

TESTING FOR INCIDENTAL REACTIVATION OF EPISODIC INFORMATION
DURING MEMORY RETRIEVAL: AN ELECTROPHYSIOLOGICAL STUDY

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MEMORY RETRIEVAL: AN ELECTROPHYSIOLOGICAL STUDY

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LIST OF ABBREVIATIONS

ANOVA:	Analysis of variance
EEG:	Electroencephalography
ERSP:	Event-related spectral perturbation
fMRI:	Functional magnetic resonance imaging
FWER:	Family-wise error rate
ICA:	Independent component analysis
ITC:	Inter-trial coherence
MVPA:	Multi-variate pattern analysis
RT:	Response time
SVM:	Support vector machine

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ABSTRACT

Neuro-computational models of memory posit that successful episodic retrieval is accompanied by reactivation of the cortical representations that were active during encoding. Several fMRI and EEG studies have shown that such reactivation effects are strongly related to conscious retrieval (recollection), consistent with the idea that this phenomenon relies on the hippocampus. The involvement of reactivation during weak and unconscious memory retrieval, however, is yet to be fully explored. One exception is a recent EEG study by Wimber, Maab, Staudigl, Richardson-Klavehn, and Hanslmayr (2012) in which words were encoded in the context of background visual flicker entrainment (at 6 and 10 Hz) and then presented at retrieval in the absence of flicker. Neural measures of the effects of the visual flicker, often referred to as phase-locking, were observed at the corresponding entrained frequencies during retrieval, consistent with the notion that the encoding representations were reactivated. Given the important implications of unconscious reactivation to established memory theories, the current study attempted to provide a direct replication of the Wimber et al. (2012) findings. Additionally, we tested whether a final memory test, in which EEG was acquired while subjects were explicitly asked to make judgments about the frequency of visual flicker present at encoding, provided further evidence for reactivation under more-ideal, intentional retrieval conditions. Our study failed to replicate the findings of Wimber et al., indicating that neural modulation due to visual frequency entrainment is reactivated neither under unconscious nor intentional retrieval conditions.

INTRODUCTION

Psychological and neurobiological theories of episodic memory have proposed that the neurocognitive processes and representations engaged when an event is encoded are re-engaged at the time of its retrieval (Rugg et al., 2008; Danker & Anderson, 2010). In the psychological domain, the principle of transfer-appropriate processing (Morris et al., 1977) accounts for the finding that retrieval is more likely to succeed when cues are processed in a manner similar to the processing at encoding (also see Tulving & Thomson, 1973). Likewise, several influential models of episodic memory are based on the idea that the brain regions active during encoding are reactivated at retrieval (Marr, 1971; Yonelinas, 2002; Norman, 2010). According to this view, a pattern of cortical activity corresponding to the sensory, perceptual, and cognitive processes engaged at encoding is stored in a sparse representation by the hippocampus (Rolls, 2000; Alvarez & Squire, 1994). Upon later presentation of an effective retrieval cue, the hippocampal representation becomes activated, thereby triggering *reinstatement* (reactivation) of the original cortical pattern (Hasselmo & Wyble, 1997; Norman & O'Reilly, 2003). Common to both the psychological and neurobiological accounts is the idea that the encoding-retrieval relationship is particularly evident during instances of conscious retrieval, or *recollection*, which comes either in the form of greater likelihood of reported retrieval success or with access to additional details not present in the cue. The study proposed here tests an alternative hypothesis recently put forth (Wimber, Maab, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012) that cortical reinstatement is additionally involved in situations in which memory retrieval is incidental or even outside of conscious awareness.

Empirical evidence for the involvement of cortical reinstatement during recollection comes from several recent neuroimaging studies (for reviews, see Rugg et al., 2008; Danker & Anderson, 2010; Rissman & Wagner, 2012). These studies employ a general approach of investigating the overlap (or similarity) in the neural correlates of encoding and retrieval in the context of different subjective measures of memory. In one study using functional magnetic resonance imaging (fMRI), Kahn et al. (2004) had subjects encode a list of words in the context of two tasks. One task required generating a mental scene depicting the item, and the other had subjects covertly pronounce the word backwards. For the retrieval phase, subjects completed a two-step response procedure in which they made a recognition judgment (*Was the word previously encountered or not?*) followed by a source-memory judgment (*Which encoding task was performed for the word?*). When subjects correctly identified the task, different sets of brain regions were selectively active: left parahippocampal cortex was active for words from the scene-generation condition and left premotor/ventrolateral prefrontal cortex was active for words from the pronunciation condition. These differences resembled those observed at the time of encoding in a previous study that used the same task conditions (Kahn, Davachi, & Wagner, 2004). Furthermore, new items eliciting an old (false alarm) response and subsequent source misattribution were associated with weaker activation in these regions, suggesting a functional relationship between cortical reinstatement and retrieval success.

Johnson and Rugg (2007) further investigated the cortical-reinstatement hypothesis by directly testing for overlap between encoding- and retrieval-related activity in a single study. Subjects encoded a series of words under two conditions: words presented on a solid background required generating a meaningful sentence that included the word, whereas those superimposed on a picture of a scene required imagining the object denoted by the word in the scene. At retrieval, subjects distinguished between words for which they “remembered”

(recollected) details from encoding (e.g., the encoding task performed or any other detail) and words that were accompanied by a sense of *familiarity* (“known”) in the absence of recollection (Tulving, 1983). An important feature of the study was that fMRI data were acquired during both the encoding and retrieval phases, allowing for the identification of brain regions that exhibited reactivation of encoding-related activity at the time of retrieval. Regions exhibiting selective activity according to encoding condition were also selectively reactivated at retrieval, with words from the scene encoding condition associated with greater activity in occipital and fusiform cortex, and words encoded with the sentence generation task exhibiting greater activity in medial prefrontal cortex. Additionally, these reactivation effects were evident in regions that also exhibited greater activity for “remember” compared to “know” responses (i.e. recollection effects), suggesting that reactivation played a role in the subjective response about retrieval. Together, the findings supported the proposal of the modeling literature that hippocampally-mediated reinstatement is associated with conscious retrieval (Hasselmo & Wyble, 1997; Norman & O’Reilly, 2003).

Subsequent studies have expanded the functional role of reinstatement during memory retrieval by showing that reactivation also occurs for other, non-recollective, memory judgments. Johnson et al. (2009) employed fMRI with a technique called multivariate pattern analysis (MVPA; see Haynes & Rees, 2006; Norman et al., 2006; Rissman & Wagner, 2012; Tong & Pratte, 2012) to test for reactivation when memory judgments were not accompanied by recollection. Subjects encoded words under three task conditions: imagining the difficulty an artist would have drawing the item, generating different functions the item could serve, and rating the difficulty of pronouncing the word backwards. Subjects then completed a recognition memory test in which they were instructed to distinguish between remembering details from encoding and, in the absence of recollection, four levels of confidence that a given item was old

or new. Consistent with previous findings, reactivation was greatest in magnitude for recollection-based judgments. Crucially, reactivation was also evident for high-confidence judgments, thus challenging the notion that reinstatement is restricted to instances of recollection. These findings also raise an uncertainty regarding the limiting conditions under which cortical reinstatement is involved in memory retrieval.

A recent study by Wimber et al. (2012) expanded the limiting conditions of cortical reinstatement by investigating reactivation in the context of unconscious retrieval. Wimber et al. acquired electroencephalographic (EEG) data in a procedure involving frequency entrainment in the visual domain. During an encoding phase, subjects judged the number of syllables (odd or even) for a series of words that were shown on backgrounds that flickered at one of two frequencies (6 and 10 Hz). On a later recognition test, words were shown in the absence of flicker, and subjects made confidence judgments (on a 6-point scale) about their memories. Wimber et al. (2012) demonstrated that the flicker stimuli produced phase-locked activity in the EEG data at encoding. Although there was no direct test of encoding-retrieval overlap (or similarity; cf. Johnson & Rugg, 2007; Johnson et al., 2009), phase-locking effects at the same frequencies were tested at retrieval. For old items correctly judged with high confidence, the phase-locked activity corresponding to the appropriate frequency condition for that word re-emerged within about 300 ms after stimulus onset. These findings are consistent with the notion that the encoding-related information was reactivated during retrieval, even though the flicker stimulus was not present. More importantly, Wimber et al. (2012) demonstrated in a separate behavioral experiment that subjects were at chance when directly asked to indicate the flicker rate associated with each word, suggesting that the phase-locking effects were evidence of reactivation during unconscious retrieval.

Given the challenge of the Wimber et al. (2012) findings to the widely-accepted position that cortical reinstatement provides conscious access to episodic information, the current study sought to further test those findings. To provide a direct methodological replication of Wimber et al., our behavioral procedures closely followed theirs, including the nature and timing of the stimuli (words and flicker), the tasks performed during the encoding and retrieval phases, and the number of items comprising each phase. At encoding, subjects completed a syllable-judgment task for a series of words, while the background flickered at either 6 or 10 Hz. After a short delay, a recognition memory test – hereafter referred to as the *indirect test* – was administered, in which subjects judged their confidence about the old/new status of each word in the absence of any visual flicker. This procedure allowed us to assess, as in Wimber et al. (2012), reactivation of encoding-related frequency information at the time of retrieval.

As noted earlier, Wimber et al. (2012) also included a behavioral experiment in which an additional sample of subjects was directly asked about the flicker stimulus previously associated with each word at encoding. Departing from this procedure, we included such a *direct test* with the same group of subjects described above, following completion of the indirect test. The purpose of administering the direct test in this manner was to obtain EEG data (cf. Wimber et al.) that allowed for the examination of neural evidence potentially indicating that flicker information was reactivated when directly probed. As Wimber et al. (2012) acknowledged, previous studies have demonstrated that visually-presented oscillatory stimuli can entrain neural networks distinct from those involved exclusively in visual processing (Rosanova et al., 2009; Thut, Schyns, & Gross, 2011). As a consequence, it is possible that reactivation at the time of retrieval would not take the form of encoding-retrieval overlap (e.g., in visual cortex), as it has in the fMRI studies described earlier. The acquisition of EEG data in the direct test of the current

study thus circumvents this problem by allowing for the localization of potential reactivation effects within the same test phase.

METHODS

Subjects

Twenty-five students from the University of Missouri (MU) participated in partial fulfillment of course credit. All subjects were right-handed, native-English speakers, with normal or corrected vision, and had no history of neurological disorders. The data from seven subjects were removed, due to either excessive artifact in the EEG (three subjects) or inadequate behavioral performance (four subjects with hit and false alarm rates within .15). The final sample of 18 subjects (12 males) ranged in age from 18 to 22 years ($M = 19$). Informed consent was obtained in accordance with the MU Institutional Review Board.

Stimuli and design

A pool of 360 words was obtained from the MRC Psycholinguistic Database (Coltheart, 1981; Wilson, 1988; http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm). Words were four to nine letters long ($M = 5.4$), had written frequencies of 1 to 50 per million ($M = 17.4$; Kucera & Francis, 1967), and had scores of at least 500 on scales of familiarity ($M = 540.1$), concreteness ($M = 581.5$), and imagability ($M = 581.0$). The words were randomly assigned to six lists (60 words each) that were rotated across the conditions across subjects. For each subject, words from two of the lists were presented during the encoding phase (one list assigned to each flicker frequency) and again as old items during the *indirect* and *direct* test phases (see Procedure). Words from the remaining lists served as new items for the indirect test. All words were shown in white uppercase 36-point Arial font (longest word: approx. 9 x 1 cm) at the center of a black rectangular box (approx. 9.3 cm long x 8.0 cm high) on the gray background of a 24-inch widescreen LCD monitor (cropped to 1024 x 768 resolution). The rectangular box flickered on and off the screen at a frequency of either 6 or 10 Hz. The display

was viewed at a distance of approximately 1 m. Stimulus presentation was controlled by the Cogent 2000 toolbox (<http://www.vislab.ucl.ac.uk>) in MATLAB (The MathWorks, Natick, MA).

Procedure

Upon arrival to the laboratory, subjects completed the required consent forms and were fitted with an electrode cap, which lasted approximately 30 minutes. Subjects then completed two cycles of the encoding phase and indirect test phase, followed finally by the direct memory test. A brief practice session was administered before each phase to ensure that subjects were familiar with the tasks.

Each encoding phase consisted of a series of 120 words presented visually, while subjects were to judge whether the words had an odd or even number of syllables. Each word was presented for 2500 ms on a background rectangular box that flickered (alternated between black and gray) at either 6 or 10 Hz (60 trials of each condition per encoding phase). A white question mark was then displayed centrally on the gray background for 1000 ms to signify that subjects should make their response. Subjects pressed the “J” key on the keyboard for the odd response and the “K” key for the even response. A white fixation cross appeared in the center of the screen for a jittered inter-stimulus interval between 750 and 1250 ms. Trials from the two flicker conditions were randomly intermixed during each encoding phase.

Following the initial encoding phase, subjects completed a brief practice version of the indirect memory test. The proper indirect test immediately followed, consisting of intermixed presentation of the 120 words encountered in the previous encoding phase and 60 new words. Subjects were instructed to indicate their confidence that each item was old or new using a 6-point scale (“sure old”, “probably old”, “maybe old”, “maybe new”, “probably new”, and “sure new”; respectively mapped to the “Z”, “X”, “C”, “,”, “.”, and “/” keys). Subjects were further

informed that they were being tested only on words from the immediately-preceding encoding phase. Test stimuli were presented against a black rectangular box for 2000 ms. A question mark then prompted subjects to make their response and remained on the screen for 1500 ms. As during the encoding phase, a white fixation cross appeared in the center of the screen for a jittered inter-stimulus interval of 750 to 1250 ms.

Following the second cycle of encoding and indirect test phases, subjects completed the direct memory test, which consisted of all of the items presented during the encoding phases. Subjects were instructed to indicate whether the rectangular background flickered at a “slow” (6 Hz) or “fast” rate (10 Hz) when the word was presented in the earlier encoding phase, by pressing the “J” and “K” keys, respectively. Words were presented on the gray background for 2000 ms each and were followed by a question mark for an additional 1500 ms. Subjects were instructed to make their response while the question mark was displayed. An inter-stimulus interval between 750 and 1250 ms was again employed, during which a white fixation cross was displayed.

EEG acquisition and analysis

EEG was continuously recorded during all phases of the experiment. Data were acquired with a BrainAmp Standard system (Brain Vision LLC; Durham, NC; <http://www.brainvision.com>) from 59 Ag/AgCl ring electrodes embedded in an elastic cap (EasyCap, Herrsching, Germany; <http://www.easycap.de>). The electrode locations were based on the extended 10-20 system (Chatrian et al., 1985; EasyCap montage 11) and included the following sites: Fpz/1/2, AFz/3/4/7/8, Fz, F1 through F8, FC1 through FC6, FT7/8, Cz, C1 through C6, T7/8, CPz, CP1 through CP6, TP7/8, Pz, P1 through P8, POz/3/4/7/8, and O1/2. Data were recorded with reference to an electrode placed at the FCz cap location, and a ground electrode was placed at FT10. Additional electrodes were adhered to the mastoids, below the left eye, and on the outer

canthi. Before the experimental procedure began, electrodes were adjusted until impedances were below 5 k Ω . Data were recorded at a sampling rate of 1000 Hz and amplifier bandwidth of 0.01-100 Hz.

Offline processing of the EEG data was implemented with the EEGLAB (Delorme & Makeig, 2004; <http://sccn.ucsd.edu/eeglab/>) and FieldTrip (Oostenveld et al., 2011; <http://fieldtrip.fcdonders.nl>) toolboxes in MATLAB. The data were downsampled to 200 Hz, high-pass filtered at .05 Hz, re-referenced to the mastoid average, and epoched from -1000 to 2495 ms relative to item onset (baseline-corrected to the pre-stimulus interval). Independent components analysis (ICA) was used to identify artifacts (e.g., eye movements, blinks, and muscle activity) that were then manually rejected on the basis of their scalp topography and power spectra (also see Jung et al., 2000). The ICA-based identification and rejection procedure was applied to the data from all of the experimental phases together (encoding, indirect, and direct test phases) so as to prevent any bias of removing components for one condition or phase versus another. Epochs were also rejected automatically if the signal exceeded ± 100 mV from baseline. The data were then low-pass filtered at 50 Hz.

The data were next transformed with a Morlet-wavelet decomposition into 73 frequencies (.5-Hz intervals from 4Hz to 40Hz) and 126 time points (20-ms bins for an epoch ranging from -500 to 2000 ms, relative to stimulus onset). A measure of phase-locking across trials, referred to as *inter-trial coherence* (ITC), was calculated for each electrode and each condition of interest throughout the experimental phases. ITC varies between 0 and 1, with larger values indicating highly synchronous activity across trials and smaller values corresponding to desynchronized (random) activity. Given the non-normality of the ITC measure, Wilcoxon sign-rank tests (rather than t-tests) were employed, as in Wimber et al. (2012). Non-parametric permutation-based

analyses were used to control the family-wise error rate (FWER) due to multiple comparisons across time, frequencies, and electrodes (see Maris & Oostenveld, 2007). Specifically, null distributions were created by randomly shuffling the condition labels for each subject 1,000 times and then testing for significance ($p < .05$ per electrode or time-frequency data-point) at the group level. Clustered effects surviving a corrected level of $p < .05$ (two-tailed, as positive and negative effects were kept separate) are reported as significant.

In addition to the ITC analyses described above, the event-related spectral perturbation (ERSP, in dB) was computed for each electrode and trial during the test phases in order to carry out multivariate pattern-classification analysis (MVPA). Prior to classification, the ERSP data were z-scored. A support vector machine (SVM) was then trained for each subject to detect differences between items from the two flicker conditions during one of the indirect test blocks. The SVM was evaluated on data from the remaining indirect test block, resulting in a measure of classifier accuracy (where chance is 0.5, due to having two conditions). This analysis was then repeated while switching the training and testing blocks. As in the previous analyses, only items eliciting a correct old response (i.e. hits) were included. To ensure that an unequal number of trials per flicker condition did not bias the classifier, trial numbers were equated via random selection from the more-plentiful condition. Analogous analyses were repeated using data from the direct test phase for training and data from the indirect test phase for evaluation.

RESULTS

Behavioral results

For the indirect test phase, the overall hit rates were equivalent for items from the 6- and 10-Hz conditions ($M = .74$ and $SD = .13$ for each), and the correct rejection rate was $.68$ ($SD = .14$). A one-way ANOVA of these data revealed no significant differences ($F_{1.1,18.2} = 1.43$, $p = 0.25$; degrees of freedom for this and subsequent analyses were Greenhouse-Geisser adjusted when appropriate). The mean response times (RTs) for the correct judgments were 2310 ms ($SD = 527$) for 6-Hz hits, 2300 ms ($SD = 527$) for 10-Hz hits, and 2372 ms ($SD = 421$) for new items. A one-way ANOVA revealed no significant differences in the RTs ($F_{1.2,19.7} = 3.14$, $p = 0.09$).

The mean response proportions and RTs according to each confidence level in the indirect test phase are shown in Table 1. A two-way ANOVA of the response proportions for old items, with factors accounting for prior frequency (6 vs. 10 Hz) and all six confidence levels, gave rise to a main effect of confidence ($F_{1.3,21.5} = 38.27$, $p < 0.001$). However, no effects involving the frequency factor were evident (both $F_s < 1$). Because of the low numbers of old items designated with low-confidence and new responses, it was not possible to compute meaningful statistics on the RTs at each confidence level. Thus, the analysis of RTs across confidence was restricted to “sure old” responses. No significant differences were observed, though, between items from the 6-Hz ($M = 2254$ ms, $SD = 551$) and 10-Hz ($M = 2244$ ms, $SD = 560$) conditions ($p = .41$).

The mean response proportions and RTs for the direct test are provided in Table 2. Accuracy at identifying the correct frequency condition ($M = .50$, $SD = .03$) was not significantly different from chance ($p = .75$). The accuracy rate for each subject was also near the chance level, with the best-performing subject only reaching a rate of 53%. A two-way ANOVA of the RTs,

employing factors of prior frequency and accuracy (correct vs. incorrect), revealed no significant effects (minimum $p = .17$).

EEG results

The analyses of the EEG data first focused on assessing the inter-trial coherence (ITC) associated with the frequencies of visual flicker at encoding, and then applying analogous analyses to the data from the indirect test phase to identify evidence for reactivation. This approach constitutes a replication attempt of the findings of Wimber et al. (2012). We next turned our attention to the EEG data from the direct test phase, which, as subjects were explicitly asked to retrieve the frequency information associated with each item, was expected to provide a stronger test for reactivation. Finally, we employed multivariate pattern-classification analysis (MVPA), using the EEG data from the indirect and direct tests, to further assess the presence of any frequency-related neural modulation during these phases.

Encoding phase

The ITC data from the encoding phase were first contrasted across the 6- and 10-Hz conditions. As in Wimber et al. (2012), we expected the EEG data to exhibit phase-locked effects at the frequency of the flicker stimulation (e.g., the 6-Hz band for 6-Hz trials) that were larger than the corresponding measure for trials from the other condition (e.g., the 6-Hz band for 10-Hz trials). Further, these effects were predicted to be maximally-distributed over the posterior scalp due to the visual nature of the stimuli (although Wimber et al. did not provide evidence of the topographic distribution at encoding) and to be relatively constant across the period of flicker presentation. As shown in Figure 1A, sustained significant differences in ITC were present when collapsing over all electrodes. Specifically, trials in the 6-Hz condition were associated with greater ITC in the 6-Hz frequency band, as well as near the harmonic frequencies of 12 and 24

Hz, compared to 10-Hz trials. Both of these effects passed the cluster-wise (frequency band x time point) corrected threshold for significance (228 adjacent effects). Likewise, trials in the 10-Hz condition elicited significantly greater ITC at 10 Hz and at harmonic frequencies (20 Hz and, to a lesser extent, 30 Hz) - all of which passed the cluster-corrected threshold. Shown in Figure 1B are the topographic maps of the averaged ITC differences at 6 Hz (averaging over 5.5 to 6.5 Hz, as in Wimber et al.) and at 10 Hz (averaging over 9.5 to 10.5 Hz) for the 0- to 2000-msec time period that the flicker was presented (as described in *EEG acquisition and analysis*, the last 500 ms of the encoding epochs was truncated due to padding for the spectral transformation). The differences in both bands were significant at every electrode (surpassing the correction for number of clustered electrodes), but were also maximal over the posterior scalp as expected (at the O1 and O2 electrodes, respectively, for both 6 and 10-Hz bands). Of particular note are the comparable sizes of effects obtained in the current study and in Wimber et al. Compared to the effect sizes obtained in the encoding phase of Wimber et al. (2012) - Cohen's d values of about 1.5 and 1.25 for the 6- and 10-Hz bands, respectively (based on Figure 2 of that paper) - differences in the 6- and 10-Hz bands in our encoding phase were associated with Cohen's d values of 2.09 and 1.68, respectively.

Indirect test phase

Having established that the flicker stimuli elicited phase-locked activity at their respective frequencies during encoding, the EEG data from the indirect test were next analyzed for evidence of frequency-specific reactivation. As was noted in the Introduction, evidence of reactivation would take the form of directional differences in ITC according to the encoding history of the test word, even though visual flicker is not present at retrieval. Figure 2A displays the ITC differences across the recording epoch, collapsing across all electrodes, for old items

that elicited correct responses (i.e. hits). With contrasts of ITC across each frequency band and time point, however, there were no significant differences surpassing the cluster-corrected threshold of 107 adjacent effects. The large change in scale between the ITC differences at encoding compared to those at test is also highlighted in Figure 2A.

Given that Wimber et al. (2012) observed reactivation effects for trials from the 6- and 10-Hz conditions at 0-300 ms after item onset, our analysis next focused on this time period. However, the analysis of ITC differences averaged over this period, as well as for periods of equal length throughout the remainder of the recording epoch, provided no evidence of flicker-related reactivation. Furthermore, ITC differences within 0-300 ms were assessed at each electrode, and the resulting topographic plots for the two frequency bands are shown in Figure 2C. These analyses again revealed significant effects at none of the electrodes. (If there were any such differences, they would have also had to occur across 12 neighboring electrodes according to the appropriate cluster-correction procedures.)

Although the analyses reported above failed to give rise to any evidence of reactivated ITC at retrieval, it remains possible that frequency-related activity is present but not in a synchronous (phase-locked) manner. To test for such effects, an additional analysis, involving multivariate pattern-classification, was conducted. For this analysis, each trial eliciting a correct response was first time-frequency transformed in the same manner as previously described. Frequency power was then averaged across 300-ms intervals beginning at item onset. A linear support vector machine (SVM) algorithm was trained and tested separately for each subject and respective time bin, including the data at each electrode and in each frequency band. Classification proceeded in a leave-one-out cross-validation manner, in which the first block served as the training set and the second block served as the test set, and then this process was

reversed. Figure 3 displays the accuracy for the classification, averaged across subjects, in each time bin across the recording epoch. To statistically test classifier accuracy against chance, a null distribution was determined via 1000 random permutations of the condition labels.

Performance did not differ significantly from chance for any of the time periods.

Direct test phase

In a final set of analyses, the EEG data from the direct test were analyzed for potential reactivation effects under conditions in which subjects were instructed to intentionally retrieve the flicker information from encoding. As in the foregoing analyses, items only eliciting correct responses were included, although this does not mean that the frequency was successfully retrieved, given that performance was near chance for each subject. Figure 4A displays the ITC differences for these items across the recording epoch, collapsed over all electrodes.

Contrasting the ITC values associated with the two frequency conditions failed to reveal any frequency band x time point clusters that passed the corrected threshold (46 adjacent effects in this case). Topographic plots also indicated the failure of ITC differences to reach significance over any part of the scalp, as shown in Figure 4B. In keeping with the foregoing analyses, the corrected significance level of 13 clustered electrodes was determined via analogous permutation tests.

To further test for effects of the flicker frequency from encoding, MVPA was employed on the data for correct trials from the direct test phase. As with done for the MVPA of the indirect test phase, frequency power was averaged across 300-ms intervals beginning at item onset. A linear SVM was then trained and tested separately for each time bin using a procedure in which 10% of the trials were withheld for testing on each cross-validation iteration. Shown in Figure 5 are the results of this analysis. Comparable to what was shown for the indirect test, the MVPA

revealed near-chance levels of accuracy across all time bins. There was thus no evidence that the prior encoding frequency associated with direct test items could be identified with the EEG data, even when subjects were explicitly asked to access such information.

DISCUSSION

The current study used EEG to test the hypothesis that encoding-related information elicits neural reactivation at the time of retrieval even when presumably inaccessible to conscious awareness. A recent study by Wimber et al. (2012) reported evidence of frequency-specific EEG effects during retrieval that corresponded to visual entrainment induced at encoding. We sought to replicate those findings here. As shown by Wimber et al., we observed statistically equivalent behavioral performance in a recognition memory (indirect test) phase for items previously associated with two background flicker rates (6 and 10 Hz). These equivalent performance measures included overall hit rates, RTs corresponding to hits, and the proportions and RTs associated with high-confidence ratings. In a subsequent test phase that probed explicit retrieval of the frequency condition at encoding, subjects were also at chance in identifying the correct frequency and exhibited no RT differences across conditions. Consistent with the behavioral results of Wimber et al., these findings suggest that subjects did not, and were unable to, consciously access the encoding information during retrieval.

EEG data were recorded during all phases of the current study - encoding and the indirect and direct tests - to investigate coherent (phase-locked) activation and reactivation due to visual entrainment at 6 and 10 Hz. During encoding, the visual flicker elicited significant inter-trial coherence (ITC) differences at the stimulated and harmonic frequencies (also see Herrmann, 2001). The encoding differences were additionally widespread across the scalp and strongest at posterior electrode sites, as was predicted due to the visual nature of the stimuli. Despite the strong effects at encoding, however, we observed no frequency-specific effects during either of the test phases. ITC measures in both the 6- and 10-Hz bands were indistinguishable according to the prior frequency condition from which the test items came. Specifically, we failed to find

such differences regardless of whether they were tested at any scalp electrode or restricted to the 0-300 ms post-stimulus onset interval in which the effects were evident in the Wimber et al. study. We also observed differences neither for hits (as in Wimber et al.) nor for higher-confidence judgments, as might be expected given that reactivation has been previously shown to correlate positively with confidence (Johnson et al., 2009, 2015). Importantly, there was no evidence of frequency effect during the direct test phase, which arguably provides more ideal conditions under which the encoding information could be retrieved. Together, the current results fail to replicate the findings of Wimber et al., suggesting that neural modulation due to frequency entrainment is not reactivated at the time of retrieval.

Given our failure to replicate the critical finding of unconscious reactivation shown by Wimber et al. (2012), it is natural to speculate about possible differences between the current and previous studies that might have given rise to the disparate results. As described in the Introduction, we set out to replicate that study as closely as possible, based on the methodological details provided. These included aspects of the design, such as the numbers of stimuli comprising each phase and the timing of stimulus presentation, as well as the EEG recording and analysis procedures. Notably, the main difference between the studies was that the same subjects completed all of the test phases in our study, whereas Wimber et al. enlisted an additional subject sample for the direct test; however, because this test was administered at the end of our session (and it was not referred to earlier in the experimenter's instructions), it should have had no impact on the previous test phases. In addition, some aspects of our findings can be taken as confirmation that our methods were similar enough to those previously employed. First, we observed differences at encoding that were comparable in magnitude to those demonstrated by Wimber et al., suggesting that our entrainment procedure was effective. This is an important finding since the potential reactivation of encoding differences would

presumably be considerably smaller in magnitude, as has been shown with fMRI (Johnson & Rugg, 2007; Johnson et al., 2009). Second, overall behavioral accuracy in the indirect test phase of our study was almost as high as in the Wimber et al. study ($d' = 1.11$ and 1.25 , respectively), with the accuracy based only on high-confidence responses being even more similar ($d' = 1.20$ and $d' \approx 1.27$, respectively; note that the latter value is estimated from Figure 1 of Wimber et al.). Although we are confident that our replication attempt included the key features of the previous study, there nonetheless might be other subtle differences that we overlooked.

One puzzling aspect of the results of Wimber et al. (2012) concerns the statistical correction procedure that was employed to control for multiple comparisons in the topographic analyses of the reactivation effects. In their Figure 2, which appears to display these results, 6 electrodes were highlighted for differences in the 6-Hz band, and 5 electrodes were highlighted for the 10-Hz band. These electrodes appear, based on the color scale provided, to correspond to locations where the differences survived a threshold of $p < .05$. However, whereas all 5 electrodes for the 10-Hz difference were adjacent to at least one other electrode, only 2 of the 6 electrodes for the 6-Hz difference were adjacent. Wimber et al. report in the text of their paper that “The overall number of electrodes showing a significant ($p < 0.05$) effect was significantly above chance in both comparisons ($p_{\text{corr}} < 0.05$).” (p. 1482) It is thus ambiguous whether the correction procedure treated each electrode independently (and thereby involved just counting the number significant electrodes) or accounted for the clustering of significant electrode-wise effects, the latter which should be used considering the correlations among proximal electrodes (for such procedures, see Maris & Oostenveld, 2007). Note that this ambiguity of Wimber et al. does not take away from the findings of the current study, since we found no significant effects even by uncorrected standards in the indirect test, thereby precluding any type of cluster correction. Due to these concerns, though, it is unclear whether the previous evidence for

unconscious reactivation of encoding-related activity at retrieval would hold up to these more-appropriate procedures.

Despite the disparities between the current and previous findings, our added use of multivariate pattern-classification analysis (MVPA) arguably provided a more-flexible and thereby potentially-stronger test of the reactivation hypothesis. This flexibility is important for multiple reasons. First, as was also noted by Wimber et al. (2012), the topographies of the frequency-related effects might be dissimilar across encoding and retrieval, given that the visual stimulation is only present at encoding. Such a finding has been demonstrated with transcranial magnetic stimulation (TMS) applied to occipital cortex, whereby increases in oscillatory activity in frontal and parietal cortices was also observed (Rosanova et al. 2011). Second, it is possible that frequency-related information is reactivated even when such reactivation is not phase-locked to test-item onset. For example, suppose that reactivation is locked to the moment of semantic access of the test item; if the timing of that moment varies from item to item, then the phase of the effect will also vary. The MVPA was designed to make use of any information to distinguish items from the two frequency conditions, thus allowing for the involvement of effects at different electrodes from encoding, at different frequencies than those entrained, and that were potentially not phase-locked. No reliable evidence of reactivation was observed with MVPA, however, even for the ideal conditions of explicit retrieval in the direct test phase.

Aside from the present study and that of Wimber et al. (2012), several prior studies that have also investigated the effects of sensory manipulations at encoding on unconscious retrieval are worth noting. In an early study, Gratton et al. (1997, Experiment 4) presented abstract line stimuli to the left or right of fixation at encoding and then had subjects make recognition-memory judgments for centrally-presented stimuli at test. Lateralized differences in the event-

related potentials (ERPs) recorded during the test corresponded to the side of presentation at encoding. Additionally, Gratton et al. showed in a subsequent experiment (Experiment 5) that subjects were at chance in identifying the side of original presentation, consistent with our and Wimber et al.'s results. Fabiani et al. (2000) extended these findings by showing that such lateralized differences distinguished between true and false recognition. Because both true and false memories were designated with the same "old" response, but only true memories exhibited the lateralized ERP effects, the authors inferred that effects were outside of conscious awareness (for analogous fMRI results, see Slotnick & Schacter, 2004). Although there are several differences between the stimulus conditions and analysis procedures of these studies and the current one, one difference stands out as a possible explanation of the discrepancy in results. That is, in the three studies noted here, the items were presented multiple times at encoding, with subjects even being instructed to remember the presentation location in two of the studies (Gratton et al., 1997; Slotnick & Schacter, 2004). By comparison, the visual flicker in our study was likely incidentally encoded (if at all), potentially leading to weaker results of reactivation.

As described in the Introduction, a class of influential neurobiological models of episodic memory states that, upon presentation of an effective retrieval cue, the hippocampus elicits cortical-pattern reinstatement, providing conscious access to encoded information. Considering the findings of the current study on their own, we interpret them as establishing a boundary condition of the involvement of such neural reactivation in memory retrieval. Whereas some prior studies have also failed to demonstrate reactivation of encoding information when subjects make low-confidence or incorrect responses to old items on a retrieval test (e.g., Johnson et al., 2009; Leiker & Johnson, 2015), one rather uninteresting explanation of those effects is that the relevant information is merely not effectively encoded.

Here, however, the neural effects at encoding due to the flicker entrainment procedure are clearly evident. The present findings thus provide stronger support that reactivation does not always occur for salient encoding information.

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TABLE 1

Mean (SD) response proportions and response times during the indirect test phase

Response Proportions						
Trial type	Sure Old	Probably Old	Maybe Old	Maybe New	Probably New	Sure New
10 Hz	0.50 (.22)	0.15 (.07)	0.09 (.08)	0.07 (.06)*	0.11 (.05)	0.07(.05)
6 Hz	0.51 (.25)	0.15 (.07)	0.08 (.08)	0.05 (.11)*	0.11 (.06)	0.07 (.04)
New	0.12 (.10)	0.10 (.06)	0.07 (.06)*	0.12 (.07)	0.21 (.10)	0.35 (.20)
Response Time (ms)						
10 Hz	2244 (560)	2435 (445)	2561 (413)	2643 (430)*	2374 (490)	2374 (454)
6 Hz	2254 (551)	2420 (405)	2597 (398)	2565 (307)*	2426 (355)	2386 (384)
New	2323 (596)	2485 (545)	2660 (450)*	2460 (376)	2455 (424)	2311 (439)

*Indicates that there were multiple subjects with fewer than 8 responses per cell.

TABLE 2

Trial type	Correct proportion	Response Time (ms)	
		Correct	Incorrect
10 Hz	.54 (.11)	2238 (488)	2279 (481)
6 Hz	.45 (.09)	2283 (490)	2259 (503)

Mean (SD) correct

response proportions

and response times

during the direct test

phase

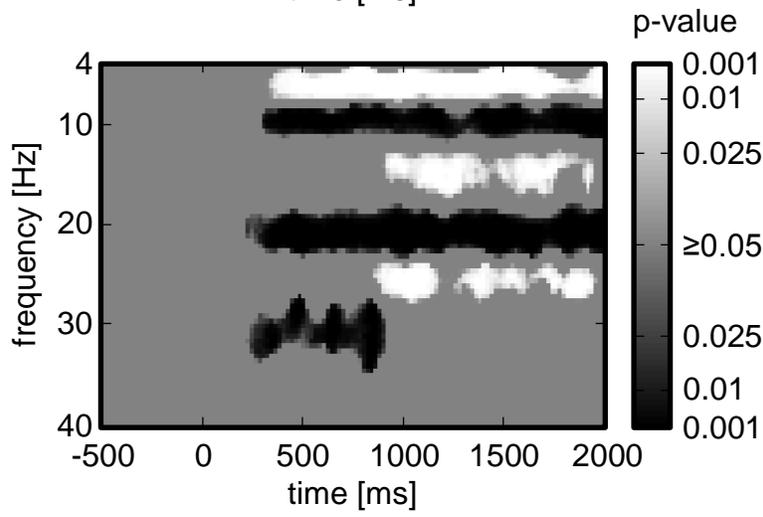
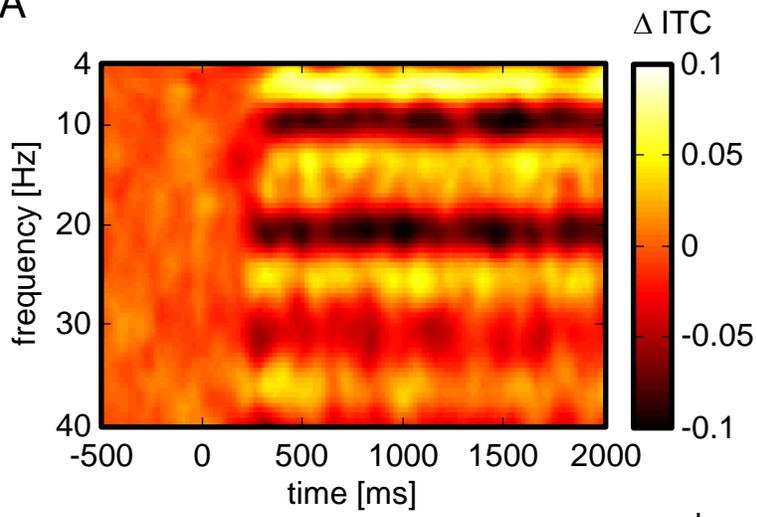
FIGURE CAPTIONS

- 1. Differences in inter-trial coherence (ITC) during the encoding phase.** (A) *Upper panel:* Group-averaged ITC differences (6- minus 10-Hz trials) for each frequency band and time-point, collapsed across all electrodes. *Lower panel:* P-values associated with ITC differences that were significant at both the element-wise (each frequency band and time-point) and cluster-wise level. (B) Topographic maps of ITC differences for the 6-Hz band (6- minus 10-Hz trials; top) and the 10-Hz band (10- minus 6-Hz trials; bottom). As shown, the differences are positive across the scalp but largest at posterior electrodes.
- 2. Differences in inter-trial coherence (ITC) during the indirect test phase.** (A) *Upper panel:* Group-averaged ITC differences (6- minus 10-Hz trials) for each frequency band and time-point, collapsed across all electrodes. *Lower panel:* The same differences as above, but plotted with the color scale used in Figure 1A (upper panel) to highlight the smaller magnitude of effects. (B) Topographic maps of ITC differences for the 6-Hz band (6- minus 10-Hz trials; top) and the 10-Hz band (10- minus 6-Hz trials; bottom). The color scale is the same as that used for the encoding-phase data in Figure 1B.
- 3. Results of the multivariate pattern-classification analysis (MVPA) for the indirect test phase.** Classifier accuracy (chance = 0.5) in discriminating 6- from 10-Hz trials, based on cross-validation of the indirect test data. Orange lines indicate the median accuracy across subjects, box edges indicate the 25th and 75th percentiles, and whiskers extend to the extreme (non-outlier) data-points. Outliers (orange plus-signs) are defined as being > 1.5 times the size of the 25-75th percentile difference

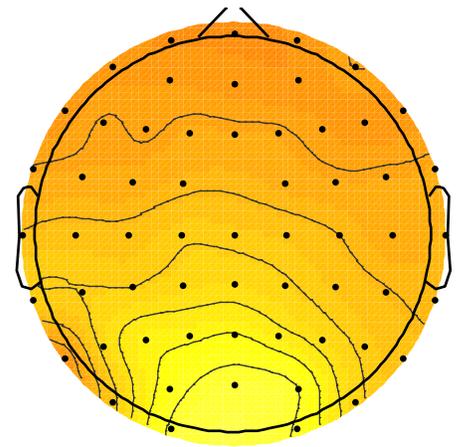
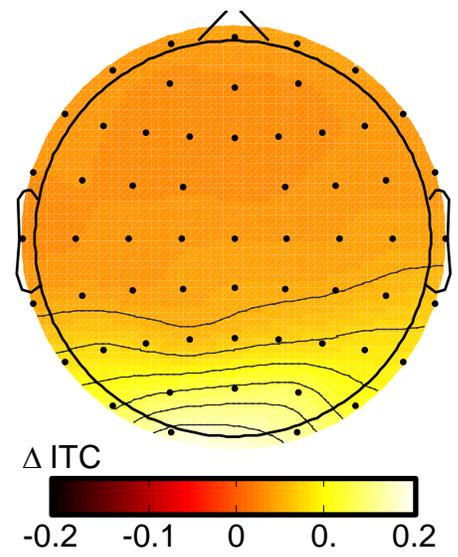
beyond the box edges. Accuracy did not significantly differ than chance during any of the latency intervals.

- 4. Differences in inter-trial coherence (ITC) during the direct test phase.** (A) *Upper panel:* Group-averaged ITC differences (6- minus 10-Hz trials) for each frequency band and time-point, collapsed across all electrodes. *Lower panel:* The same differences as above, but plotted with the color scale used in Figure 1A (upper panel) to highlight the smaller magnitude of effects. (B) Topographic maps of ITC differences for the 6-Hz band (6- minus 10-Hz trials; top) and the 10-Hz band (10- minus 6-Hz trials; bottom). The color scale is the same as that used for the encoding-phase data in Figure 1B.
- 5. Results of the multivariate pattern-classification analysis (MVPA) for the direct test phase.** Classifier accuracy (chance = 0.5) in discriminating 6- from 10-Hz trials, based on cross-validation of the indirect test data. Orange lines indicate the median accuracy across subjects, box edges indicate the 25th and 75th percentiles, and whiskers extend to the extreme (non-outlier) data-points. Outliers (orange plus-signs) are defined as being > 1.5 times the size of the 25-75th percentile difference beyond the box edges. Accuracy did not significantly differ than chance during any of the latency intervals.

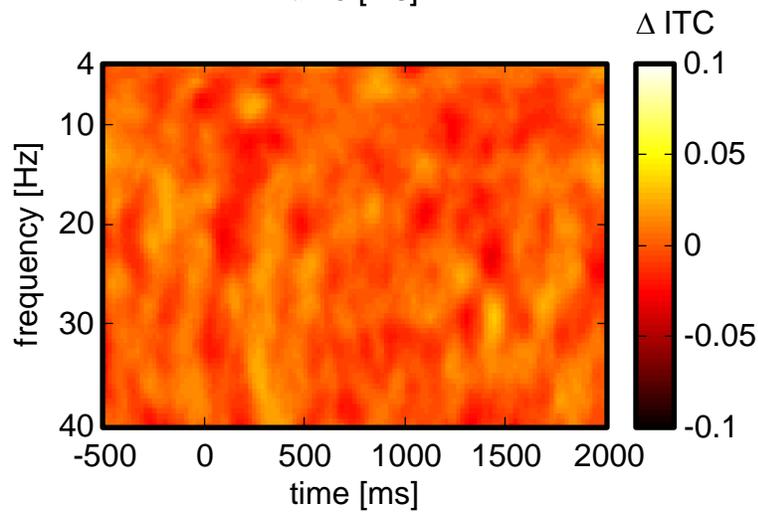
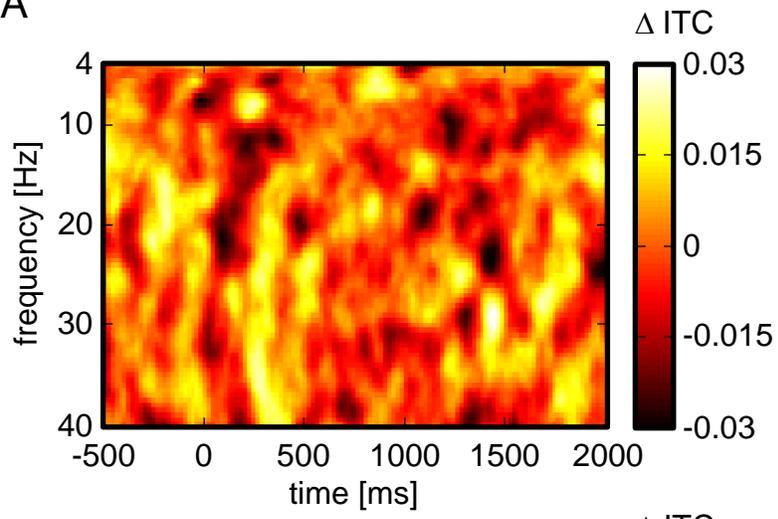
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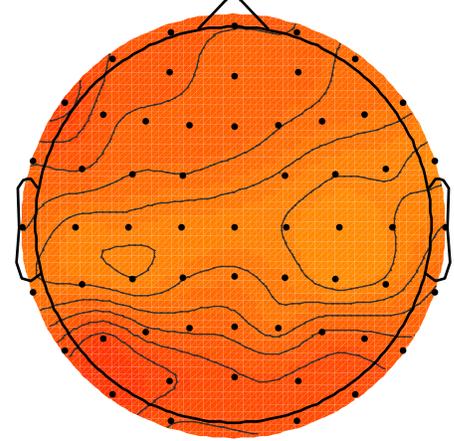
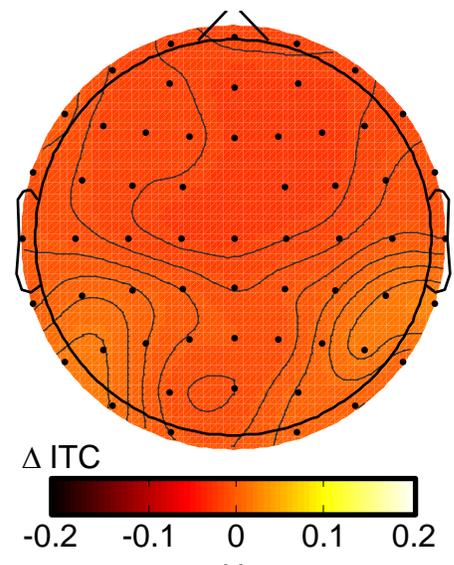
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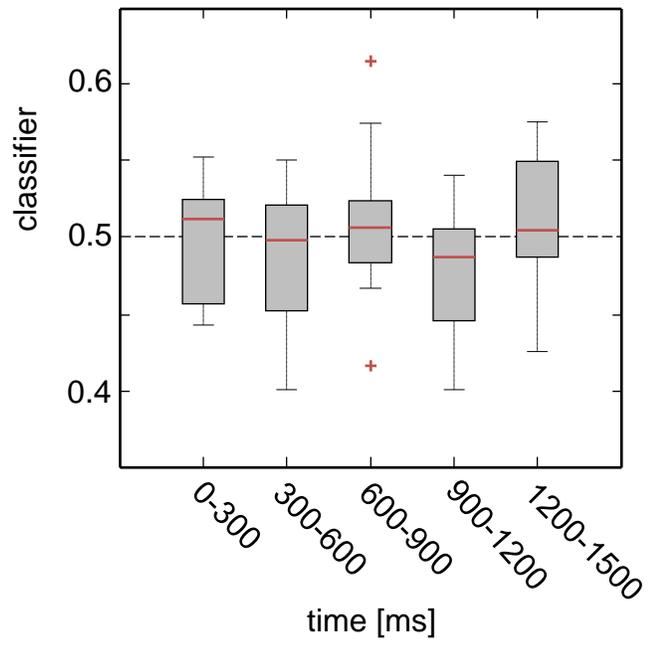


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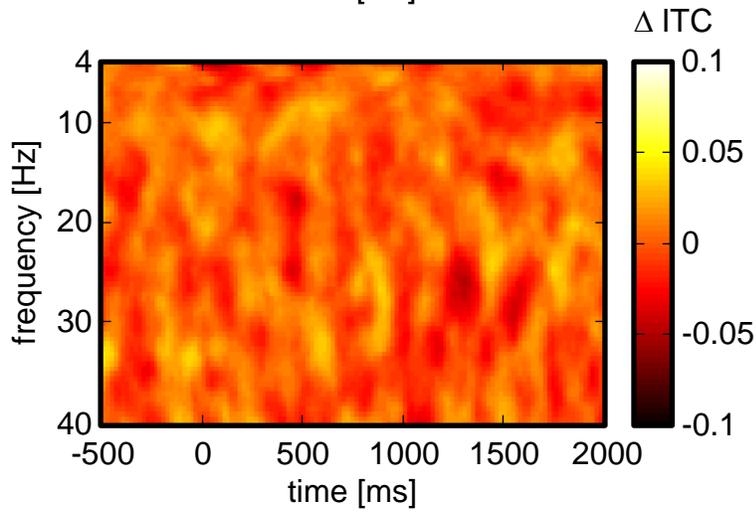
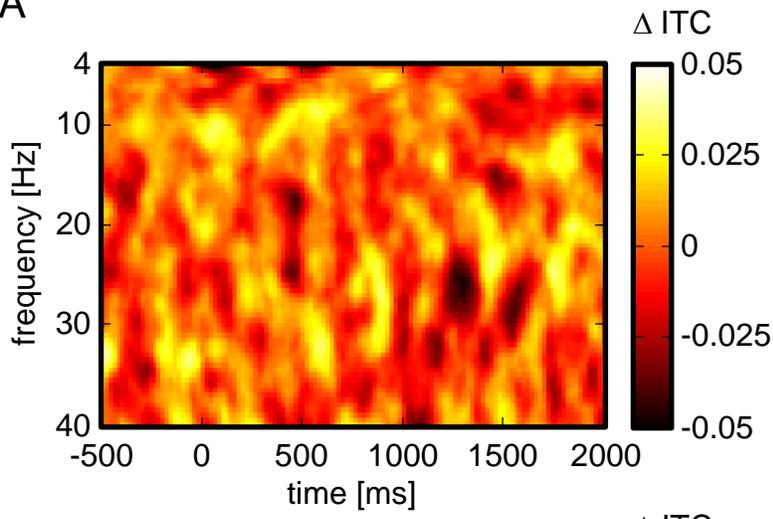


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