Communication Through Coherence With Inter-areal Delays

Andre M. Bastos[1,2,*], Julien Vezoli[1,*], Pascal Fries[1,3]

[1]Ernst Strüngmann Institute (ESI) for Neuroscience in Cooperation with Max Planck Society, 60528 Frankfurt, Germany.

[2]Picower Institute for Learning and Memory, Massachusetts Institute of Technology, Cambridge, MA 02139, USA.

[3]Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, 6525 EN Nijmegen, Netherlands.

*These authors contributed equally to this work.

Corresponding author: andrembastos@gmail.com

Abstract

The communication-through-coherence (CTC) hypothesis proposes that anatomical connections are dynamically rendered effective or ineffective through the presence or absence of rhythmic synchronization, in particular in the gamma and beta bands. The original CTC statement proposed that uni-directional communication is due to rhythmic entrainment with an inter-areal delay and a resulting non-zero phase relation, whereas bi-directional communication is due to zero-phase synchronization. Recent studies found that inter-areal gamma-band synchronization entails a non-zero phase lag. We therefore modify the CTC hypothesis and propose that bi-directional cortical communication is realized separately for the two directions by uni-directional CTC mechanisms entailing delays in both directions. We review evidence suggesting that inter-areal influences in the feedforward and feedback directions are segregated both anatomically and spectrally.

Highlights

- CTC considered delayed uni-directional and zero-phase bi-directional communication.
- Recent studies show that inter-areal gamma coherence has a non-zero phase lag.
- Therefore, feedforward and feedback communication likely use CTC separately.
- Feedforward-input receiving and feedback-output sending neurons are separate.
- Gamma dominates feedforward, beta dominates feedback communication.

Acknowledgments

Introduction / Main text review / Conclusions

Rhythmic neuronal synchronization in the gamma-frequency band has been described in the primary visual cortex (areas 17 and 18) of anesthetized cats [1]. These recordings demonstrated that separate groups of cells within the same area could establish oscillatory synchrony when their receptive fields were simultaneously stimulated by a single visual stimulus spanning both receptive fields. This oscillatory synchrony was evident in the cross-correlation function between the spike trains as a peak at approximately zero lag (**Figure 1A**), with additional oscillatory side lobes. These observations were the basis for the proposal that oscillatory synchrony at zero-phase lag could be a mechanism for binding cells into a functional assembly [2]. Further observations supported this proposal: pairs of cells between area 17 and area 18, between two visual areas with well-defined hierarchical relationship (area 17 and PMLS) [3], and between areas 17 of the two cerebral hemispheres [4] were all reported to engage in oscillatory synchrony with near-zero phase lag when activated by appropriate stimuli. Furthermore, when the physical distance between the cell pairs in primary visual cortex increased, pairs with synchronous spikes were almost always associated with zero-phase oscillations [5], supporting the notion that oscillations might be necessary for assembly formation over long distances. In support of this, simultaneous recordings from multiple areas of the cat neocortex showed long-range beta-band synchrony at zero phase between the field potentials of primary and secondary visual areas, somatosensory and motor cortex [6]. Finally, other studies helped solidify the link between synchronous oscillatory activity and cognitive functions like perception and attention [7,8].

These studies provided experimental evidence that synchrony could provide the mechanism for binding disparate neuronal groups into a coherent assembly (Binding By Synchrony, or BBS) [2,9]. BBS considered primarily zero-phase oscillatory synchrony as the underlying mechanism that binds together a neuronal group representing an active percept. Another hypothesis about the functional role of rhythmic neuronal synchronization is the Communication Through Coherence (CTC) hypothesis. CTC and BBS are distinct, yet consistent with each other, and experiments testing the CTC hypothesis have also provided strong evidence for the BBS hypothesis [10]. CTC states that local rhythmic synchronization leads to rhythmic modulations in synaptic input gain, and a sending group of neurons will have the highest impact on a receiving group, if its inputs consistently arrive when gain is high. This entails that effective connectivity requires synchronization between sender and receiver [11-14]. Indeed, enhanced synchronization between V1 and V4 has been found for V1 neurons activated by an attended as compared to an un-attended stimulus, likely leading to the selective enhancement of effective connectivity for attended signals [10,15]. Furthermore, a metric of effective connectivity within and between brain areas was found to depend on the precise phase relation between local gamma-band rhythms [12]. Yet, the fundamental CTC prediction, that the phase of the local gamma rhythm modulates synaptic input gain, so far received equivocal experimental support. On the one hand, simultaneous recordings in anesthetized monkey V1 and V2 suggested "that the coupling of V1-V2 spiking activity follows more closely the V1 than the V2 gamma rhythm" [16]. On the other hand, when fast-spiking interneurons in somatosensory cortex were optogenetically driven with a 40 Hz pulse train, both neuronal [17] and behavioral [18] responses to vibrissae deflections were modulated by the phase of the deflection relative to the 40 Hz cycle. Similar effects have been demonstrated for the physiological beta rhythm in the cortico-spinal projection [19], and will need to be tested for naturally occurring cortico-cortical beta- and gamma-band synchronization.

The original statement of the CTC hypothesis [11] differentiated between uni-directional and bi-directional communication. "For unidirectional communication, an oscillation in a sending group might entrain an oscillation that is intrinsically generated in the receiving group or it might even simply drive an oscillation in the receiving group. In this case, the conduction delay would, for a given

Bastos, Vezoli, Fries: Communication Through Coherence With Inter-areal Delays

frequency, directly translate into a relative [non-zero] phase [...]". For bi-directional inter-areal communication, the original CTC statement assumed that neurons participating in a communication link were synchronized at zero phase both within and between areas. As reviewed above, experiments had demonstrated such zero-phase synchronization. CTC considered inter-areal conduction delays explicitly and suggested that they were short relative to the respective cycle lengths. Thereby, two communicating areas, oscillating at zero phase, send output at the same time in the oscillation cycle, and their mutual inputs arrive shortly afterward, still within the excitatory phase of the same cycle. A given cycle length, i.e. given oscillation frequency, can in this scheme only subserve communication up to a certain conduction delay. This led to the prediction that longer delays, observed between more distant brain areas, result in communication through coherence at lower frequencies. While this has sometimes been assumed to be the case [20], it has recently been shown that inter-areal neuronal synchronization, even over very large cortico-cortical distances, occurs also in the gamma-frequency band [10,15,21,22].

Modeling studies proposed a number of solutions to the problem of how to engage neuronal groups in zero-phase synchrony despite conduction delays. For example, Vicente and colleagues showed that two neuronal groups, if they were both bi-directionally connected to a third population, could display oscillatory coherence at zero phase [23]. Since this motif of common input is often observed in anatomical networks involving cortical [24] or sub-cortical sources [25], areas with widespread anatomical connectivity were envisioned to stabilize phase relationships by bringing the oscillations to zero phase across the network despite non-negligible spike transmission times. Several modeling studies explored the underlying connectivity structures that could produce zero-phase offsets, and converged on the importance of common inputs and recurrent connections to coordinate such a zero-phase phenomenon [26,27]. Other mechanisms were explored to maintain zero phase over long conduction delays, such as the spike-doublet phenomenon [28]. Although these models demonstrated the biophysical plausibility of zero-phase synchronization despite long conduction delays, several conditions need to be met. Typically, the situation needs to be symmetric, i.e. the two synchronized local circuits should be similar e.g. in their local organization and activity level, their conduction delays to the respective other circuit, and the strength of their feed-forward inhibition. While these conditions might be met for inter-hemispheric connections, they are likely often not met for connections between visual areas at different hierarchical levels. Indeed, there is increasing experimental evidence that different visual areas are gamma-band synchronized with a non-zero phase lag.

For example, it has been shown that between areas V1 and V2 in the monkey, spike-spike cross-correlograms display gamma oscillations with an average phase shift of 2.7 ms, with V2 spikes following V1 spikes (**Figure 1B)** [16]. Another recent study found that spikes in V4 were coherent with fields in V1 of awake monkeys, with the V1 gamma preceding the V4 spikes by a few milliseconds (**Figure 1C)** [15]. Areas separated by greater cortical distances display greater phase delays. For example, FEF and area V4 show inter-areal spike-LFP coherence in the gamma band with a phase shift corresponding to approximately 10 ms (**Figure 1D**) [21]. In human cortex, frontal-to-visual gamma coherence has been associated with even longer (~20ms) delays [22]. Similar observations have also been made outside visual cortex, e.g. in the hippocampus, where a gamma oscillation emerging in CA3 entrains CA1 [29]. Note that these non-zero phase relations likely reflect several distinct processes necessary for inter-neuronal influences, like pre-synaptic spike transmission and post-synaptic dendritic charge accumulation and diffusion. While it is difficult to predict the combined delay due to all these processes, particularly in the context of rhythmic coupling, the reported paired recordings directly provide the resulting net phase relation. Here, we integrate these new insights with previous evidence and propose a modified CTC hypothesis for the bi-directional communication between cortical areas.

If gamma-band synchronization between two cortical areas A and B entails a relative phase consistent with an A-to-B conduction delay, this suggests that the gamma rhythm is generated in A and either entrains a gamma rhythm generated in B, or simply drives a gamma rhythm in B. As mentioned above, this corresponds to CTC for uni-directional communication, and it provides the core CTC mechanism: When gamma in B is phase locked to the gamma in A, then input from A to B can consistently arrive at moments of high input gain. Yet, at first sight it appears as if this could subserve only the communication in the A-to-B direction. If output in one gamma cycle of A triggers spiking in a phase-lagged gamma cycle of B, then feedback from B to A will arrive in A after the excitatory phase of the gamma cycle in which A had sent its output. Thus, CTC would subserve communication in the feedforward direction, but would not at the same time strengthen the corresponding feedback. One potential solution could be that feedback arrives at the excitable phase of the following gamma cycle. Assuming that inter-areal delays are fixed, this would require that gamma cycle lengths are fixed, and thus that the gamma frequency is fixed. By contrast, gamma frequency changes dynamically with stimulus parameters [30-33] and with selective attention [10]. However, laminar anatomy together with laminar electrophysiology suggests a different scenario, in which CTC subserves bi-directional cortical communication separately in the two directions.

Anatomical tracing studies suggest that those neurons of a given area that receive input and those that send output are almost completely separate [34,35]. Thus, one set of neurons might entrain to incoming rhythmic input, and a different set might provide rhythmic output. Those separate, yet neighboring, sets of neurons might locally communicate via rate-based mechanisms and/or be synchronized in a non-rhythmic way [5]. Alternatively, receiving and sending neurons within a given area might have a particular non-zero phase relation to each other, which should be visible if the separate sets of neurons were not intermingled, but segregated e.g. in layers. In fact, neurons receiving feedforward input are primarily located in layer 4 [35]. These layer 4 neurons send intra-columnar projections to supragranular layers [36]. Supragranular neurons send output projections feedforward and also feedback to nearby areas, e.g. from supragranular V2 to supragranular V1 [34]. Intriguingly, Livingstone showed in the granular and supragranular layers of monkey V1 that gamma-band synchronization entails a systematic inter-laminar delay of 1 ms per 100 micron, with more superficial neurons lagging deeper neurons [37]. We show an example pair of neurons from Livingstone that was recorded at a separation of 300 micron and showed gamma-band synchronization with a 3 ms delay (**Figure 1E).** This suggests the mechanism illustrated in **Figure 2:** Bi-directional cortical communication might be realized by CTC acting separately in the two directions, with both inter-areal and inter-laminar delays (see the thick red and blue arrows in the lower left). Inter-laminar delays might delay the supragranular gamma phase such that reentrant feedback arrives at the excitable phase of the same – delayed – gamma cycle. This mechanism should function with variable gamma frequencies, as long as inter-areal and inter-laminar delays remain stable. The precise laminar level at which reentrant feedback hits a matching phase might be determined by spike-timing dependent plasticity mechanisms. For pairs of very distant areas, reentrant feedback would arrive too late to hit a matching phase. Intriguingly, we found that for those area pairs, gamma-band influences exist essentially only in the feedforward direction [38].

Note that the presented scenario simplifies the local rhythm as an oscillating line with a particular phase at a particular time. In reality, the rhythm is a process that entails excitatory and inhibitory neurons firing in a characteristic sequence [29,39-41]. Future research will need to investigate how inter-laminar and inter-areal synchronization with the observed delays is brought about by locally triggered and/or feedforward inhibition. Predictions from this scenario are confirmed by several recent studies. The Livingstone result was recently replicated and extended by current-source density recordings from laminar multi-contact electrodes [42]. Other studies showed that neuronal signals recorded from different cortical depths show consistent phase differences [40,43,44]. Also, the delayed inter-areal gamma-band synchronization should be visible as Granger-causal (GC) influences

in the gamma band, because a GC influence indicates that variance in one signal explains otherwise unexplained variance in another signal several millisecond later. Indeed, we recently demonstrated GC influences between V1 and V4 in both directions (**Figure 1F**) [10].

Furthermore, a combination of laminar anatomy and electrophysiology with inter-areal GC influence analysis suggests an additional mechanism that maintains bidirectional communication between pairs of areas that span multiple hierarchical levels. While feedforward projections between these areas originate primarily from supragranular layers, feedback projections originate primarily from infragranular layers [34]. This anatomical asymmetry strongly suggests that the above mentioned models of long-range zero-phase synchrony based on symmetricity do not apply between hierarchically distant areas. Rather, feedback and feedforward communication appear not only anatomically but also functionally distinct. Locally, infragranular neurons show synchronization primarily at slower frequencies than gamma, such as alpha and beta [45-47]. Correspondingly, feedback communication deriving from infragranular neurons is expected to use slower frequencies (**Figure 2**, right side), a prediction that we have recently verified [38] (see also [42,48]): Directed inter-areal influences in the beta and gamma bands were systematically related to the laminar origin of the corresponding anatomical projections. Across 28 pairs of visual areas, we found that an increasing asymmetry in the GC influence was strongly correlated to an increasing anatomical asymmetry (neurons increasingly projecting from supragranular layers) [38]. This correlation between anatomical and functional asymmetry was significantly positive in the theta- and gamma-band and significantly negative in the beta-band, indicating that theta and gamma frequencies contribute to feedforward communication and beta frequencies to feedback communication. Thus, long-distance communication channels in the feedforward and feedback directions are separated not only anatomically but also spectrally. While such a spectral segregation of the counter-streams solves the problem of bi-directional communication with non-zero phase lags, it raises the question of how the segregated streams are integrated where they meet in a given area. This might be achieved through cross-frequency coupling [49,50] or through non-rhythmic coupling [5], which will require further investigation.

We propose that the mechanisms described above operate concurrently to subserve bi-directional cortical communication. Future studies will need to dissect out these possibilities with greater mechanistic detail. We would like to emphasize that existing anatomical studies provide many clues about the functional influences that might be observed. Many other relationships between structure and function are likely to be uncovered as the understanding of widespread cortico-cortical interactions matures [51-53]. In this context, we note that despite the evidence for non-zero phase synchrony reviewed here, cortico-cortical networks also engage in zero-phase synchrony. Long-distance cortico-cortical synchronization in the beta band can exist at zero or near-zero phase lag [6,54,55]. For beta band influences, long distance zero-phase synchronization is consistent with the original CTC mechanism: input from the sending group can arrive at the receiving group within the same oscillation cycle because the conduction delay is short relative to the cycle length. In fact, in the beta-frequency band, recent studies described the coexistence of long-range synchronization at zero phase and non-zero phase [54,55], and rapid task-dependent switches between stable near-antiphase synchronization and stable near-zero-phase synchronization [54]. These spatially specific and dynamic phase relations might modulate connection strength according to CTC mechanisms.

While anatomical connectivity will shape neuronal communication, it does not fully determine it, because cognitive variables can act as powerful gates to open or close communication links [10,15]. In fact anatomy presents a backbone that can give rise to a diversity of functional interactions [56]. Cortical hierarchy models do not specify a single "perfect" hierarchy [34,57]. Many pairwise connections do not agree with the global hierarchical model [34], which may be cause and/or consequence of the flexibility in functional interactions, which change the balance between

Bastos, Vezoli, Fries: Communication Through Coherence With Inter-areal Delays

feedforward and feedback signaling depending on the cognitive context [21,38,58]. For example, area FEF can change its directed influence on area V4 dynamically [21], and we found corresponding changes in the pattern of influences between FEF and several other visual areas [38]. These dynamic changes in functional interactions are likely at the heart of our cognitive dynamics, which subserves adaptive behavior.

In summary, we have reviewed evidence showing that there is a diversity of phase relationships between areas and cortical layers at which synchronization can occur. This calls for consideration of non-zero phase relationships as important aspects for theories on the function of oscillations such as BBS and CTC. Non-zero phase synchronization has by now been observed both within and between areas, and therefore likely has a key role in the establishment of communication links. These communication links exist within hierarchically distributed cortical areas with exquisitely structured feedforward and feedback counter-streams which appear ideally suited for segregating the streams either anatomically, spectrally, or by a combination of both mechanisms.

Figure Legends

Figure 1: Inter-areal gamma-band synchronization entails time delays.
For all cross-correlograms in this figure, the arrows above the panels indicate the alignment event, i.e. what happens at time zero, and the arrows inside the panels indicate what is averaged relative to those alignment events. **A.** Cross-correlogram between two multi-unit recordings from cat primary visual cortex showing zero-phase lag synchronization when the stimulus moves over both neurons' receptive fields. Modified from [1]. **B.** Jitter-corrected cross-correlogram between V1 and V2 spikes showing inter-areal gamma coherence with a delay between V1 and V2. Modified from [16]. **C.** Spike-triggered averages of V1 LFPs relative to V4 spikes, consistent with an inter-areal delay. Modified from [15]. **D.** Spike-triggered average of FEF LFPs relative to V4 spikes, suggesting an inter-areal delay of approximately 10 ms. Modified from [21]. **E.** Cross-correlogram between two neurons in the superficial layers of monkey V1, showing gamma coherence with a 3 ms delay between the deeper and the 300 micron more superficial cell. Modified from [37]. **F.** Granger-causal influence between V1 and V4 recording sites showing directed influence in the gamma band in both directions. Granger-causal influences are due to delayed interactions. Modified from [10].

Figure2: CTC with inter-areal delays between hierarchically arranged areas.
Schematic illustration of the modified CTC hypothesis incorporating delays between areas and between the layers of a given area. Purple lines illustrate supragranular gamma oscillations with a systematic delay from layer 4 toward layer 1. Such systematic delays have been found with paired recordings at two depths [37] and with multi-contact laminar probes [42]. Red arrows indicate feedforward signals, entering in the lower left into layer 4, and proceeding through supragranular layers onwards to layer 4 of the next higher area. Blue arrows indicate supragranular feedback between closely neighboring areas. The thick red and blue arrows highlight one complete cycle of feedforward and reentrant feedback signaling. Note that the reentrant feedback arrives at the excitable phase of the local gamma, because it targets more superficial sub-layers, which are delayed relative to layer 4. Brown lines illustrate infragranular beta oscillations, green arrows infragranular feedback.

References:

1. Gray CM, König P, Engel AK, Singer W: **Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties**. *Nature* 1989, **338**:334-337.

2. Singer W, Gray CM: **Visual feature integration and the temporal correlation hypothesis**. *Annu Rev Neurosci* 1995, **18**:555-586.

3. Engel AK, Kreiter AK, Konig P, Singer W: **Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat**. *Proc Natl Acad Sci U S A* 1991, **88**:6048-6052.

4. Engel AK, König P, Kreiter AK, Singer W: **Interhemispheric synchronization of oscillatory neuronal responses in cat visual cortex**. *Science* 1991, **252**:1177-1179.

5. König P, Engel AK, Singer W: **Relation between oscillatory activity and long-range synchronization in cat visual cortex**. *Proc Natl Acad Sci U S A* 1995, **92**:290-294.

6. Roelfsema PR, Engel AK, König P, Singer W: **Visuomotor integration is associated with zero time-lag synchronization among cortical areas**. *Nature* 1997, **385**:157-161.

7. Fries P, Roelfsema PR, Engel AK, König P, Singer W: **Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry**. *Proc Natl Acad Sci U S A* 1997, **94**:12699-12704.

8. Fries P, Womelsdorf T, Oostenveld R, Desimone R: **The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4**. *J Neurosci* 2008, **28**:4823-4835.

9. Singer W: **Neuronal synchrony: a versatile code for the definition of relations?** *Neuron* 1999, **24**:49-65, 111-125.

10. Bosman CA, Schoffelen JM, Brunet N, Oostenveld R, Bastos AM, Womelsdorf T, Rubehn B, Stieglitz T, De Weerd P, Fries P: **Attentional stimulus selection through selective synchronization between monkey visual areas**. *Neuron* 2012, **75**:875-888.
●● *Study of interactions between awake monkey V1 and V4, showing Granger-causal influences in the gamma band in both directions.*

11. Fries P: **A mechanism for cognitive dynamics: neuronal communication through neuronal coherence**. *Trends Cogn Sci* 2005, **9**:474-480.

12. Womelsdorf T, Schoffelen JM, Oostenveld R, Singer W, Desimone R, Engel AK, Fries P: **Modulation of neuronal interactions through neuronal synchronization**. *Science* 2007, **316**:1609-1612.

13. Schoffelen JM, Oostenveld R, Fries P: **Neuronal coherence as a mechanism of effective corticospinal interaction**. *Science* 2005, **308**:111-113.

14. Schoffelen JM, Poort J, Oostenveld R, Fries P: **Selective movement preparation is subserved by selective increases in corticomuscular gamma-band coherence**. *J Neurosci* 2011, **31**:6750-6758.

15. Grothe I, Neitzel SD, Mandon S, Kreiter AK: **Switching neuronal inputs by differential modulations of gamma-band phase-coherence**. *J Neurosci* 2012, **32**:16172-16180.
●● Study of gamma-band synchronization between monkey areas V1 and V4, showing average V1 LFP aligned to V4 spikes, and suggesting several milliseconds inter-areal delay.

16. Jia X, Tanabe S, Kohn A: **Gamma and the coordination of spiking activity in early visual cortex**. *Neuron* 2013, **77**:762-774.
●● Study of gamma-band synchronization between monkey areas V1 and V2, showing an average 2.7 ms inter-areal delay.

17. Cardin JA, Carlén M, Meletis K, Knoblich U, Zhang F, Deisseroth K, Tsai LH, Moore CI: **Driving fast-spiking cells induces gamma rhythm and controls sensory responses**. *Nature 2009*, **459**:663-667.
●● Study showing that optogenetic driving of mouse somatosensory cortex interneurons at 40 Hz leads to phase-dependent modulations in the neuronal response to vibrissae deflections.

18. Siegle JH, Pritchett DL, Moore CI: **Gamma-range synchronization of fast-spiking interneurons can enhance detection of tactile stimuli**. *Nat Neurosci 2014*.
●● Study showing that optogenetic driving of mouse somatosensory cortex interneurons at 40 Hz leads to phase-dependent modulations in behavioral responses to vibrissae deflections.

19. van Elswijk G, Maij F, Schoffelen JM, Overeem S, Stegeman DF, Fries P: **Corticospinal beta-band synchronization entails rhythmic gain modulation**. *J Neurosci 2010*, **30**:4481-4488.
20. von Stein A, Sarnthein J: **Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization**. *Int J Psychophysiol 2000*, **38**:301-313.
21. Gregoriou GG, Gotts SJ, Zhou H, Desimone R: **High-frequency, long-range coupling between prefrontal and visual cortex during attention**. *Science 2009*, **324**:1207-1210.
22. Baldauf D, Desimone R: **Neural mechanisms of object-based attention**. *Science 2014*, **344**:424-427.
●● Study of gamma-band synchronization between frontal and temporal areas in human subjects, estimating a 20 ms delay.

23. Vicente R, Gollo LL, Mirasso CR, Fischer I, Pipa G: **Dynamical relaying can yield zero time lag neuronal synchrony despite long conduction delays**. *Proc Natl Acad Sci U S A 2008*, **105**:17157-17162.
24. Markov NT, Ercsey-Ravasz MM, Ribeiro Gomes AR, Lamy C, Magrou L, Vezoli J, Misery P, Falchier A, Quilodran R, Gariel MA, et al.: **A weighted and directed interareal connectivity matrix for macaque cerebral cortex**. *Cereb Cortex 2014*, **24**:17-36.
25. Shipp S: **The functional logic of cortico-pulvinar connections**. *Philos Trans R Soc Lond B Biol Sci 2003*, **358**:1605-1624.
26. Chawla D, Friston KJ, Lumer ED: **Zero-lag synchronous dynamics in triplets of interconnected cortical areas**. *Neural Netw 2001*, **14**:727-735.
27. Rajagovindan R, Ding M: **Decomposing neural synchrony: toward an explanation for near-zero phase-lag in cortical oscillatory networks**. *PLoS One 2008*, **3**:e3649.
28. Traub RD, Whittington MA, Stanford IM, Jefferys JG: **A mechanism for generation of long-range synchronous fast oscillations in the cortex**. *Nature 1996*, **383**:621-624.
29. Csicsvari J, Jamieson B, Wise KD, Buzsáki G: **Mechanisms of gamma oscillations in the hippocampus of the behaving rat**. *Neuron 2003*, **37**:311-322.
30. Ray S, Maunsell JH: **Differences in gamma frequencies across visual cortex restrict their possible use in computation**. *Neuron 2010*, **67**:885-896.
31. Roberts MJ, Lowet E, Brunet NM, Ter Wal M, Tiesinga P, Fries P, De Weerd P: **Robust gamma coherence between macaque V1 and V2 by dynamic frequency matching**. *Neuron 2013*, **78**:523-536.
32. van Pelt S, Fries P: **Visual stimulus eccentricity affects human gamma peak frequency**. *Neuroimage 2013*, **78**:439-447.
33. Swettenham JB, Muthukumaraswamy SD, Singh KD: **Spectral properties of induced and evoked gamma oscillations in human early visual cortex to moving and stationary stimuli**. *J Neurophysiol 2009*, **102**:1241-1253.

34. *Markov NT, Vezoli J, Chameau P, Falchier A, Quilodran R, Huissoud C, Lamy C, Misery P, Giroud P, Ullman S, et al.:* **Anatomy of hierarchy: feedforward and feedback pathways in macaque visual cortex**. *J Comp Neurol 2014,* **522**:*225-259.*

●● A paper summarizing recent findings in quantitative anatomy of hierarchical connections, emphasizing two distinct counter-streams for feedforward and feedback influences: first, for areas nearby in hierarchical distance, a supragranular counter stream with "deep superficial" feedforward projections and a "shallow superficial" feedback projection. And second, for areas far in hierarchical distance, a long range supragranular feedforward projection and infragranular feedback projection.

35. *Felleman DJ, Van Essen DC:* **Distributed hierarchical processing in the primate cerebral cortex**. *Cereb Cortex 1991,* **1**:*1-47.*

36. *Douglas RJ, Martin KA:* **Neuronal circuits of the neocortex**. *Annu Rev Neurosci 2004,* **27**:*419-451.*

37. *Livingstone MS:* **Oscillatory firing and interneuronal correlations in squirrel monkey striate cortex**. *J Neurophysiol 1996,* **75**:*2467-2485.*

●● Seminal study of monkey V1 gamma-band synchronization with laminar resolution. Gamma-band synchronization was primarily found in granular and supragranular layers, and entailed a systematic inter-laminar delay of 1 ms per 100 micron, with more superficial neurons lagging deeper neurons.

38. *Bastos AM, Vezoli J, Bosman CA, Schoffelen JM, Oostenveld R, Dowdall JR, De Weerd P, Kennedy H, Fries P:* **Visual areas exert feedforward and feedback influences through distinct frequency channels**. *bioRxiv 2014.*

●● A study showing that across 28 pairs of visual areas, feedforward connectivity uses theta and gamma frequencies, and feedback connectivity uses beta frequency. These functional asymmetries become increasingly apparent as two given areas move further apart in hierarchical distance. The study shows that rhythmic influences between areas are Granger-causal in both directions.

39. *Hasenstaub A, Shu Y, Haider B, Kraushaar U, Duque A, McCormick DA:* **Inhibitory postsynaptic potentials carry synchronized frequency information in active cortical networks**. *Neuron 2005,* **47**:*423-435.*

40. *Vinck M, Womelsdorf T, Buffalo EA, Desimone R, Fries P:* **Attentional modulation of cell-class-specific gamma-band synchronization in awake monkey area V4**. *Neuron 2013,* **80**:*1077-1089.*

41. *Buzsáki G, Wang XJ:* **Mechanisms of gamma oscillations**. *Annu Rev Neurosci 2012,* **35**:*203-225.*

42. *van Kerkoerle T, Self MW, Dagnino B, Gariel-Mathis MA, Poort J, van der Togt C, Roelfsema PR:* **Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex**. *Proc Natl Acad Sci U S A 2014.*

43. *Vinck M, Lima B, Womelsdorf T, Oostenveld R, Singer W, Neuenschwander S, Fries P:* **Gamma-phase shifting in awake monkey visual cortex**. *J Neurosci 2010,* **30**:*1250-1257.*

44. *Maris E, Womelsdorf T, Desimone R, Fries P:* **Rhythmic neuronal synchronization in visual cortex entails spatial phase relation diversity that is modulated by stimulation and attention**. *Neuroimage 2013,* **74**:*99-116.*

45. *Buffalo EA, Fries P, Landman R, Buschman TJ, Desimone R:* **Laminar differences in gamma and alpha coherence in the ventral stream**. *Proc Natl Acad Sci U S A 2011,* **108**:*11262-11267.*

46. *Smith MA, Jia X, Zandvakili A, Kohn A:* **Laminar dependence of neuronal correlations in visual cortex**. *J Neurophysiol 2013,* **109**:*940-947.*

47. *Maier A, Adams GK, Aura C, Leopold DA:* **Distinct superficial and deep laminar domains of activity in the visual cortex during rest and stimulation**. *Front Syst Neurosci 2010,* **4**.

Bastos, Vezoli, Fries: Communication Through Coherence With Inter-areal Delays

48. *Bressler SL, Richter CG:* **Interareal oscillatory synchronization in top-down neocortical processing**. *Curr Opin Neurobiol 2014,* **31C***:62-66.*

49. *Roopun AK, Kramer MA, Carracedo LM, Kaiser M, Davies CH, Traub RD, Kopell NJ, Whittington MA:* **Period concatenation underlies interactions between gamma and beta rhythms in neocortex**. *Front Cell Neurosci 2008,* **2***:1.*

50. *Lee JH, Whittington MA, Kopell NJ:* **Top-down beta rhythms support selective attention via interlaminar interaction: a model**. *PLoS Comput Biol 2013,* **9***:e1003164.*

51. *Miranda-Dominguez O, Mills BD, Grayson D, Woodall A, Grant KA, Kroenke CD, Fair DA:* **Bridging the gap between the human and macaque connectome: a quantitative comparison of global interspecies structure-function relationships and network topology**. *J Neurosci 2014,* **34***:5552-5563.*

52. *Ding Z, Newton AT, Xu R, Anderson AW, Morgan VL, Gore JC:* **Spatio-temporal correlation tensors reveal functional structure in human brain**. *PLoS One 2013,* **8***:e82107.*

53. *Honey CJ, Kötter R, Breakspear M, Sporns O:* **Network structure of cerebral cortex shapes functional connectivity on multiple time scales**. *Proc Natl Acad Sci U S A 2007,* **104***:10240-10245.*

54. *Dotson NM, Salazar RF, Gray CM:* **Frontoparietal Correlation Dynamics Reveal Interplay between Integration and Segregation during Visual Working Memory**. *J Neurosci 2014,* **34***:13600-13613.*

55. *Stetson C, Andersen RA:* **The parietal reach region selectively anti-synchronizes with dorsal premotor cortex during planning**. *J Neurosci 2014,* **34***:11948-11958.*

56. *Battaglia D, Witt A, Wolf F, Geisel T:* **Dynamic effective connectivity of inter-areal brain circuits**. *PLoS Comput Biol 2012,* **8***:e1002438.*

57. *Reid AT, Krumnack A, Wanke E, Kötter R:* **Optimization of cortical hierarchies with continuous scales and ranges**. *Neuroimage 2009,* **47***:611-617.*

58. *Buschman TJ, Miller EK:* **Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices**. *Science 2007,* **315***:1860-1862.*
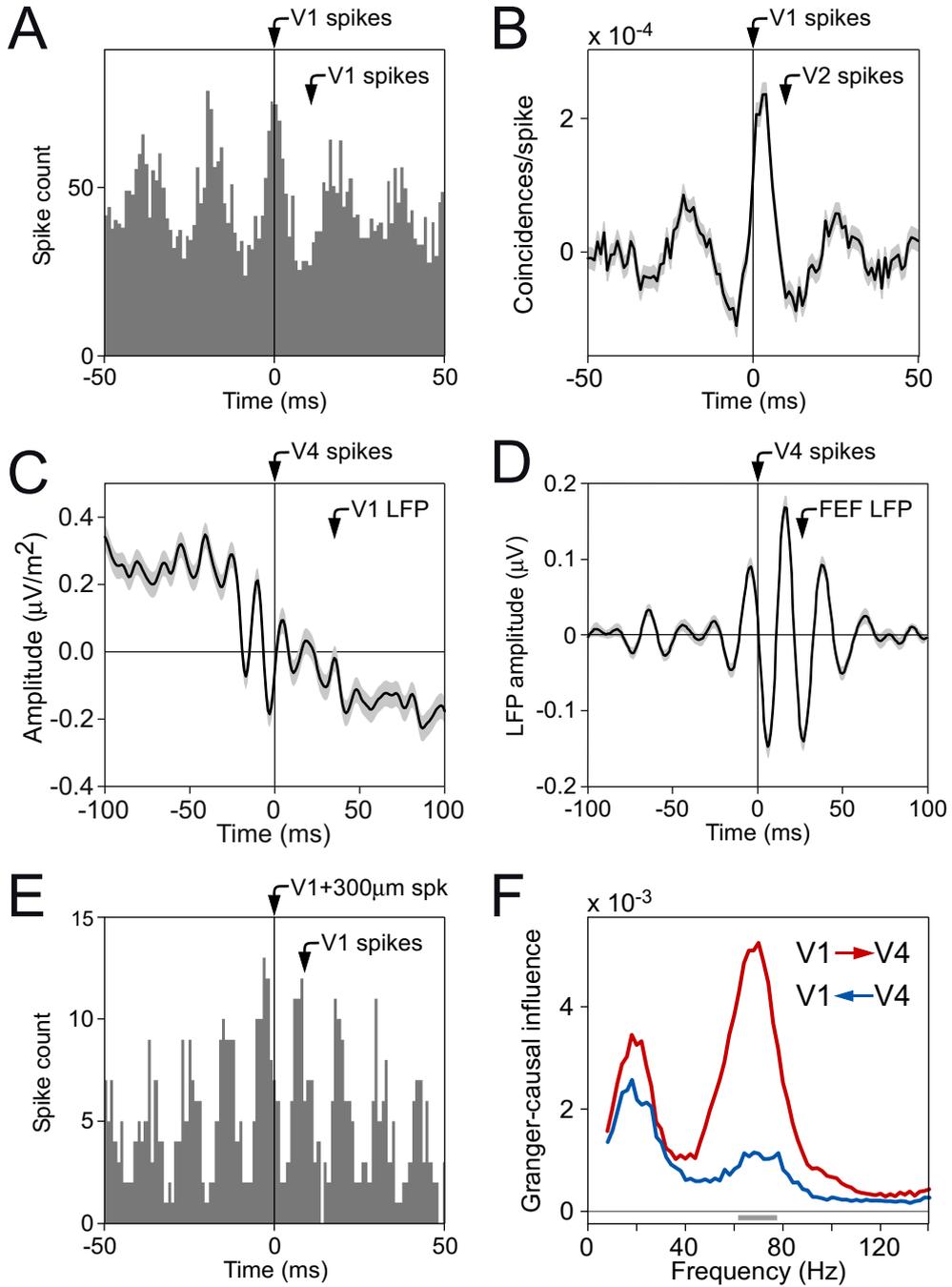
Figure 1

Figure 2