(\mathrm{fdf} \mid \mathrm{H0}) = 0.5 \times p(f_{e1}) \times p(d_{e2}) \times p(f_t)$. A corresponding probability tree illustrating this procedure and averaging resulting values across all subjects is displayed in Figure 2. To obtain normalized values of triplet proportions, we then subtracted the H0 triplet proportions from the observed proportions in the experimental and control condition separate for each subject.

iEEG Analyses

Signals from depth electrodes were recorded at a sampling rate of 1 kHz, band-pass filtered from 0.01 Hz (6 dB/octave) to 300 Hz (12 dB/octave), and referenced to linked mastoids. For each subject ERPs collapsing all conditions were computed. Electrode-location was determined by visual inspection of the post-implantation MRI. The hippocampal contact with the maximum peak amplitude of the average event-related potential between 500 and 1000 ms was chosen for further analysis because the corresponding hippocampal P600 component had been demonstrated to be closely related to the processing of visually presented words (e.g., Fernández et al., 1999; Klaver et al., 2005). By selecting this electrode contact in each patient we aimed to reduce the influence of processes that are not specifically related to the word pair task. Artifact-rejection (e.g., epileptic spikes) was performed manually.

For further ERP analyses, the data were low-pass filtered at 30 Hz. Signals of individual trials were segmented according to the onset of the stimulus (stimulus-locked analyses). Furthermore, signals were also segmented according to the onset of the "fit" and "do not fit judgments" (response-locked analyses) to assess interactions of memory with decision making, i.e., the semantic judgments. Individual trials were either normalized to the average of the signal from −200 ms to stimulus onset (stimulus-locked analyses), or to the average of the signal of the whole segment (−1.5 s to 1.5 s; response-locked analyses).

Statistical contrasts were computed using cluster-based permutation tests (Maris & Oostenveld, 2007) as implemented in the fieldtrip toolbox (http://fieldtrip.fcdonders.nl) for MATLAB (http://www.mathworks.com). Here, a series of dependent-samples *t* tests using the patient averages of two conditions is calculated at each time-point after stimulus onset. Contingent time-points at which the *t* tests reach a threshold of $P < 0.05$ are entered in a cluster. The sum of *t* values in that cluster is taken as the cluster-statistic. These cluster statistics are then computed a 1,000 times for random assignments of condition-labels to individual ERPs (i.e., "label-shuffling"). The reported *P* value reflects the percentile that the test-statistic of the actual assignment of labels to the data reaches in the distribution of cluster-statistics obtained by label-shuffling.

RESULTS

Behavioral Results

In the interview after the main experiment, one patient reported to have noticed repeating words, i.e., the AB BC scheme, but did not notice the indirect relations, i.e., the AB BC AC scheme. The remaining eight subjects reported not to have noticed anything particular about the sequence of word

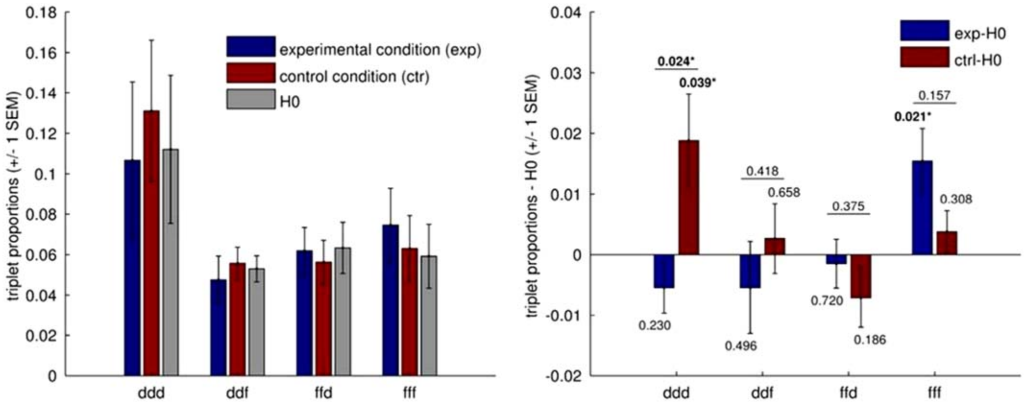

FIGURE 3. **The left panel depicts H0 triplet proportions next to the observed proportions for the experimental and control condition. Observed triplet proportions of the experimental and control condition were normalized by subtraction oft the corresponding H0 triplet proportions (right panel). Normalized triplet proportions were subjected to pairwise *t* tests of experimental vs. control condition for each triplet. *P* values of these tests are denoted above horizontal lines. Furthermore, one-sample *t* tests against what would be expected by chance, i.e., H0, were computed for each triplet separate for the experimental and control condition. *P* values of these tests are denoted above/below the corresponding bars. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]**

pairs they saw during the experiment. Hence, all participants were classified as unaware of indirect relations. Did indirect relations nevertheless influence participants' semantic decisions on indirect relations at test?

Unlike previous implicit inference studies using subliminal encoding procedures (Reber and Henke, 2012; Reber et al., 2012; Henke et al., 2013), no effects of relational memory and inference were evident in overall contrasts. The mean percentage of fit answers given to AC pairs ($M = 41.5\%$, SEM = 4.1%) was comparable to fit answers given to AD pairs ($M = 40.7\%$ SEM = 5.0%); $t = 0.875$, $P = 0.407$. Also, no significant difference was evident at encoding phase II as the percentage of fit answers was 43.9 (7.5) % for BC pairs, 40.7 (6.8) % for CD pairs ($t = 0.854$, $P = 0.418$). Furthermore, the percentage of fit answers (SEM) was 53.1 (7.6) % for AB pairs in the experimental condition, and 46.9 (6.0) % for AB pairs in the control condition; $t = 2.053$, $P = 0.075$. This tendency is surprising because it cannot result from our experimental manipulation since during encoding-phase I the word-pairs did not differ in their encoding history.

The mean reaction latencies of semantic judgments (SEM) was 1,833 (301) ms for AB pairs in the experimental condition, 1,857 (308) ms for AB pairs in the control condition (encoding-phase I, AB_{exp} vs. AB_{ctrl}: $t = -1.195$, $P = 0.266$), 1,889 (372) ms for BC pairs, 1,907 (370) ms for CD pairs (encoding-phase II, BC vs. CD: $t = -1.119$, $P = 0.296$), 2,216 (431) ms for AC pairs, and 2,194 (424) ms for AD pairs (test-phase AC vs. AD: $t = 0.581$, $P = 0.577$).

In contrast to studies using subliminal encoding procedures (Reber and Henke, 2012; Reber et al., 2012; Henke et al., 2013), participants in the current study received encoding pairs supraliminally and judged the semantic fit between two words in a pair also at encoding. Response behavior during encoding might impact on semantic judgments made on following word pairs at test. Therefore, we calculated proportions by which certain combinations of responses for corresponding word pairs, i.e., triplets, occurred (see Methods). We excluded triplets containing a "fit" answer in encoding phase I and a "do not fit answer" in encoding phase II and vice versa, i.e., triplets starting with either fd or df, as the outcome of successful inference at test seems ill defined for these cases. We restricted our analyses to triplets with either consistent "fit" or consistent "do not fit" answers during encoding I and II (triplets starting with either ff or dd). Here, the presence or absence of indirect relations at test (experimental vs. control condition) might affect whether participants judge words in the test pair consistent with responses given to corresponding encoding pairs (fff, ddd) or not (ffd, ddf). The following analyses of triplet proportions were not planned a priori, concern only a subset of the trials recorded, and should therefore be considered exploratory (a descriptive overview of all triplet proportions is given in Supporting Information Fig. 1).

Generally, we hypothesize that implicit inference may influence how participants judge the semantic fit between words in test pairs. Considering the above, we computed a 2 × 2 × 2 repeated-measures ANOVA as omnibus test, which included the factors Condition (experimental vs. control), Encoding History (triplets starting with ff vs. dd), Consistency (consistent, i.e., fff, ddd vs. inconsistent, i.e., ddf, ffd), and the normalized triplet proportions as dependent variable. The interaction of Condition × Encoding History × Consistency reached significance; $F(1,8) = 6.779$, $P = 0.031$. Furthermore, the interaction of Condition × Encoding History approached significance; $F(1,8) = 4.702$, $P = 0.062$. As both of these interactions included the factor Condition, these results suggest that the presence or absence of indirect relations affected observed triplet proportions. These results could hence be taken as evidence for inference in the current study. All further effects in this ANOVA were insignificant ($F \leq 3.073$, $P \geq 0.117$).

Specifically, we hypothesized that implicit inference on indirect relations in the experimental condition may reduce the perceived semantic distance between two words in a test pair, and would therefore foster "fit" judgments in the experimental condition (Henke, et al., 2013). To address this, we investigated the nature of the above interactions with a series of post-hoc *t* tests (see Fig. 3). Paired t-tests were performed between normalized triplet proportions in the experimental and control condition of individual triplets. One-sample *t* tests of individual triplet proportions against what would be expected by chance (H0) were performed to assess which of the observed triplet proportions deviate from what would be expected if no inference were at play (H0, see Methods). We found that fff triplet frequency was comparable between the experimental condition ($M = 0.015$, SEM = 0.005) and the control condition ($M = 0.004$, SEM = 0.003); $t = 1.563$, $P = 0.156$. Interestingly, however, there were significantly more fff triplets in the experimental condition than would be expected by chance (H0; $t = 2.861$, $P = 0.021$). By contrast, fff triplet frequency was not significantly higher than would be expected by chance in the control condition ($M = 0.004$, SEM = 0.003, $t = 1.088$, $P = 0.308$). These results could be taken as support for the notion that implicit inference results in reduced perceived semantic distance in test-pairs containing an indirect relation.

Furthermore, ddd pairs were more frequent in the control condition ($M = 0.019$, SEM = 0.008) than in the experimental condition ($M = -0.005$, SEM = 0.004); $t = -2.773$, $P = 0.024$, and ddd pairs in the control condition were significantly more frequent than would be expected by chance (H0); $t = 2.461$, $P = 0.039$. In contrast, ddd pairs in the experimental condition ($M = -0.005$, SEM = 0.004) were not significantly more frequent than would be expected by chance (H0); $t = -1.299$, $P = 0.230$. There were no differences in triplet frequencies between experimental and control condition on either ddf or ffd triplets, and none of these triplets occurred significantly more often than would be expected by chance (H0) in either the experimental or the control condition ($P \geq 0.186$, see Fig. 3). A possible explanation for the finding of more frequent ddd pairs in the control condition could be that AD pairs at test may trigger the reactivation of both corresponding encoding word pairs, even if no indirect relation was established by encoding word pairs (AB CD) as they did not contain a common word. Note, that this bias toward "do not fit" answers in the control condition could not have happened already during encoding phase II since at that time the corresponding word pairs did not contain a common word and a relationship between AB and CD pairs could therefore not be inferred. It appears that two 'do not fit' answers during encoding together with the lack of an indirect relation in AD pairs increases the semantic distance between words in test pairs of the control condition (AD).

In conclusion, it seems that presence of indirect relations fosters "fit" answers by reducing the perceived semantic distance when corresponding encoding word pairs were consistently judged with "fit" judgments. On the other hand, the absence of indirect relations increases the perceived semantic distance between test pairs and fosters "do not fit" judgments when corresponding encoding word pairs were consistently judged with "do not fit" judgments. This description of the pattern of results also corresponds well with the condition × encoding history × consistency interaction found in the ANOVA.

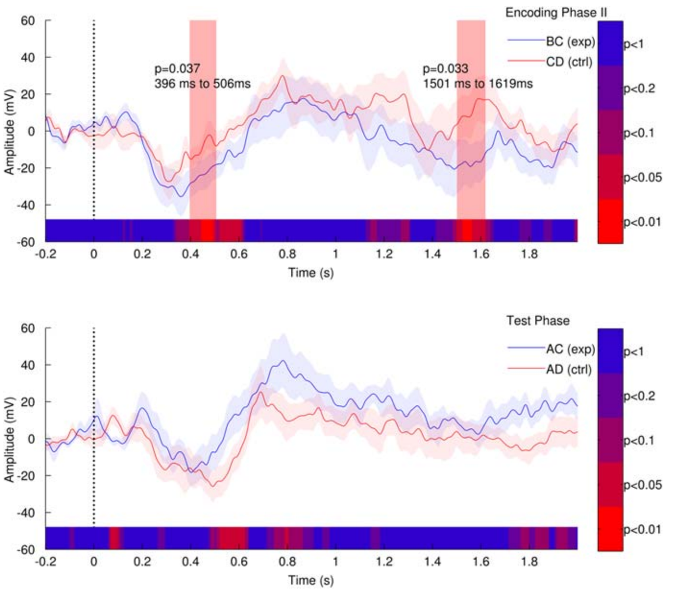

FIGURE 4. **Event related potentials locked to stimulus-onset (dotted vertical line) during encoding phase II (BC vs. CD) and during the test phase (AC vs. AD pairs). Shaded areas delineate ±1 standard errors of the mean. The colored area along the *x*-axis signifies *P* values of paired-samples *t* tests in 5 ms time bins. Red rectangles depict clusters which reached significance in the cluster permutation statistics. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]**

Importantly, it seems unlikely that the tendency of overall more frequent "fit" judgments for AB pairs in the experimental versus control condition reported above can be responsible for the results of normalized triplet frequencies we report as evidence for implicit inference. If this difference on AB pairs were also evident in the contrasts of normalized triplet frequencies, there should be significant differences between experimental and control condition also on ddf vs. ffd triplets (see above), which is not the case.

Intracranial EEG Results

First, we analyzed ERP differences locked to stimulus onset between the experimental and the control condition collapsed across "fit" and "do not fit" judgments. Significant differences were evident during encoding phase II, but not during the test-phase (Fig. 4). At encoding phase II, a stronger negativity for BC (experimental condition) than CD (control condition) pairs emerged from 396 to 506 ms, and from 1,501 to 1,619 ms after stimulus onset. Note, that it seems unlikely that this effect is solely due to the single word repetition of the B-word in the experimental condition (AB-BC) pairs because word repetitions usually yield reduced neural signals (see discussion;

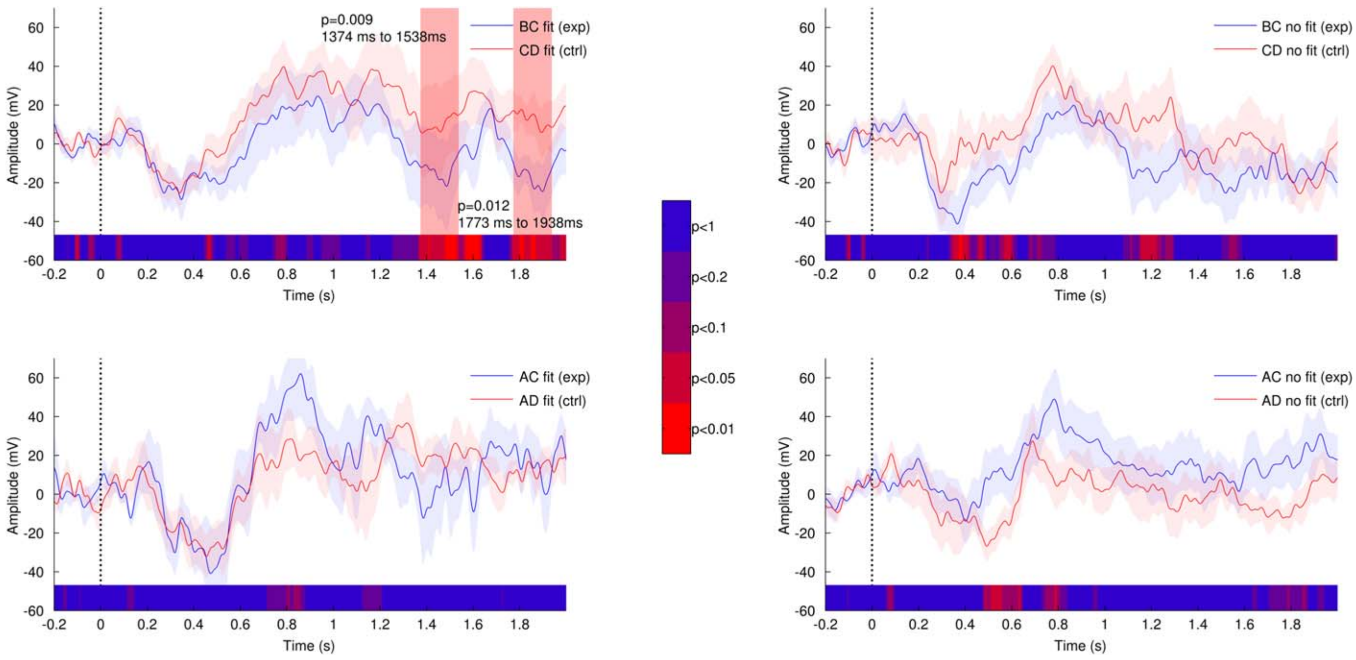

FIGURE 5. **Event related potentials locked to stimulus onset (dotted vertical line) contrasting experimental and control condition during encoding phase II (BC vs. CD) and test (AC vs. AD), separately for word pairs that received "fit" answers, and for word pairs that received "do not fit" answers. Shaded areas indicate ±1 standard errors of the mean. The colored area along the *x*-axis signifies *P* values of paired-samples *t* tests in 5 ms time bins. Red rectangles depict clusters which reached significance in the cluster permutation statistics. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]**

Rugg, 1985; Holcomb, 1988; Nobre and McCarthy, 1995; Henson, 2003). Two further clusters did not reach significance ($P \geq 0.214$). At the test phase, no difference between indirectly related (AC) and unrelated word pairs (AD) was found with the cluster-based permutation statistics (five clusters, $P \geq 0.134$). These results suggest that an integration of overlapping memory traces (A-B, B-C → A-B-C) may have already occurred during encoding of the overlapping word pair (BC; Shohamy and Wagner, 2008).

Visual inspection of the curves may suggest sustained effects emerging around 300–400 ms and extending until the end of the considered segments (2,000 ms). To investigate this possibility, we computed pairwise t tests of the average signals from a time window ranging from 300 to 2,000 ms. Here, the mean of ERPs to BC pairs ($M = -7.03$ mV, SEM = 8.03 mV) was significantly lower than to CD pairs ($M = 5.25$ mV, SEM = 6.42 mV); $t = -2.825$, $P = 0.022$. At test, mean ERPs to AC pairs ($M = 14.27$, SEM = 4.56) pairs did not differ significantly from AD pairs ($M = 1.21$, SEM = 6.43); $t = 1.600$, $P = 0.148$. Together, analyses for sustained effects support the notion that differences of experimental versus control condition arose rather during the encoding phase than during the test phase.

The behavioral data suggest that indirectly related word pairs (AC) bias the participants' responses towards more frequent "fit" answers. Thus, we were interested whether the response a word pair received would modulate the ERPs. We analyzed stimulus-locked ERPs at encoding phase II and at test separately for trials in which the word pairs received "fit" and "do not fit" judgments at test. Using cluster-based permutation tests, differences were evident during encoding phase II but not during the test phase (Fig. 5). Significant ERP differences emerged for the contrast of overlapping word pairs (BC) versus non-overlapping word pairs (CD) that received a "fit" answer. Stronger negativities for BC than CD word pairs that received a fit answer were indicated by the cluster-permutation statistics from 1,374 to 1,538 ms, and from 1,773 to 1938 ms. One further negative cluster approached significance (1,560–1,639 ms, $P = 0.59$), and three further negative clusters were clearly insignificant ($P \geq 0.370$; no positive clusters). The analogous contrast for "do not fit" answers did not reveal any significant difference (one positive and four negative clusters, $P \geq 0.123$). At test, all clusters were insignificant (AC-fit vs. AD-fit: no clusters, AC-no fit vs. AD no-fit: four negative clusters, $P \geq 0.146$).

Again visual inspection may suggest sustained effects and we conducted pairwise t tests on average signals between 300 and 2,000 ms post-stimulus. ERPs following BC pairs that received a "fit" answer ($M = -0.91$ mV, SEM = 10.92 mV) were significantly lower than CD pair that received a "fit" answer ($M = 16.29$, SEM = 11.64); $t = -2.646$, $P = 0.029$. The same contrast for "do not fit" answers was insignificant ($M_{\text{BC-no fit}} = 9.71$ mV, $\text{SEM}_{\text{BC-no fit}} = 8.03$ mV, $M_{\text{CD-no fit}} = 4.32$ mV, $\text{SEM}_{\text{CD-no fit}} = 8.13$ mV; $t = -1.732$, $P = 0.122$). Furthermore, no sustained differences between experimental and control condition at test were evident for both, word pairs that received "fit" answer ($M_{\text{AC-fit}} = 13.05$ mV, $\text{SEM}_{\text{AC-fit}} = 11.16$ mV, $M_{\text{AD-fit}} = 9.51$ mV, $\text{SEM}_{\text{AD-fit}} = 6.76$ mV; $t = 0.256$

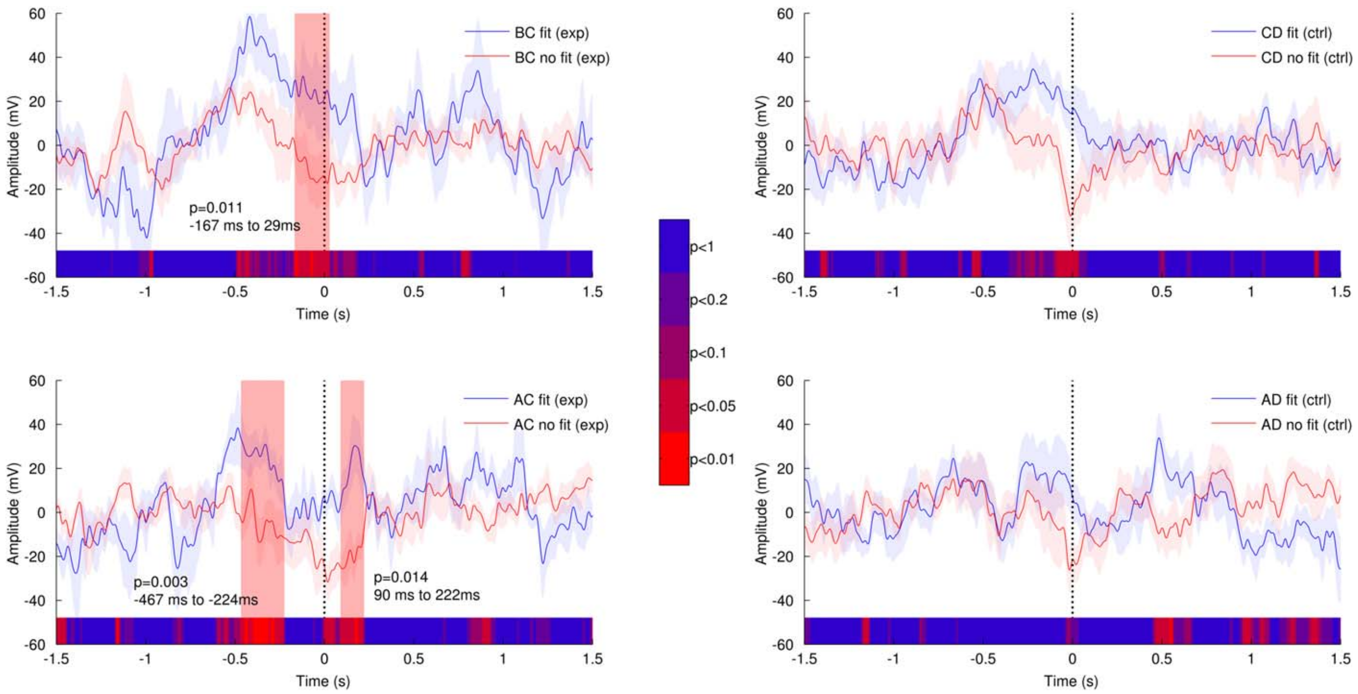

FIGURE 6. Event related potentials locked to the response (dotted vertical line). Significant differences between ERPs following "fit" and "do not fit" responses were evident within the experimental condition during encoding phase II (BC, CD), and during the test-phase (AC, AD). Shaded areas indicate ±1 standard errors of the mean. The colored area along the *x* axis signify *P* values of paired-samples *t* tests in 5 ms time-bins. Red rectangles depict clusters which reached significance in the cluster permutation statistics. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

$P = 0.804$), and "do not fit" answer ($M_{\text{AC-no fit}} = 15.86$ mV, $\text{SEM}_{\text{AC-fit}} = 8.97$ mV, $M_{\text{AD-no fit}} = -1.05$ mV, $\text{SEM}_{\text{AD-fit}} = 7.88$ mV; $t = 1.272$, $P = 0.239$). Together, these results agree with the results from cluster-based permutation statistics in that effects of experimental versus control trials emerged during encoding-phase II and are observable on pairs that received a 'fit' answer.

Next, we were interested in the interaction of implicit memory with decision making, i.e., the semantic judgments. Therefore, we analyzed ERPs locked to responses. Significant response-locked ERP effects were found when contrasting "fit" with "do not fit" judgments (Fig. 6). During encoding phase II, overlapping (BC) pairs that received a "fit" judgment displayed a significantly stronger positivity than overlapping pairs that received "do not fit" judgments from −167 to 26 ms. Further five positive and one negative cluster did not reach significance ($P \geq 0.393$). The analog contrast on CD pairs revealed one positive cluster approaching significance (−89 to 34 ms, $P = 0.052$), and two further positive and three negative clusters that are clearly insignificant ($P \geq 0.391$).

Unlike the stimulus-locked analyses, the response-locked analyses also revealed effects at test (Fig. 5). Here, indirectly related (AC) pairs that received a "fit" judgment were associated with increased positivities from −467 to −224 ms, and from 90 to 222 ms (further four positive and two negative clusters, $P \geq 0.209$). Contrasting "fit" versus "do not fit" judgments on AD pairs revealed one positive cluster with a trend (468–568 ms, $P = 0.090$) and five negative clusters that were clearly insignificant ($P \geq 0.399$; Fig. 6).

DISCUSSION

This research investigated the time-course of implicit inference within the hippocampus. Behavioral results suggest that indirect relations established by overlapping word pairs during encoding (winter–red, red–computer) influenced participants' semantic judgments at test (winter–computer). We suggest that participants implicitly recognized and encoded indirect relations from overlapping word pairs into long-term memory. From these integrated memories, the participants likely drew inferences that guided their choices at inference test. That indirect relations were implicitly recognized and encoded as such already at encoding was suggested by stimulus-locked ERPs from within the hippocampus. Encoding-based inference-processing seemed reflected in a more pronounced early negativity of the ERP signal for overlapping word pairs (BC) as compared to non-overlapping word pairs (CD). Integrated memories biasing the participants' semantic judgments seemed likely to be reflected in later ERP effects that were associated with distinct semantic judgments.

Some previous implicit inference studies used subliminal encoding procedures in combination with objective tests of discrimination performance of the stimuli (Reber and Henke, 2012; Reber et al., 2012; Henke et al., 2013). While the use of subliminal presentations make claims of unawareness compelling, great care has to be taken that stimuli are presented with just the right intensity so that they cannot be seen consciously but nevertheless get processed. This narrow window of feasible stimulus intensities may vary between subjects. Conservative subliminal presentation comes at the risk of presenting stimuli too weak (low contrast, short presentation duration, strong masking, etc.) to be processed by some subjects, which may result in rather weak or absent overall effects. Consequently, our previous subliminal studies tested either 33 or more subjects (e.g., Reber et al., 2012: $N = 33$, or Reber and Henke, 2012: $N = 72$), or tested each subject for longer periods of time and on multiple days of testing (Duss et al., 2014). Subliminal encoding procedures seem unfit in the context of the current study as testing time and the amount of patients was limited. Additionally, patients were tested at bedside, which results e.g. in less control over lighting conditions that is required for subliminal studies. Finally, subliminal studies result in unawareness of the mere presence of stimuli. For inference to be implicit, however, unawareness of relations between stimuli and not of the stimuli per se is the relevant criterion.

The current and previous implicit inference studies (Gross and Greene, 2007; Leo and Greene, 2008; Greene et al., 2001) present encoding stimuli visibly throughout the experiment but use post-experimental interviews to assess awareness of indirect relations. In these and our current study, conscious access/recovery of encoded content was not required by the task, and awareness thereof was not as strictly controlled as in subliminal studies. Nevertheless, participants in the current study were kept naive as to the purpose of the experiment and were told that we would be interested only in how they judged the semantic relatedness of two words in pair. They were not informed of taking part in a memory experiment and of the indirect relations that were introduced in the word pairs. None of the participants reported to have had noticed indirect relations during the experiment. Nevertheless semantic judgments were biased by indirect relations in the word pairs. However, one could argue that subjects may have noticed indirect relations during the experiment and either forgot about them or were not confident enough to report their insight by the time of the post-experiment interview (Björkman et al., 1993). Furthermore, patients in the current study were impaired on neuropsychological test of memory, which might further contribute to under-reporting of conscious awareness of indirect relations. While these explanations cannot be ruled out completely, it seems also important to note that this underconfidence phenomenon (Björkman et al., 1993) was described for perceptual judgments, and that it seems unlikely that gaining sudden conscious insight into the hidden relational structure of the task will easily be forgotten (Auble et al., 1979). Furthermore, although patients were overall impaired in the memory domain, the test-scores indicate that the impairment was not severe except for one patient. The fact that we do find behavioral effects of indirect relations also supports that memory deficits were not too serious for the purposes of this study and may suggest that participants were not in principle incapable of reporting their experiences. Nevertheless, to what extent memory impairment might have impacted on effects of implicit inference should be investigated in future studies using the same task with healthy participants. In conclusion, we suggest that behavioral effects we find are due to relational inference and were expressed implicitly.

We suggest that implicit inference was relational because non-relational “inference-like” strategies cannot account for the behavioral effect we find. Non-relational or “inference-like” behavior refers to simple shortcuts to solve inference-tasks that were intended to measure relational inference (Frank et al., 2006; Greene, 2007; Frank et al., 2008; Leo and Greene, 2008). Non-relational “inference-like” behavior can only occur if encoding entails choosing the “correct” element of an encoding pair over the other (e.g., A over B, and B over C), and if correct choices are rewarded (Van Elzakker et al., 2003; Frank et al., 2006). Furthermore, multiple encoding trials of the same associations are needed. In such study designs, rules such as “the choice of A was always rewarded,” or “the choice of C was never rewarded” can be learned. These simple rules would enable correct choice of A over C, but the underlying memory representation would not be relational and would be unlikely to rely on the hippocampus (Van Elzakker et al., 2003; Frank et al., 2006). In our current design, there were no objectively correct or incorrect choices because participants judged the semantic relatedness of two words in a pair by their own standards. Participants saw the encoding word pairs only one time, and rewarding feedback was neither given at encoding nor at test. Thus we conclude that the memory representations in the current task needed to get established in a single trial, were relational, and were hence likely to require hippocampal memory functions.

Accordingly, we think of the intracranial ERP effects from within the hippocampus as a plausible correlate of implicit relational inference. Our data thus add an intracranial record of implicit inference to previous studies, which have assessed implicit inference either behaviorally (Greene et al., 2001; Greene, 2007; Gross and Greene, 2007; Leo and Greene, 2008; Reber and Henke, 2012; Henke et al., 2013), or in combination with fMRI (Greene et al., 2006; Greene, 2007; Reber et al., 2012). IEEG from within the hippocampus enabled us to take a closer look at hippocampal contributions to implicit inference in the temporal domain.

Early significant ERP differences during encoding phase II (BC vs. CD) occur within a similar time-window as the N400 component in scalp EEG (Kutas and Federmeier, 2011), which has been associated with semantic processing in general and semantic integration specifically. However, it seems unlikely that the reported effect from within the hippocampus reflects N400 because a corresponding intracranial potential, the anterior medial temporal lobe N400 (AMTL-N400, e.g., McCarthy et al., 1995, Fernandez et al., 1999) has been observed in areas adjacent to but not within the hippocampus (McCarthy et al., 1995; Nobre and McCarty, 1995; Elger et al., 1997), and has been suggested to be generated in the perirhinal cortex (McCarthy et al., 1995, Fernandez et al., 2002). We therefore suppose that early deflections at encoding reflect not so much semantic but relational integration and episodic memory.

Further support for the notion that the early ERP effect at encoding could reflect relational processes and episodic memory can be derived from previous intracranial EEG studies from within the hippocampus (e.g., McCarthy et al., 1989; Grunwald et al., 1999) and scalp EEG studies of relational memory (Hannula et al., 2006; Bonnefond et al., 2014). Although the significant differences in the early effect is evident between 396 and 506 ms, the negative peak of the component we find is around 350 ms, and corresponds well with results of intracranial studies reporting similar wave-forms (Halgren et al., 1980; McCarthy et al., 1989, Grunwald et al., 1999). These studies conclude that the early negativity peaking between 300 and 400 ms is generated within the hippocampus and is functionally related to—at least to some degree (see also Polich, 2007)—the P300 observed in scalp EEG. The scalp P300, in turn, has been reported to be the earliest component that distinguishes between intact and recombined or new face-scene associations (Hannula et al., 2006), and between matching and non-matching overlapping associations (Bonnefond et al., 2014). Our data support this view of early relational processing and add that these effects of relational memory and inference can also be observed within the hippocampus.

Alternatively, one could argue that the early effect we find may be caused by the repetition of a single word alone, namely one repeated word (B in BC) as compared to entirely new words (CD). Although future studies may include additional control conditions such as complete repetitions of the word pairs from encoding phase I (AB) also in encoding phase II and maybe also at test to elaborate on this possibility, it seems unlikely that the early effect reflects a mere single word repetition effect (priming). Single word repetition and priming usually elicit reduced responses in scalp EEG (Rugg, 1985; Holcomb, 1988), intracranial EEG (Nobre and McCarthy, 1995) and fMRI (Henson, 2003). In our data, however, the ERPs following BC word pairs actually displayed a stronger negativity than ERPs following CD word pairs, indicating increased processing for the BC word pairs, which entailed a repeated word (B). Increased processing following BC than CD pairs might suggest that the integration of a word pair containing a repeated word is more effortful than an entirely new pair. Especially the early ERP difference following BC vs. CD pairs corresponds well with the notion that implicit inference may be enabled by an automatic—and therefore also fast—integration of experiences into pre-existing knowledge structures (Shohamy and Wagner, 2008; Wimmer and Shohamy, 2012).

Late ERP differences evident during encoding phase II (BC vs. CD) occur at times when previous studies found effects of successful versus unsuccessful memory encoding in intracranial EEG from within the hippocampus (Fernández et al., 1999, 2002). Here, stronger positivities for subsequently remembered versus forgotten words have been found to emerge after 500 ms (Fernández et al., 1999) or 800 ms (Fernández et al., 2002) post-stimulus and persisted up to 2,000 ms. In the current behavioral data, "correctness" of relational inference was suggested to foster "fit" judgments in the experimental condition at test when corresponding encoding pairs were consistently also judged with a "fit" answer (fff triplets). Considering only trials at encoding phase II (BC vs. CD) that corresponded to a test word pair that received a "fit" answer, stimulus-locked ERP effects emerged within the temporal window of late memory related effects (1,374–1,539 ms and 1,773–1,938 ms) but—in contrast to these previous studies (Fernández et al., 1999, 2000)—were characterized by negative deflections for experimental pairs (BC) versus positive deflections for control pairs (CD). Response-locked ERP effects during encoding phase II, in contrast, revealed stronger positive deflections to "fit" versus "do not fit" judgments in the experimental condition. As behavioral responses during encoding approximately occur 1,900 ms post-stimulus these results may be taken as support for the notion that "correctness" of inference is reflected in late stronger positivity during encoding.

Both, the early and late stimulus-locked effects were obtained during encoding phase II suggesting that the crucial part of relational integration and inference can already occur during encoding. Our data thus add to a recent view that mnemonic integration at encoding may suffice for apparently effortless inference at the time of test (Shohamy and Wagner, 2008; Zeithamova and Preston, 2010). Mnemonic integration is achieved by associating a current episode to a previous episode through their common elements. This associative binding across the temporal domain is considered as one of the core functions of the hippocampus (Lisman, 1999; Staresina and Davachi, 2009). Thus, associative binding is also considered central to episodic memory formation (Davachi and Wagner, 2002). Because inference was implicit in our current study, associative binding and mnemonic integration was taking place automatically and without deliberation or effort. Associative binding and mnemonic integration could hence be perpetual hippocampal processes by which the essence of the stream of experiences of our everyday lives gets laid down in memory (Olsen et al., 2012).

Perpetual mnemonic integration in the hippocampus may thus yield memories that may often bias our choices in new situations implicitly. We suggest ERP effects that were either modulated by or locked to the responses as potential correlate of this interaction of implicit memory with decision making. First, late stimulus-locked ERP differences between BC and CD word pairs were also evident when considering word pairs that received a "fit" judgment but not for word pairs that received a "do not fit" judgment. Second, response-locked ERPs revealed differences between "fit" and "do not fit" judgments at encoding and at test. All of these response-dependent ERP effects were evident late after stimulus onset, suggesting that they do not reflect automatic processes but rather the interaction of implicit memory with the seemingly conscious and deliberate mental act of judging the semantic fit between two words in a pair.

Our results are at odds with a standard model of human long-term memory (Squire, 1992) because we report relational inference that occurs automatically and hence implicitly but nevertheless recruits the hippocampus. Relational inference is thought to depend on the hippocampus and hence on the episodic memory system (Eichenbaum, 2004), which—according to the standard view—requires awareness of encoding and retrieval to operate (Squire, 1992; Smith and Squire, 2005). Our results hence favor more recent models of human long-term memory (Reder et al., 2009; Henke, 2010; Hannula and Greene, 2012), which do not posit awareness as a precondition for the functioning of hippocampal memory encoding or retrieval.

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