Title: Binding of cortical functional modules by synchronous high frequency oscillations

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Abstract:

High-frequency phase-locked oscillations have been hypothesized to facilitate integration ('binding') of information encoded across widespread cortical areas. Ripples (~100ms long ~90Hz oscillations) co-occur ('co-ripple') broadly in multiple states and locations, but have only been associated with memory replay. We tested whether cortico-cortical co-ripples subserve a general role in binding by recording intracranial EEG during reading. Co-rippling increased to words versus consonant-strings between visual, wordform and semantic cortical areas when letters are binding into words, and words to meaning. Similarly, co-ripples strongly increased before correct responses between executive, response, wordform and semantic areas when word meanings bind instructions and response. Task-selective co-rippling dissociated from non-oscillatory activation and memory reinstatement. Co-ripples were phase-locked at zero-lag, even at long distances (>12cm), supporting a general role in cognitive binding.

One Sentence Summary: Widespread visual, lexical, semantic, executive and response processing areas phase-lock during integrative processing.

Main Text:

A central unanswered question in neuroscience is how information is integrated across the cortex. One model, Binding-by-synchrony, posits that objects are 'bound' by coordinating activity representing constituent features via coherent oscillations acting as coupled oscillators (*1*), facilitating selective communication through coincidence detection (*2*) and gain modulation (*3*). Cortical ripples are a promising candidate for binding-by-synchrony. Anatomically and behaviorally ubiquitous, they strongly phase-modulate local cell-firing, and co-firing across sites (*4, 5*).

Ripples were discovered in the rat hippocampus, where they mark the replay of encoded spatial sequences during non-rapid eye movement (NREM) sleep, critical for cortical memory consolidation (*6-9*). In humans, ripples occur throughout the hippocampus and neocortex (*10-12*) and also contribute to memory (*5, 13-16*). Human ripples often co-occur, and even phase-lock between cortical sites, largely independent of distance (*5*). Co-rippling increases during successful cued recall to co-activate distinct cortical sites, suggesting that co-rippling helps bind memory elements (*5*): a form of binding-by-synchrony (*17, 18*). However, a possible general role for cortical co-ripples in binding diverse cognitive functions remains untested.

A reading task evokes widespread cortical co-ripples. Here we tested this possible role by examining ripple co-occurrence (i.e., co-rippling) during reading, when letters need to be bound into words, words with their meanings, and meanings with task instructions and behavioral response (Fig. 1A). Subjects were implanted with electrodes on cortical language areas for diagnosis of epilepsy. They read words presented continuously at 600ms intervals, and key-pressed to words referring to an animal. Consonant strings matched for length served as sensory controls. Overall, during the task, ripples occurred with mean frequency 90.3Hz, amplitude 10.6µV, duration 113.5ms (median 90ms), and rate 18.6/minute, similar to those previously found during spontaneous waking and declarative memory testing (*5, 12, 14-16*) (Fig. S1). Ripples in different sites had a strong tendency to co-occur, at a rate that decrements very slowly with distance (Fig. S2B). Ripples in early visual areas were more likely to have high amplitude and density, and low synchrony with other sites (Figs. S11-13).

Word-selective co-ripples are evoked between visual, wordform and semantic areas. We grouped contacts in anatomo-functional regions (Fig. 2I) and tested for differential binding between regions that encode information that needs to be bound, at the post-stimulus latencies when the binding needs to occur (Fig. 2A). Word-selective co-rippling is maximal from 200 to 400ms after stimulus onset, when it is significant between early visual processing areas in occipital cortex, the ventral wordform area in medial fusiform gyrus (*19*), and the supramarginal and angular gyri, which support accessing the meaning of words (*20*) (Figs. 2C, S3). The 200-400ms post-stimulus interval is when local potentials and high gamma in the word-form area distinguishes between words and nonwords (*21*), and widespread areas produce activity indicating if the meaning of words match their context (*22*). Thus, word-selective co-ripples occur in the appropriate anatomical locations and post-stimulus latencies for binding letters into words, and words with their meaning.

Binding wordforms to their meanings is not hippocampus-dependent (*23*), and thus does not *require* reinstatement of a recent memory trace. However, our task included repeated words which presumably formed a trace associating the word with the task, and which could be reinstated when the words are repeated. Such reinstatement would be hippocampal-dependent due to the long distractor-filled delay between repetitions. This, if the co-rippling we observe is due to reinstatement then it would be selective for repeated words. However, repeated words evoked *less* co-rippling than novel words presented the first time (Fig. S3). This is consistent with the oft-observed phenomenon of repetition-suppression due to facilitated encoding (*24*), and thus provides further support for our hypothesis that such processes, rather than reinstatement, account for the cortical co-rippling we observed.

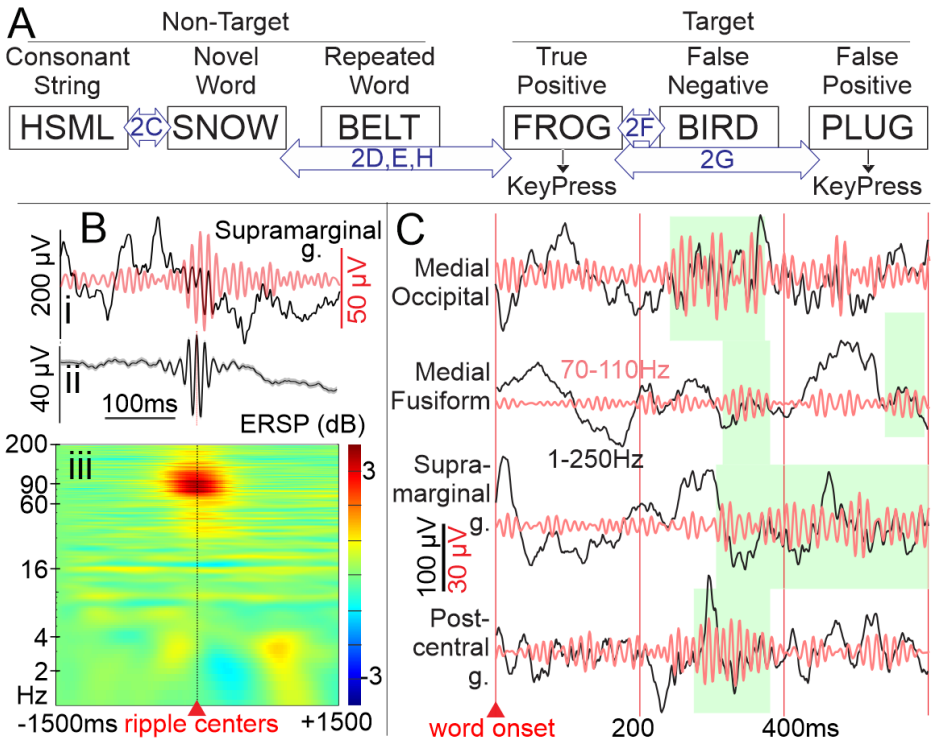

Fig. 1. Cortical Ripples and Co-Ripples During a Reading Task. **A**. Subjects read words and control stimuli (including consonant strings) and key-pressed to names of animals. Blue arrows indicate panels in Fig. 2 with the indicated comparisons. **B**. High frequency bursts ('ripples') from typical disc electrode on the cortical surface as single sweep (**Bi**; broadband (black) or band-passed (red)), average waveform (**Bii**), or average time-frequency plot (**Biii**). **C**. Example Co-Ripple, single sweep to a novel word, multiple sites with overlapping ripples (green shading), broadband and band-passed.

Correctly-detected target words selectively evoke co-ripples between visual, wordform, semantic, executive and response areas. Co-rippling strongly increased on trials where the subject key-pressed correctly to animate words, compared to non-target words. Increases were significant in 54% of connections between left hemisphere areas, where the increase could be greater than ten-fold (Figs. 2DE, S6; Table S7). Co-rippling to targets was similar to non-targets until ~400ms post-stimulus onset, then increased between occipital visual, ventral temporal wordform, parieto-temporal semantic, prefrontal executive, and central response areas (Fig. 2D). Peak co-rippling occurred in the response period (600-800ms), and continued into the post-response period (800-1000ms).

Correct performance in this task requires that the meaning of the word be evaluated against the criterion 'animate,' and if it matches to respond with a keypress. Maintenance of the response criterion and consequent action in active memory, comparison of stimulus word meaning to the response criterion, and procedural sequence control, are all critical but poorly understood 'executive' processes that are supported by prefrontal and parietal cortices (*25, 26*). In the critical response epoch (600-800ms), prefrontal and superior parietal cortices are strongly coupled with areas thought crucial for encoding word meaning, which could support comparison of stimulus word meaning to the response criterion. Prefrontal coupling is also very strong with motor areas, which could support linking the target detection to the required response. Thus, target-selective co-ripples peak in appropriate anatomical locations and post-stimulus latencies for binding stimulus word meaning to target meaning, and for binding stimulus-target matches to appropriate motor response, as predicted by our hypothesis.

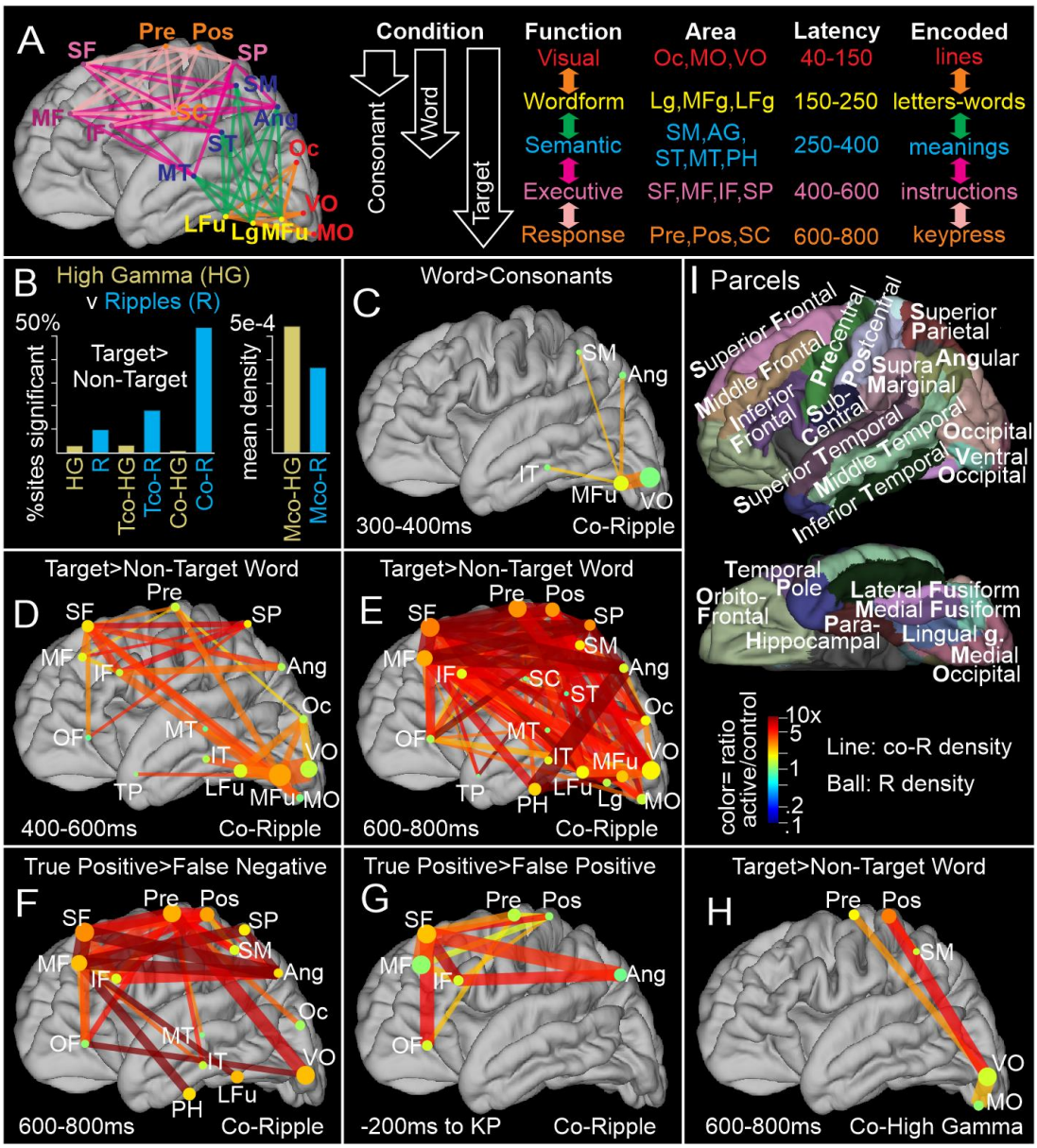

Fig. 2. Cortical Co-Ripples Selective for Words and Semantic Decisions. A. Schema of successive stages of binding from visual input to keypress response. **B**. Proportion of left hemisphere sites that ripple (R), or co-ripple with any other site (Tco-R), and of area-pairs that co-ripple during specific time periods (Co-R), to Targets versus Non-Target contrasts, is higher than for High Gamma Bursts (left), despite the mean density of co-ripples across the entire task period (Mco-R) being less than that of Mco-HG (right). **C-G**. Line color indicates ratio of co-ripple density between the connected sites evoked by active versus control conditions, and line thickness is proportional to co-ripple density in the active condition. All lines are $p<0.01$, 1-tailed, randomization test, FDR-corrected. Dot color indicates ratio of ripple density at that site by active versus control conditions, and dot area is proportional to ripple density in the active condition. **C**. Words evoke more co-rippling between visual (V), wordform (MFu) and semantic (SM, Ang) areas when letters are bound into words, and words with meaning. **D-E**. Co-rippling to target versus nontarget words links visual and wordform areas, and especially semantic, executive and response areas during the response period (600-800ms). No significant T>N responses occurred prior to 400ms. Correct keypresses elicit greater co-rippling than omitted (**F**) or wrong keypresses (**G**) mainly between semantic, executive and response areas. **H**. High gamma bursts co-occur much less selectively than co-ripples during the same contrast as in panel E. No significant co-High Gamma bursts were recorded in the Words>Consonants contrast. **I**. Sites in 13 subjects are gathered into regions for analysis. See Figs. S3-S7 for additional latencies and views.

Although we cannot disrupt co-rippling in humans to test if it is necessary for binding, we were able to examine if incorrect responses were associated with decreased co-rippling. Compared to missed responses to targets, correct responses were associated with strongly increased co-rippling between semantic (supramarginal and angular), executive (prefrontal), and response (pre- and post-central) areas (Fig. 2F; S7). A similar but weaker pattern of increased co-rippling occurred in the 200ms immediately preceding True Positive versus False Positive keypresses (Fig. 2G, S7; this comparison was only possible in the 6 subjects with sufficient key-presses to non-target words). Note that on both True and False Positive trials, the subject read a word and made a keypress; thus sensory and motor components of the trial were matched. Thus, correct detection of target words was differentiated from incorrect detections by increased co-rippling between executive, semantic and response areas, the critical interactions where binding is predicted to be necessary for correct performance.

Task-related co-high-gamma bursts (co-HG) are rare. In order to test the assertion that ripples do not actively facilitate transcortical integration but are simply a byproduct of nonspecific activation (*27, 28*), we compared co-rippling to the co-occurrence of bursts of non-oscillatory very high gamma ('co-HG'; 120-190 Hz), a measure of nonspecific activation (*29*). Increased connectivity to targets versus non-targets occurred in 54% of inter-areal connections with co-ripples, compared to only 1% with co-HG (Fig. 2E, 2H, S6). Furthermore, co-HG between cortical areas were not modulated at any latency by any of the other task contrasts in this study (Figs. S3, S7), despite their overall rate during the task being slightly greater than that of co-ripples (Figs. 2B, S2C). The proportion of left hemisphere contacts with task-related increases were also higher for co-rippling versus co-HG (29 versus 7%), or simple rippling versus HG (14 versus 4%; Figs. 2B, S4, S5). Thus, while co-HG do occur during reading, they are less specifically focused than co-R to the particular task conditions, latencies, and pairs of anatomical areas that are engaged by critical language processes. These findings indicate that co-ripple effects are unlikely to be secondary to high gamma activation.

Co-rippling sites are often strongly phase-locked, at zero phase-lag. If co-rippling between cortical locations facilitates binding of their encoding unit-firing patterns, then there should be indications of non-random interaction of the ripples in those locations. One such indication is the increased occurrence of co-ripples above what would be expected by chance (Fig. 2, S2A, S4-5). Another indication would be a tendency of such co-occurring ripples to oscillate with a consistent phase-lag relative to each other. The consistency of phase across co-ripples was quantified for each electrode pair as the Phase Locking Value (PLV). PLV was found to be significant between 90.5% of the 210 region-pairs ($p<0.01$, FDR-corrected; Fig. 3A, Table S10), with the exceptions mainly in early visual areas (Fig. S12). PLV amplitude was independent of the distance between recording electrodes (Fig. 3D), but increases with the proportion of recorded sites co-rippling, with PLV = 0.17 when ~6% of sites co-rippling and increasing to 0.86 when ~34% are co-rippling (Fig. 3EF; S9). Thus, co-ripples between left hemisphere locations generally phase-lock with each other during the reading task, especially when a large proportion of the sites are co-rippling.

The phase-lag between phase-locked oscillations can suggest the flow of information between them. The phase-lag between sites was significantly concentrated around zero in 98.4% of the connections with significant PLV (Fig. 3A, S11, Table S10), or examining the phase histogram of all co-ripples between individual areas, or of all areas and contact-pairs (Fig. 3BC). Zero-lag suggests that the communications between areas occurring during co-ripples are not being driven by one of the areas but are interactive.

The synchronization of distant locations as quantified by PLV and zero-lag is facilitated by the high consistency of ripple frequency across areas, whose mean frequency varies by a maximum of ~1Hz (Fig. 3A). Across contact pairs, PLV was negatively correlated with difference in mean ripple frequency ($p=0.002$, $b=-0.011$/Hz). Further, as more sites co-ripple, their ripple frequencies

become more similar (r^2=0.68; p<0.005, Fig. S10). Thus, as co-ripples engage more sites, they tend to become more synchronous and oscillate at similar frequencies.

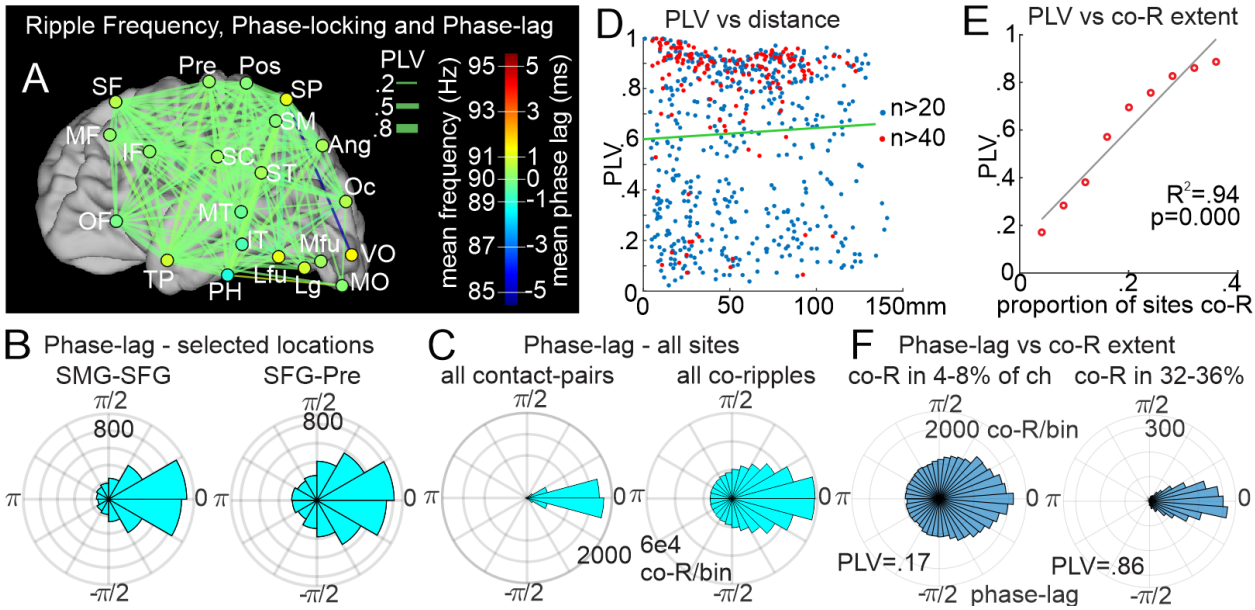

Fig. 3. Widespread Left Hemisphere Phase-locking. **A**. Areas with significant PLV during the task are connected with lines; line color indicates average phase-lag (±5.5ms =±π at 90Hz); dot color indicates average ripple frequency. **B**. Phase-lag plots of all co-ripples between the indicated example structures (see also Fig. S12). **C**. Phase-lag of all co-ripples (left, total N=615,441) and average phase-lag for all significant contact-pairs (right, total N=4,021). **D**. PLV versus distance. Each dot is an electrode pair, blue with 21-40 co-ripples; red with >40. R^2=0.0009, B=0.00044, n.s. **E**. PLV versus percent of contacts co-rippling. **F**. Phase of individual co-ripples when 4-8% or 32-36% of recorded contacts are co-rippling (see also Fig. S7). PLV is the vector-sum of phase-lags, ranging from 0 (no consistency) to 1 (perfect consistency).

Conclusion

In the current study we tested the hypothesis that co-ripples facilitate the integration ('binding') of information encoded in different cortical locations. This hypothesis predicts, and we found, that co-rippling would be elevated in task conditions requiring binding, between cortical areas that encode information that needs to be bound, and at latencies when binding needs to occur. Compared to controls not requiring binding, words evoked increased co-rippling between early visual, wordform, and semantic areas, in the epoch when those processes occur. Correctly recognized target words additionally evoked in subsequent epochs co-rippling between these locations and cortical areas maintaining target criteria, implementing task instructions, and executing movements. Co-ripples were strongly phase-locked at zero-lag, supporting the hypothesis that they facilitate interaction between the co-rippling areas.

Ripples have been related to the consolidation and retrieval of recent declarative memories in rodents and humans, in the hippocampus and cortex. The tasks utilized all required associating various arbitrary elements (for example, paired-associates learning), and the ripple itself is associated with the reinstatement of the firing-patterns encoding the various elements unified in the memory. Successful recall is associated not only with increased rippling, but increased cortico-cortical and cortico-hippocampal co-rippling (*5, 15*). These properties are typically interpreted as supporting a role of ripples in recent declarative memory. However, the task used in the current study did not require recent memory, and the task contrasts, latencies and structures associated with increased co-rippling were those expected for reading and semantic judgment. Conversely, a task manipulation (delayed repetition of some words) that rendered the word capable of reinstatement did not increase co-rippling but rather decreased it. Repetition suppression is a well-

known phenomenon that reduces neural activation associated with lexical access (*24*), and thus the reduced co-rippling to repeated words between wordform and semantic areas further supports our hypothesis that previous findings of co-ripple involvement in recent memory replay and recall may represent a special case of a more general role of co-ripples in binding.

This general role is consistent with the philosophical concept of binding, which extends to all contents of the stream of awareness (*30*). In contrast, the binding of different sensory characteristics of visual stimuli is the most commonly studied form of binding in psychological experiments (*31*). Accordingly, the role of oscillations in binding elements of visual stimuli has been extensively tested in neurophysiological recordings from visual cortex of animals, where it is generally of lower and more variable frequency, and thus may be a related but not necessarily identical phenomenon to that studied here (*18*). Indeed, we found that ripples in early visual areas were often larger, more frequent, and less phase-locked than in other areas.

The potential power of synchronized oscillations to facilitate the binding of diverse elements encoded in different cortical areas into an integrated mental event has long been recognized (*17*), specifically when phase-modulation enables phase-selection (*3*), and facilitates coincidence-detection (*2*). In the current study, we found strong phase-locking between co-rippling sites, and prior studies have found that ripples strongly phase-modulate neuronal firing (*5, 12, 16*). Thus, the basic pre-requisites for phase-modulation and coincidence-detection appear to be supported by co-rippling during binding in the reading task. Further tests of the binding-by-synchrony hypothesis should more directly examine if co-ripples facilitate integration of neuronal firing across the cortical surface.

Some have criticized synchronous high gamma oscillations such as co-ripples as providing no mechanism for neuronal interaction beyond generic activation (*27, 28*). We found that a common marker for generic activation, non-oscillatory high gamma, also weakly tended to co-occur across some areas likely to be involved in performing the task. It is expected that ripples and high gamma would often co-occur because ripples are associated with increased neuronal firing as well as increased high gamma during waking (*12*). However, the co-activation of high gamma was much less related to task variables than were co-ripples. Thus, it is unlikely that the strong and specific association of co-rippling with functional areas and epochs which encode elements that need to be bound in our task is secondary to non-oscillatory high gamma co-activations which generally lack such associations.

By a large margin, the intensity and extent of co-rippling was greatest in epochs containing correct behavioral responses. The greater co-rippling to targets may reflect the larger number of cortical areas which need binding, and/or the less well-learned mapping of those elements for task performance compared to the mapping of letters to wordforms, or wordforms to meanings. Correct detection of target words was differentiated from incorrect by increased co-rippling between executive, semantic and response areas. Since these are the critical interactions where binding is predicted to be necessary for correct performance, this finding suggests that information integration during co-ripples contributes to successful task performance.

In contrast to models of cortical function wherein stimulus and response are connected via a narrow pathway where activation is focal and sequential, we found that co-rippling during the response period connected not only executive sites maintaining target information and task instruction with motor areas, but also semantic, wordform and visual processing areas connected in prior epochs. This pattern replicates that of event-related intracranial potentials in a similar task wherein following an initial sweep from visual to wordform areas, activation is simultaneously present in widespread cortical sites up to and beyond the behavioral response (*32, 33*). It is also consistent with the widespread activation of cells distributed across the cortex in rodents during decision-making (*34*).

An extended post-sequential interactive processing period leading to the response is consistent with the zero phase-lag between co-rippling sites. Given that cortico-cortical conduction times are ~10m/s, the distances between co-rippling sites would result in phase-delays of >15ms at widely separated sites if communication were unidirectional. However, phase-delays between all sites were <1ms, and were not related to distance. The possibility that cortical synchrony is due to ripple-frequency driving by a subcortical structure is unlikely because phase-locking has not been observed between cortex and hippocampus (*5*) or thalamus (*35*). It is also unlikely that zero-lags were due to the shared distant extracranial reference because they were replicated using local bipolar derivations (Fig. S6). Rather, computational modeling indicates that zero-phase gamma oscillations can arise in neural networks with dense interconnections (*36*). The mechanism seems to involve bidirectional entrainment of ongoing activity by loosely coupled oscillators. Such a mechanism would be facilitated by the similarity of ripple frequency in different locations, and indeed, phase-locking was stronger when ripple frequencies were closer. Both higher phase-locking and smaller ripple frequency differences are strongly enhanced as a larger proportion of cortical sites are co-rippling, suggesting an interactive network mechanism that intensifies as more elements are engaged.

In summary, we show that ripples co-occur between early visual, wordform, semantic, executive and motor areas in the epochs and task conditions where binding between letters, words, meanings, instructions and actions need to occur for successful semantic judgements in a reading task. This supports a general role for co-rippling in binding cognitive elements encoded in different cortical areas.

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Conceptualization: EH; Data Curation: JCG, EK, IAV, TT; Formal analysis: JCG, IAV, EH; Funding acquisition: EH, TT, OD; Investigation: TT, CC, WKD, OD, EH; Methodology: JCG, EH; Project administration: EH, TT, OD; Resources: OD, WKD, CC; Software: JCG, IAV; Supervision: EH, TT; Visualization: JCG; Writing – original draft: EH, JCG; Writing – review & editing: EH, JCG

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Data and Materials availability: All data, code, and materials used in the analysis are available to any researcher for purposes of reproducing or extending the analysis.

Supplementary Materials: Materials and Methods; Figs. S1 to S13; Tables S1 to S10; References (*37-46*)