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DOI:

[10.1016/j.cub.2012.05.054](https://doi.org/10.1016/j.cub.2012.05.054)

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Document Version

Publisher's PDF, also known as Version of record

Citation for published version (Harvard):

Wimber, M, Maaß, A, Staudigl, T, Richardson-Klavehn, A & Hanslmayr, S 2012, 'Rapid memory reactivation revealed by oscillatory entrainment', *Current Biology*, vol. 22, no. 16, pp. 1482-6.
<https://doi.org/10.1016/j.cub.2012.05.054>

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Rapid Memory Reactivation Revealed by Oscillatory Entrainment

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Summary

Episodic memory refers to humans' unique ability to mentally reconstruct past events. Neurocomputational models predict that remembering entails the reinstatement of brain activity that was present when an event was initially experienced [1–5], a claim that has recently gained support from functional imaging work in humans [6–14]. The nature of this reactivation, however, is still unclear. Cognitive models claim that retrieval is set off by an early reactivation of stored memory representations (“ecphory”) [15–17]. However, reinstatement as found in imaging studies might also reflect postretrieval processes that operate on the products of retrieval and are thus a consequence rather than a precondition of remembering. Here, we used frequency entrainment as a novel method of tagging memories in the human electroencephalogram (EEG). Participants studied words presented on flickering backgrounds, entraining a steady-state brain response at either 6 or 10 Hz. We found that these frequency signatures rapidly reemerged during a later memory test when participants successfully recognized a word. An additional behavioral experiment suggested that this reactivation occurs in the absence of conscious memory for the frequencies entrained during study. The findings provide empirical evidence for the role of rapid, likely unconscious memory reactivation during retrieval.

Results and Discussion

Our method takes advantage of the known property of flickering stimuli to entrain a so-called steady-state brain response at the stimulation frequency [18], which is easily detectable in the human electroencephalogram (EEG). Participants encoded words on backgrounds that flickered at either 6 or 10 Hz (Figure 1A). During a later memory test involving no flicker, subjects judged how confidently they recognized each item as previously studied on a scale from one to six (C1–6). We hypothesized that the frequencies entrained during encoding are reactivated during successful recognition, and that this reactivation would occur rapidly and outside of awareness if representing a neural signature of “ecphory” [15–17].

Behaviorally, flicker frequency had no significant effect on memory performance as measured by recognition sensitivity

d' and response bias β ($d'_{6\text{Hz}} = 1.26 \pm 0.14$ [SEM]; $d'_{10\text{Hz}} = 1.24 \pm 0.13$; $t_{15} = 0.33$; $p_{\text{two-tailed}} = 0.75$; $\beta_{6\text{Hz}} = 0.08 \pm 0.06$; $\beta_{10\text{Hz}} = 0.09 \pm 0.07$; $t_{15} = 0.45$, $p_{\text{two-tailed}} = 0.66$). Figure 1B shows the highly overlapping receiver operating characteristic (ROC) curves from the two conditions. The behavioral results thus indicate that words were encoded equally well in both conditions, such that any electrophysiological differences found during recognition are unlikely to be driven by differential memory performance.

Steady-state brain responses are strongly time locked to stimulation onset [18], and electrophysiological analyses were therefore focused on phase locking (also known as intertrial coherence) [19]. EEG recordings during encoding confirmed that phase locking was significantly stronger at 6 Hz when comparing 6 Hz with 10 Hz items (Figure 2A) and significantly stronger at 10 Hz when comparing 10 Hz with 6 Hz items (Figure 2B). Differences between conditions were significant ($p < 0.05$) over 62 and 61 electrodes, respectively, confirming that our manipulation evoked frequency-specific phase locking over almost every single electrode.

To test our main hypothesis that the frequencies entrained during encoding are reinstated during recognition, we first directly contrasted EEG activity elicited by correctly recognized 6 and 10 Hz words. The analysis was restricted to correct trials because previous studies using both univariate and multivariate fMRI approaches only consistently found reinstatement during successful retrieval [6–8, 14, 20]. Consistent with our hypothesis, 6 Hz words elicited significantly stronger phase locking at 6 Hz than 10 Hz words (Figure 2C), whereas 10 Hz words elicited significantly stronger phase locking at 10 Hz than 6 Hz words (Figure 2D). The overall number of electrodes showing a significant ($p < 0.05$) effect was significantly above chance in both comparisons ($p_{\text{corr}} < 0.05$). The encoding-specific frequencies thus reemerged during retrieval, an effect that was evident in a very early time window around 100–300 ms.

Regarding the time course of reactivation, studies using event-related potentials [20–22] have reported effects that largely coincided with the so-called parietal old-new effect, which is widely regarded as an electrophysiological correlate of conscious recollection and typically onsets around 400–500 ms after a reminder [23]. The present data suggest that reinstatement can occur considerably earlier, within 300 ms after cue presentation. Note that differences in both conditions peaked early, but clearly poststimulus, with the apparent prestimulus onset resulting from temporal blurring inherent in the time-frequency transformation. Even though no causal claims can be made based on the earliness of the effect, the data still suggest that an episodic, contextual signal can precede conscious stages of the retrieval process.

The present study is the first to use frequency rather than spatial patterns of neural activity as an index of memory reactivation, and we therefore had no a priori hypotheses about topography. Generally consistent with prior fMRI studies demonstrating that reactivation occurs in a subset of the brain regions activated by the encoding task [11, 12, 24], we found frequency-specific reinstatement over a subset of the electrodes responsive to the initial flickering stimulation. Not

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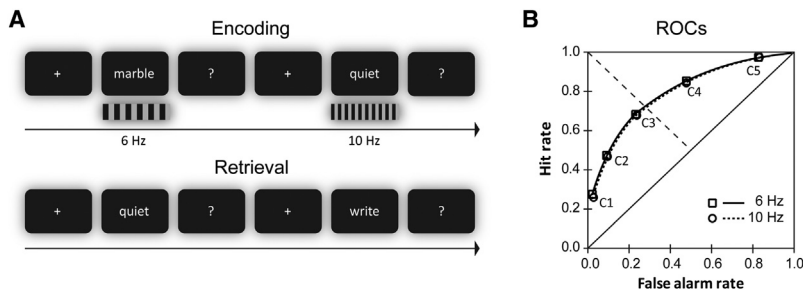


Figure 1. Experimental Paradigm and Memory Performance

(A) During encoding, participants counted the syllables of words that were presented on backgrounds flickering at either 6 or 10 Hz. During recognition, participants saw a mixture of old and new words, presented on nonflickering backgrounds, and indicated how confidently they recognized each word as old on a scale from one to six (C1–6). (B) Receiver operating characteristic (ROC) curves showing the cumulative hit rate (proportion of correctly recognized old words) as a function of the cumulative false alarm rate (proportion of new words incorrectly classified old) at varying levels of confidence (C1–6). Diagonals indicate chance performance (solid line) and the neutral response criterion (dashed line).

surprisingly, the study and test topographies still differed considerably, as indicated by a significant location \times stage interaction in the 6 Hz condition ($F_{5,3,150} = 6.75$, $p_{\text{corr}} < 0.05$) and a marginally significant interaction in the 10 Hz condition ($F_{5,2,150} = 1.87$, $p_{\text{corr}} = 0.11$). The electrodes showing reinstatement during retrieval only minimally overlapped between conditions, but there was no significant location \times condition interaction ($F_{5,6,150} = 0.82$, $p_{\text{corr}} = 0.55$). Based on previous studies showing that rhythmic stimulation at different frequencies can entrain endogenous oscillatory activity in distinct brain networks [25–27], it is still possible that the two flicker conditions entrained distinct neural populations and that these population codes (rather than the entrained rhythms themselves) were in turn reengaged during retrieval.

Another theoretically relevant question concerns the degree to which reinstatement is functionally related to memory success. fMRI studies reported that cortical reinstatement is most pronounced when participants consciously retrieve

contextual details [6, 7, 14], although recent evidence using more sensitive multivariate pattern classifiers revealed reactivation also during familiarity-based recognition [6]. We conducted two complementary analyses to formally test whether the phase information at the respective frequency of interest (6 and 10 Hz) varies as a function of memory success. First, we directly compared phase information between items recognized with high confidence (C1) and items not recognized as previously encoded (misses, C4–6) in a fixed-effects analysis. The phase distributions of high-confidence hits and misses differed in a frequency-specific manner, with differences peaking at 6 Hz during the recognition of 6 Hz words (Figure 3A) and at 10 Hz during the recognition of 10 Hz words (Figure 3B; see Figure S1 and Supplemental Discussion available online for the pattern in low-confidence hits C2–3). Differences between high-confidence hits and misses were significantly larger in the 6 Hz range when contrasting 6 Hz with 10 Hz items (Figure 3C) and in the 10 Hz range when

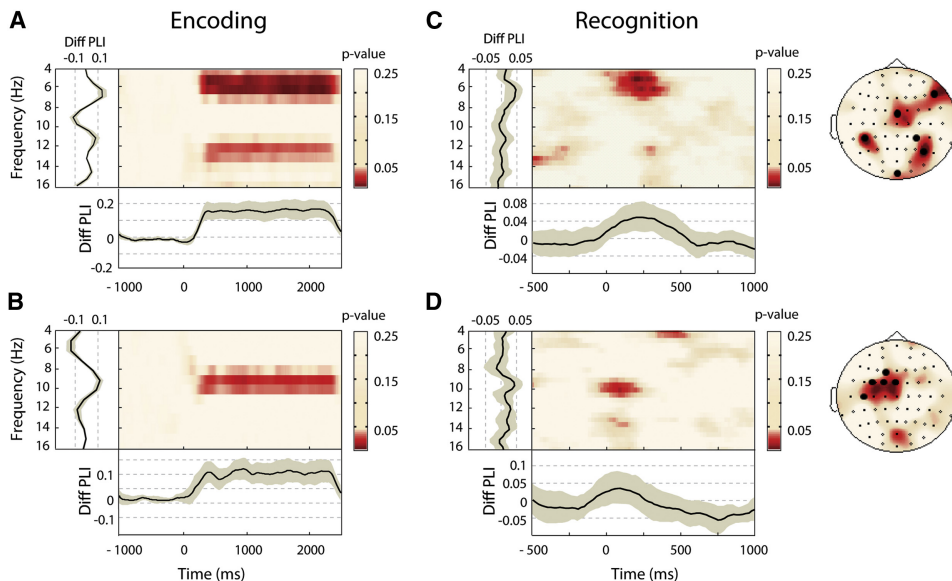


Figure 2. Differences in Phase Locking Index during Encoding and Recognition

(A and B) Phase locking index (PLI) elicited by stimuli flickering at 6 Hz compared with 10 Hz (A) and at 10 Hz compared with 6 Hz (B). Significantly more phase locking was evident at the expected frequency over all 62 electrodes in the 6 Hz condition and over 61 electrodes in the 10 Hz condition.

(C and D) Reinstatement of the encoding-specific frequencies is indicated by significant differences in PLI during successful recognition of 6 Hz compared with 10 Hz items (C) and 10 Hz compared with 6 Hz items (D).

In all panels, time-frequency plots depict p values corresponding to the mean difference across significant electrodes. Line plots to the left show the average difference in PLI across the time window of interest (0–2,000 ms during study; 0–300 ms during recognition) as a function of frequency; line plots at the bottom show the average difference in PLI at the frequency of interest (6 and 10 Hz, respectively) as a function of time. Shaded areas correspond to 95% confidence intervals.

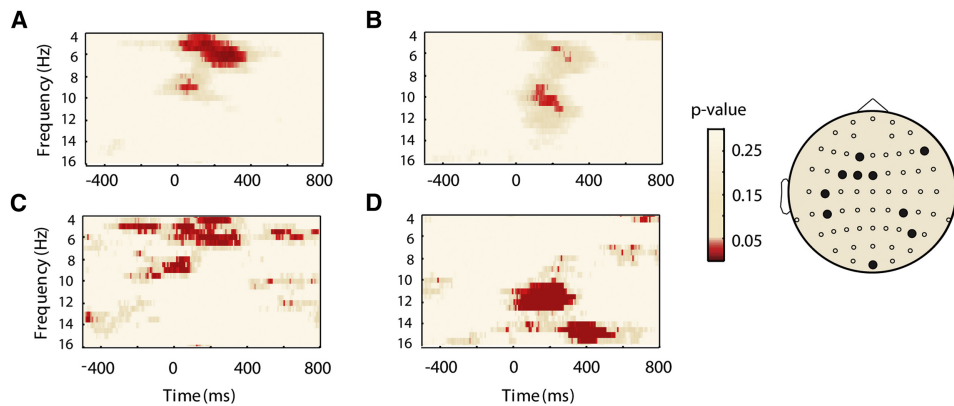


Figure 3. Results from a Fixed-Effects Analysis Assessing the Relationship between Reactivation and Memory Performance

Kuiper's tests were used to assess differences in the phase distributions of items recognized with high confidence (C1) and items that were missed (C4–6); corresponding p values were derived from permutation tests. Differences in the phase distributions of high-confidence hits and misses peaked at 6 Hz in the 6 Hz condition (A) and at 10 Hz in the 10 Hz condition (B). This pattern was confirmed by a direct comparison of these difference values between 6 and 10 Hz items (C and D). All analyses were performed over the ten (highlighted) electrodes that generally showed reinstatement effects (see Figures 2C and 2D). See also Figure S1.

comparing 10 Hz with 6 Hz items (Figure 3D). Interestingly, peaks in both comparisons were found in the same early time window in which the basic reinstatement effects (Figure 2) were evident, pointing toward a common underlying mechanism. However, it remains open why memory success was related to distinct aspects of the phase distributions (mean orientation and variance, respectively) in the two conditions (see Figure S1 and Supplemental Discussion).

Note that phase differences between hits and misses (Figures 3A and 3B) are likely to be influenced by unspecific memory success effects at various biologically relevant frequencies, potentially adding on top of any frequency-specific effects driven by contextual reinstatement. Moreover, electrode selection might have favored differences in phase distributions between item types, because the electrodes of interest were chosen based on an analysis in which they exhibit high phase locking at 6 and 10 Hz, respectively, in hits (including high-confidence hits; see Figure 2). Such unspecific effects, however, will theoretically affect 6 and 10 Hz items to the same extent and should therefore cancel out in any direct comparison between conditions (Figures 3C and 3D). Despite the general limitations associated with fixed-effects approaches (e.g., limited generalizability), these results indicate a positive relationship between frequency-specific reinstatement and memory performance.

To complement and confirm these findings, we conducted an additional single-trial, random-effects analysis in which single trials from each subject were binned according to their distance from the mean phase at the respective frequency of interest (Figure 4A). We hypothesized that trials with a low distance from the mean phase (reflecting high phase locking) would have a relatively high likelihood of being hits, and that trials with a large distance from the mean phase (reflecting low phase locking) will have a relatively high likelihood of being misses. Indeed, we found that bins with a phase close to the mean contained a disproportionately high number of confidently recognized items, and bins with a phase far from the mean contained a disproportionately high number of missed items. Across bins, the deviation from a uniform response distribution was significantly positive in both 6 Hz ($t_{15} = 1.85$, $p < 0.05$) and 10 Hz ($t_{15} = 2.12$, $p < 0.05$) items and showed

a strong trends toward being negative in the opposite bins ($t_{15} = 1.70$, $p = 0.054$ and $t_{15} = 1.58$, $p = 0.068$, respectively; Figure 4B). Results from this single-trial analysis thus confirmed the tight link between context reactivation and behavioral performance, supporting the idea that cortical reinstatement gives rise to a memory strength signal that is positively related to successful recognition [6, 28]. Important for the functional interpretation of these effects, our data additionally suggest that the brain-behavior link holds true for an early reactivation signal that is unlikely to be the product of conscious recollection.

One goal of the present study was to use “memory tags” that are unlikely to come to mind during the later recognition test. An additional behavioral experiment was therefore conducted to assess the degree to which participants were able to remember the frequency tags associated with each word. Despite good recognition memory for the words themselves ($d'_{6\text{Hz}} = 1.31 \pm 0.13$; $d'_{10\text{Hz}} = 1.34 \pm 0.13$; $\beta_{6\text{Hz}} = 0.13 \pm 0.17$; $\beta_{10\text{Hz}} = 0.13 \pm 0.16$), forced-choice performance with respect to the flicker information (“Was this word initially presented on a fast or slow flickering background?”) was not significantly different from guessing ($P_{\text{correct}} = 0.49 \pm 0.01$; $t_{17} = 0.77$, $p = 0.45$), suggesting that during recognition, participants were unaware of the encoding-related frequencies. By contrast, previous studies often used memory tests that required explicit source judgments or active recall of contextual details (e.g., “Was the word initially paired with a picture or sound?”) [9, 10, 21, 24, 29]. Even though other investigations have found reactivation with simple old/new [11] or remember/know/guess [6, 13, 20] instructions that do not make explicit reference to such information, it is still likely that participants incidentally recover details from the encoding context. Crucially, our findings suggest that neural activity specific to an encoding episode can be reactivated without the corresponding information being necessarily consciously accessible.

Indeed, Tulving [16, 17] argued that ephoric information is the result of a rapid, unconscious interaction between a reminder and a stored memory trace. Recent behavioral evidence supports the view that contextual, episodic information can have a critical influence already on early, implicit processes [30, 31]. Based on this evidence and building on

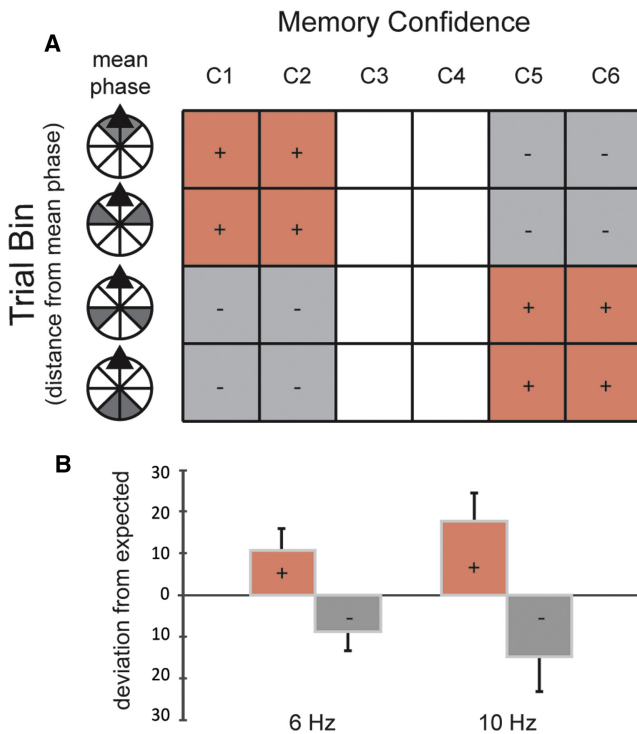


Figure 4. Results of a Random-Effects Analysis Linking Phase Information with Memory Performance

(A) Single trials were sorted into four bins (signified by circles on the left) based on their distance from the mean phase. The observed frequencies of each memory judgment per bin were then contrasted with the frequencies expected under a uniform distribution across bins.

(B) Consistent with our hypotheses (indicated by red coloring of the matrix), hits (C1–2) occurred significantly more often than expected in bins with a low distance from the mean phase, and misses (C5–6) occurred significantly more often than expected in bins with a high distance from the mean phase. Error bars represent SEM.

Tulving's framework, Moscovitch [15] proposed that retrieval might be a two-stage process, initiated by an early, unconscious signal (ecphory) that is automatically elicited by a proximal cue and a later stage involving conscious operations on the retrieved contents. The present findings provide neural evidence for the first of these two hypothetical stages, demonstrating that brain activity in a surprisingly early time window already carries specific contextual information, even in the absence of overt memory for these contextual details. The positive relationship to subjective memory strength suggests that ecphory may be contingent on further bottom-up (e.g., the proximity of the cue) or top-down (e.g., retrieval mode) factors [16]. Future work will help to elucidate the exact nature of the underlying mechanism and its significance for different forms of remembering.

Besides its theoretical implications, the present study is, to our knowledge, the first to use frequency tagging in a memory paradigm. Steady-state evoked potentials have proven a powerful tool in attention research, providing a neural index for tracking attention online [32, 33]. We found that the brain is capable of reproducing an offline echo of these entrained rhythms, such that frequency tagging might become a useful general tool in the memory domain. In particular, EEG has practical advantages over fMRI in areas like sleep research, and frequency tags in different modalities might thus be useful

for tracking memory reactivation in quasi-real time during both sleep and wake states in the human EEG (e.g., [34]) or in intracranial recordings in animals [35, 36]. Moreover, it will be interesting to see whether the present findings generalize to different methods of rhythmic entrainment, like transcranial magnetic or current stimulation.

To summarize, we have used a novel frequency tagging approach to test for the incidental reactivation of contextual memory information in the human EEG. Our findings indicate that when presented with a reminder, the brain rapidly reactivates the frequencies associated with an episode during encoding, preferentially when people confidently remember the corresponding event. Such early reactivation might represent a neural signature of ecphory, a rapid, resonance-like signal that evokes a memory trace from its latent state [15–17].

Experimental Procedures

Participants

EEG was recorded from 16 healthy volunteers, and another 18 volunteers participated in the behavioral experiment. All participants gave written informed consent for participation, in line with the ethics guidelines of the Otto-von-Guericke University Magdeburg Medical Faculty.

Materials and Procedure

Stimuli consisted of 360 German words that have been successfully used in previous memory studies (e.g., [37]). During study, participants counted the syllables of 240 words overall, each presented in white font on top of a black, rectangular box flickering regularly at either 6 or 10 Hz during word presentation. During a later recognition test, participants saw the same 240 words intermixed with 120 unstudied words on stable backgrounds and were asked to judge, on a scale from one to six (C1–6), how confidently they recognized a word as previously studied.

EEG Analyses

EEG was recorded from 62 electrodes during both phases of the experiment. Analyses were focused on phase locking, an index of how consistently oscillatory phases in a given frequency band are aligned across trials relative to stimulus onset [19]. Epochs were Gabor transformed into time-frequency space, and phase locking was calculated separately for 6 Hz and 10 Hz items correctly judged old (C1–3). Significant differences between conditions were assessed using a two-stage procedure controlling for multiple testing, as described in detail elsewhere [38]. A number of planned location \times condition interactions (see Supplemental Experimental Procedures) were performed to test for topographical differences.

Two additional analyses were conducted to assess whether phase information at the relevant frequency is related to memory performance. Importantly, both analyses were restricted to the ten electrodes of interest (see topography in Figure 3) that showed significant reactivation effects (Figure 2) in either direction. The rationale behind this electrode selection was to choose a theoretically meaningful electrode pool so as to minimize the influence of unspecific memory success effects on the one hand, and to ensure at the same time that any potential statistical bias toward high phase locking would equally affect both frequencies of interest. First, we compared the phase distributions of old items recognized with high confidence (HC hits, C1) and those of old items not recognized as studied (misses, C4–6). Because phase locking is highly susceptible to differences in trial numbers [39], this comparison was conducted in a fixed-effects model (see [40] for a similar approach), yielding comparable trial numbers across conditions. Single trials were collapsed across subjects, and Kuiper's k , a circular test statistic indicating the likelihood that two phase distributions are unequal, was computed at each time/frequency bin. Empirical p values (one-tailed) corresponding to a given k value were obtained from bootstrapping ($n = 1,000$), randomly permuting trial labels while keeping the trial numbers per condition constant.

Second, we performed a random-effects analysis relating the phase information at the respective frequencies of interest on each single trial to memory performance. We first computed the mean phase across all trials and then classified each single trial according to its distance from the mean. Four equal-sized trial bins were created based on these distances (Figure 4A). We hypothesized that bins with a low distance from the mean

should contain a disproportionately high number of confident hits (C1–2) and that bins with a high distance from the mean should contain a disproportionately high number of misses (C5–6). In contrast, if phase information is unrelated to memory performance, confidence judgments should distribute uniformly across bins. One-tailed *t* tests ($\alpha = 0.05$) were performed to test for significant differences between the observed response frequencies in each bin and the frequencies expected under the assumption of a uniform distribution.

Supplemental Information

Supplemental Information includes one figure, Supplemental Discussion, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.05.054>.

Acknowledgments

We thank Marcus Heldmann for technical support and Leona Hellwig for help with data collection. Michael Anderson, Rik Henson, Peter Lakatos, Kimron Shapiro, and Bernhard Staresina provided helpful comments on earlier versions of the manuscript. This work was supported by grants from the German Research Foundation (DFG; WI3784/1-1 to M.W., RI1847/1-1 to A.R.-K., and HA5622/1-1 to S.H.).

Received: March 2, 2012

Revised: May 1, 2012

Accepted: May 25, 2012

Published online: July 12, 2012

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