Do cortical co-ripples bind lines, letters, words, meanings, strategy and action in reading?

Summary: Widespread lexical, semantic, executive and response processing areas co-ripple and phase-lock when detecting target words.

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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 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 strongly increased to words versus consonant-strings in visual, wordform and semantic areas when letters are binding into words, and words to meaning. Similarly, co-ripples increased prior to correct responses between executive, response, wordform and semantic sites when word meanings are binding to instructions and response. These effects dissociated from non-oscillatory activation and memory reinstatement. Co-ripples were phase-locked at zero-lag, even at long distances, supporting a general role in cognitive binding.

Ripples are high frequency oscillations originally discovered in the rat hippocampus, where they mark the replay of encoded spatial sequences during non-rapid eye movement (NREM) sleep, critical for memory consolidation in the cortex (*1-4*). Ripples occur in human hippocampus (*5, 6*) and cortex (*7*) where they also contribute to memory (*8-12*). In humans, ripples occur in every region of neocortex and hippocampus throughout waking and NREM (*7*). They are highly stereotyped, with frequency closely distributed around 90 Hz for both hippocampal and cortical ripples. In humans, ripples often co-occur, and even phase-lock between cortical sites, largely independent of distance (*11*). This co-rippling increases during successful cued recall which requires co-activation of distinct cortical sites, suggesting that co-rippling may help bind memory elements (*11*) as a form of binding-by-synchrony (*13, 14*).

Binding-by-synchrony posits that objects are 'bound' by coordinating activity representing constituent features via coherent oscillations acting as coupled oscillators (*15*), facilitating selective communication through coincidence detection (*16*) and gain modulation (*17*). Cortical ripples appear to be a promising candidate for serving this function. In addition to their anatomical and behavioral ubiquity, they strongly phase-modulate local cell-firing, and co-firing across sites (*11*). However, cortical ripples have only been shown to be modulated by tasks and conditions requiring recent declarative memory, so the possibility of a general cognitive function in binding remains untested.

A reading task evokes widespread cortical co-ripples. Here we examine the possibility that ripples could facilitate binding of cortically distributed representations regardless of the involvement of recent declarative memory. Specifically, we tested for 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). Patients read words presented continuously at 600ms intervals, and key-pressed to words referring to a living thing. Consonant strings and false fonts matched for length served as sensory controls. Overall, during the task, ripples occurred with mean frequency 90.6 Hz, amplitude 10.2 µV, duration 132 ms (median 97 ms), and density 18.4/minute similar to those previously found during spontaneous waking and declarative memory testing (*7, 9-12*) (Fig. S1). Ripples in different sites had a strong tendency to co-occur, at a rate that did not decrement with distance (Fig. 1CDE). Some have suggested that ripples do not actively facilitate transcortical integration but are simply a byproduct of nonspecific activation (*18*). We thus compared co-rippling to the co-occurrence of bursts of non-oscillatory very high gamma (120-190 Hz), a measure of nonspecific activation (Fig. 1F).

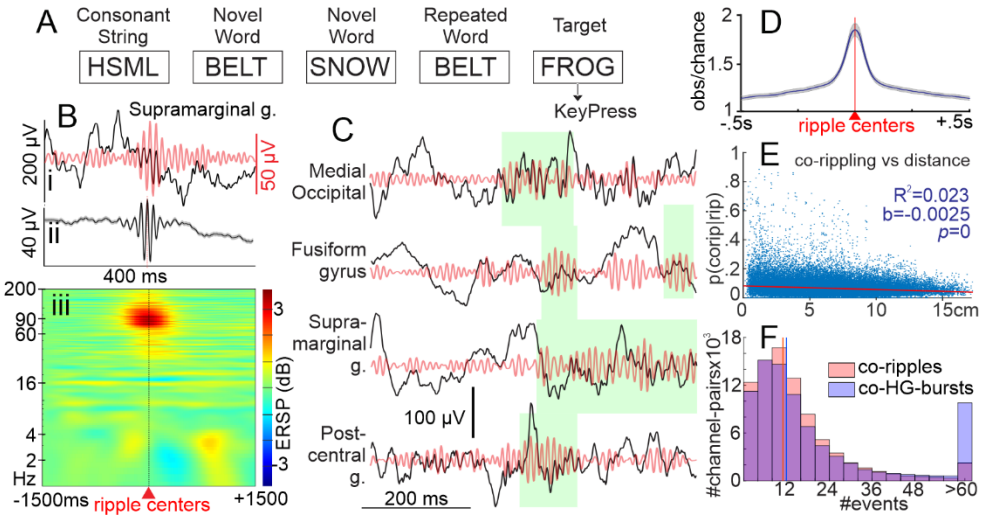

Fig. 1. Cortical Ripples and Co-Ripples During a Reading Task. **A**. Participants read words and control stimuli (including consonant strings) and key-press to animate words. **B**. High frequency bursts ('ripples') from typical disc electrode on the cortical surface as single sweep (**Bi**; broadband (black) or band-passed (red)), average waveform (**Bii**), or average time-frequency plot (**Biii**). **C**. Example Co-Ripple, single sweep, multiple sites with overlapping ripples (green shading), broadband and band-passed. **D**. Ripple overlap with center of occurrence in other simultaneously recorded sites (blue) relative to baseline (gray, s.e.m). **E**. Probability that two sites will co-ripple (given that one of them ripples) versus Euclidean distance. **F**. Number of channel pairs with the indicated number of co-ripples (blue; mean=26, median=12) and co-high gamma bursts (blue; mean=15, median=11).

Word-selective co-ripples are evoked between visual, wordform and semantic areas. We grouped contacts in anatomo-functional regions 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 predominantly between occipital, ventral occipitotemporal fusiform and lingual gyri), and temporo-parietal areas (supramarginal, angular, superior temporal gyri). The co-rippling between occipital and ventral occipitotemporal areas connects cortex performing early visual processing with the ventral wordform area. The co-rippling between ventral occipitotemporal and temporo-parietal areas connects cortex encoding wordforms (*19*) with the supramarginal and angular gyri, which comprise classical Wernicke's area for accessing the meaning of words (*20*). 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 distinguish 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.

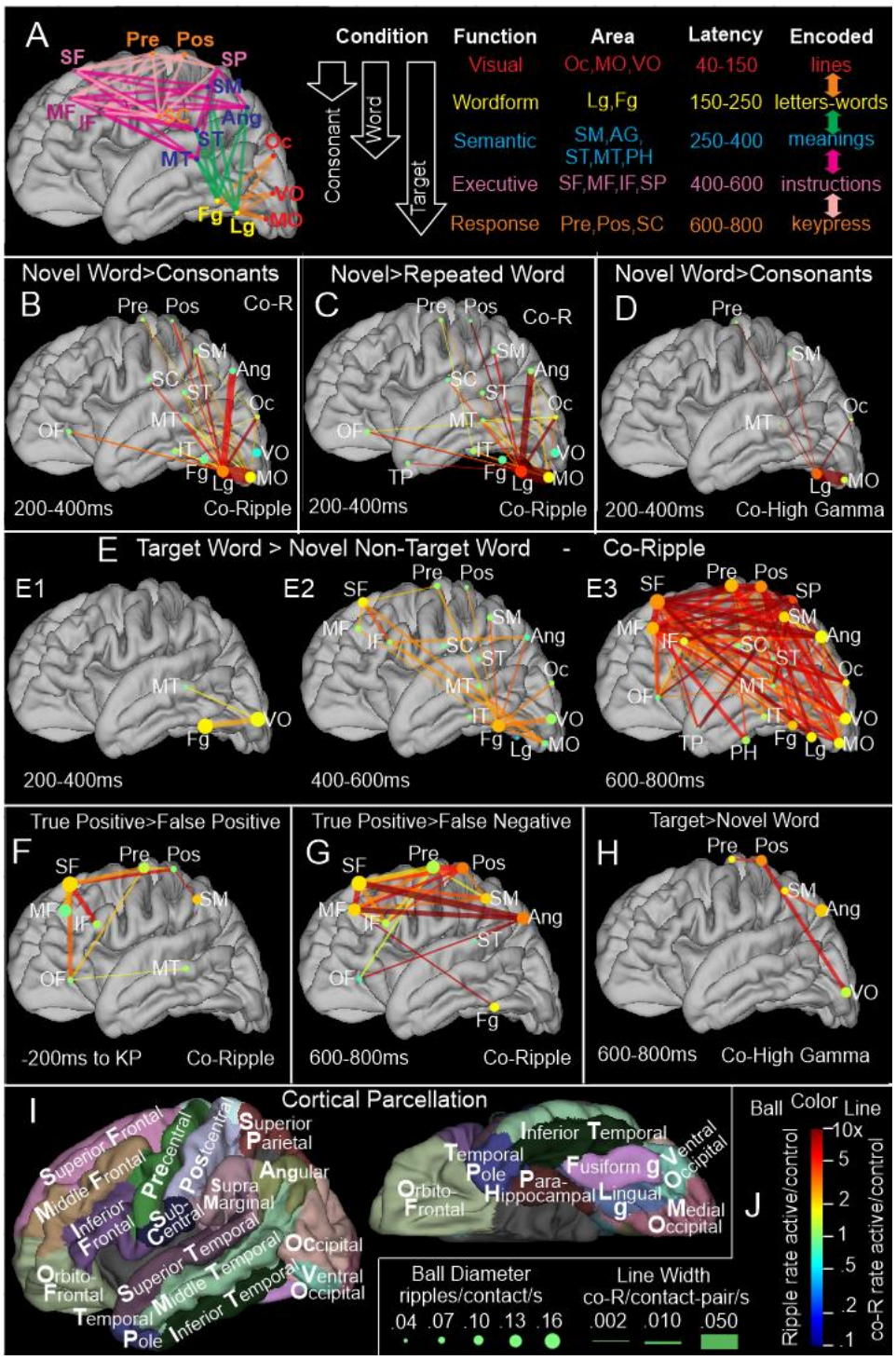

Fig. 2. Cortical Co-Ripples Selective for Words and Semantic Decisions. A. Successive stages of binding from visual input to keypress response, with their approximate locations, functions and latencies, and the task conditions which engage them. **B-H**. Significant increases in co-activation between the indicated sites and task contrasts, during the indicated latencies. **B**. Words evoke more co-rippling between wordform and their input (occipital) and output (semantic) areas when line segments are bound into letters, letters into words, and words with their meaning. **C**. This co-rippling is stronger to words the first time they are presented. **D**. High gamma bursts co-occur much less selectively than co-ripples during the same contrast as in panel B. **E**. Co-rippling to target versus nontarget words initially links visual and wordform areas, and eventually engage semantic, executive and response areas during the response period (600-800ms). Correct keypresses elicit greater co-rippling than omitted (**F**) or wrong keypresses (**G**) mainly between semantic, executive and response areas. **H**. Selective co-occurrence of high-gamma bursts is much smaller than that of ripples in panel E3. **I**. Sites in 13 subjects are gathered into regions for analysis. **J**. Legend for B-H. Color indicates ratio of Ripples (dots) or Co-Ripples (lines) to active versus control conditions. Dot diameter and line thickness indicate number of ripples or co-ripples to active condition. All lines $p<0.01$, 1-tailed, randomization test, FDR-corrected. All latencies and views for these contrasts are in Fig. S2-S5.

Although binding wordforms to their meanings entails accessing long term semantic memory, this does not require the hippocampus (*23*), and does not require reinstatement of a recent memory trace which has been associated with co-ripples. Nonetheless, to test if reinstatement of a recent memory trace could account for the co-ripples in our reading task, some of the non-target words were repeated multiple times. Repetition of a given word was separated by at least 15s (median 25s) and 24 (median 42) intervening trials, a distraction-filled delay that would render re-instatement of those items hippocampal-dependent. However, repeated words evoked *less* co-rippling than novel words presented the first time (Fig. 2C; Fig. S3). This is consistent with the often-observed phenomenon of repetition-suppression due to facilitated encoding (*24*), and thus provides further support for our hypothesis that it is such processes, rather than reinstatement, that are supported by cortical co-rippling. Also note that although co-occurrence of high gamma bursts linked some of the same sites as co-ripples, their effect was much weaker than that of co-ripples, an observation inconsistent with the suggestion that co-ripple linkage is secondary to that of high gamma linkage (Fig. 2D compared to 2B; Fig S2). Thus, co-rippling was increased to letter-strings that could be bound into words, but not by consonant strings that could not be bound; this association was stronger to words *not* stored in recent memory, and stronger than that of co-high gamma bursts.

Correctly-detected target words selectively evoke co-ripples between visual, wordform, semantic, executive and response areas. Co-rippling strongly increased on trials where the patient key-pressed correctly to animate words, compared to non-target words, across a large proportion of left hemisphere contacts (22.9% of 861 contacts; Fig. S4). Co-rippling to targets was similar to non-targets until ~400ms post-stimulus onset (Fig. 2E1), then increasing between wordform areas (fusiform and lingual gyri) and visual (occipital pole), semantic (supramarginal and angular), executive (prefrontal) and response (pre- and post-central) areas (Fig. 2E2). Peak co-rippling occurred in the response period (600-800ms) between these and related sites (Fig. 2E3), and continued into the post-response period (800-1000ms) at somewhat lower levels (Fig. S4).

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. Implicitly, correct performance also requires that these procedures be embedded in a regular sequence synchronized with the stimuli. 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 cortex (*25*). Increased co-rippling to targets compared to non-target words is initially (in the 400-600ms epoch) very similar to the co-rippling to non-target words in the previous epoch, with additional weak coupling between wordform and prefrontal areas. In the following, critical response (600-800ms) epoch, prefrontal sites (especially middle and superior frontal gyri) are coupled with all other cortical areas. Prefrontal coupling is very strong with areas thought crucial for encoding word meaning (especially supramarginal and angular gyri, and more weakly, anteroventral and lateral temporal areas), which could support comparison of stimulus word meaning to the response criterion. Prefrontal coupling is also very strong with motor areas (pre-, post- and sub-central gyri), which could support linking the target detection to the required response. Co-rippling also increases between other areas (such as motor and visual) whose function, if any, is unclear. The function of co-rippling in the post-response (800-1000ms) epoch is also unclear, although it may contribute to response monitoring. In any case, 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. Co-occurrence of high gamma bursts were only slightly modulated by target versus nontarget words, again failing to support

the suggestion that co-ripple effects are secondary to high gamma activation (compare Fig. 2H to E3).

Although there is no known method to disrupt co-rippling to test if it is necessary for binding, we were able to examine if incorrect responses were associated with decreased co-rippling. Compared to a failure to respond 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; Fig. S5). A similar but weaker pattern of increased co-rippling was observed in the 200ms immediately preceding to True Positive versus False Positive keypresses (Fig.2G.; this comparison was only possible in the 5 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. As noted above, these are the critical interactions where binding is predicted to be necessary for correct performance.

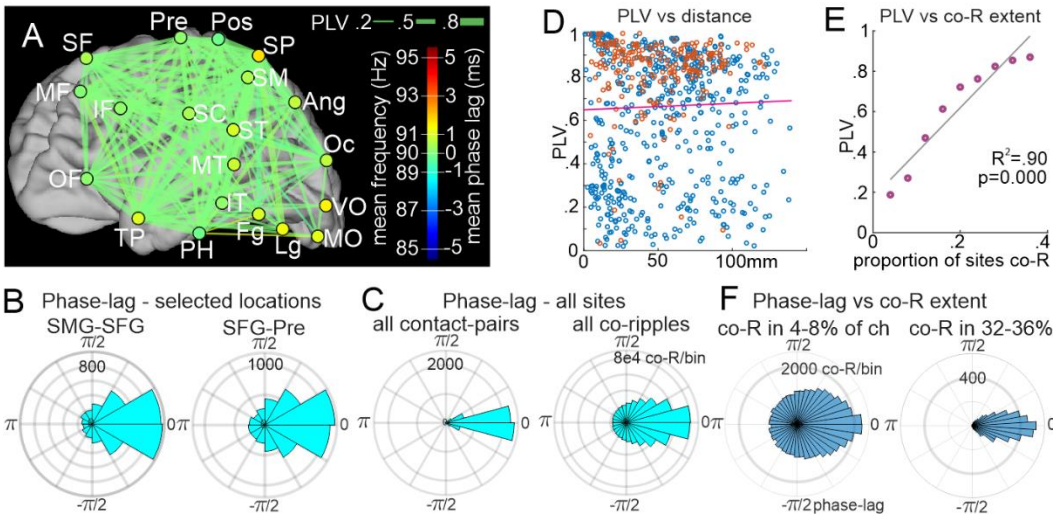

Fig. 3. Consistent Long-Distance Ripple Frequency, Phase, and Phase-locking. **A**. Areas with significant PLV during the task are connected with lines; line color indicates average phase-lag (±5.5ms =±π at 90Hz); dot color indicates average ripple frequency. **B**. Phase-lag plots of all co-ripples between the indicated example structures (see also Fig. S6). **C**. Phase-lag of all co-ripples (left, total N=762492) and average phase-lag for all significant contact-pairs (right, total N=6367). **D**. PLV versus distance (n.s.). Each dot is an electrode pair, blue with 21-40 co-ripples; red with >40. **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).

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. 1D). 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; the vector-sum of phase-lags ranging from 0 (no consistency) to 1 (perfect consistency). PLV was found to be significant between all areas with sufficient co-ripples (172% of 180 region pairs; Fig. 3A), and consistent phase is visible in plots of all co-ripples between specific areas (Fig. 3B). or all left hemisphere co-ripples and contact-pairs (Fig. 3C). PLV amplitude was independent of the distance between recording electrodes (Fig. 3D), but increases with the proportion of recorded sites co-rippling, with PLV = 0.19 when ~6% of sites co-rippling and increasing to 0.85 when ~30% are co-rippling (Fig. 3EF).

Thus, co-ripples between left hemisphere locations are generally phase-locked 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 consistently not distinguishable from zero when plotting all connections between areas that had significant PLV (Fig. 4A), or examining the phase histogram of all co-ripples between individual areas, or of all areas and contact-pairs (Fig. 4BC). 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 a maximum of ~1Hz (Fig. 3A). Across contact-pairs, those with significant PLV have smaller absolute differences in their mean ripple frequency (Significant PLV frequency difference = 1.42±1.16Hz. Non-significant= 1.71±1.51Hz, t=-11.63; $p<10^{-30}$). Further, as more sites co-ripple, their ripple frequencies become more similar (r^2=0.82; $p<10^{-3}$). Thus, as co-ripples engage more sites, they tend to become more synchronous and oscillate at similar frequencies.

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. Correct responses to 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 (see introduction). 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 (*10, 11*). 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 strongly. Repetition suppression is a well-known phenomenon that reduces neural activation associated with lexical access, 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 (*26*). In contrast, the binding of different sensory characteristics of visual stimuli is the most commonly studied form of binding in psychological experiments (*27*). 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 (*14*).

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 (*13*), specifically when phase-modulation enables phase-selection (*17*), and facilitate coincidence-detection (*16*). 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 (*7, 11*). 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 (*18*) We found that a common marker for generic activation, non-oscillatory high gamma, also tended to co-occur across 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 (*7*). However, the co-activation of high gamma was much less related to task variables than that of 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 lack such associations.

By a large margin, the intensity and extent of co-rippling was greatest in epochs containing correct behavioral responses. 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 (*28, 29*). It is also consistent with the widespread activation of cells distributed across the cortex in rodents during decision-making (*30*).

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 (*11*) or thalamus (*31*). Rather, computational modeling indicates that zero-phase gamma oscillations can arise in neural networks with dense interconnections (*32*). 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 accelerates as more elements are engaged.

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 is consistent with the possibility that information integration during co-ripples is a necessary part of successful task performance. Conversely, co-rippling with sensory and wordform areas was *not* different between correct and incorrect trials implying that they may underly an aspect of cortical

function not directed toward current performance, such as integrating all cortical levels to tune circuits for future trials, or procedural sequencing to redirect perceptual and cognitive resources in a rapidly presented task.

In summary, we show that co-ripples occur between early visual, wordform, semantic, executive and motor areas in the epochs and task conditions where binding between lines, 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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Supplementary Materials
Materials and Methods
Figs. S1 to S7
Tables S1 to S3
References (*1-14*)