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Cognition is an emergent property

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Cognition relies on the flexible organization of neural activity. In this discussion, we explore how many aspects of this organization can be described as emergent properties, not reducible to their constituent parts. We discuss how electrical fields in the brain can serve as a medium for propagating activity nearly instantaneously, and how population-level patterns of neural activity can organize computations through subspace coding.

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Introduction

Emergent properties are those that are not predictable from or reducible to their individual parts [1]. Take, for example, sports fans performing 'the wave' or the collective behavior of an ant colony. You cannot observe the wave or understand the operations of the colony by studying each person or ant separately, even if you examined every individual. The organization arises from real-time interactions and a few simple rules. If sports fans can take advantage of this to organize themselves, imagine what evolution can do with that principle. Evolution seems to have done this by exploiting the influences of the brain's electric fields (EFs).

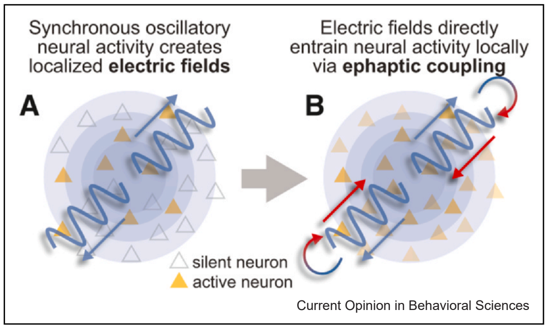
Electric fields have bidirectional influence on neural activity

Emergent organization is evident in mesoscale neural EFs, measured within the brain as local field potentials (LFPs) and at the scalp as the electroencephalogram (EEG). They show oscillations, which reflect synchronized dynamics in excitability across millions of neurons [2,3]. This is an emergent property, as the fields generated by unsynchronized signals would cancel out rather than summate into observable oscillations, and most individual neurons are individually weakly oscillatory. Coordination at this scale is crucial for attention, decision-making, action generation, and memory retrieval [4–6]. Cognitive state is reflected in patterns of EF synchrony [7–9] as are changes in attentional focus [10–13]. Further, EFs can provide stable information sources, free from the representational drift of neurons [14]. This is not to say that spiking is unimportant; it absolutely is. Spikes create and couple to oscillations, and in turn, oscillations are an excellent way to organize spiking.

Crucially, EFs not only reflect the underlying activity, but they can also shape it via ephaptic coupling (Figure 1), a direct influence of extracellular potential on neural activity [14–18]. Some influence of EFs seems almost inevitable. Many cortical neurons rest close to spiking threshold, spending much of their time teetering on the edge of spiking. It can take just small changes in the surrounding EFs to push them one way or another, as suggested by several models [11,15,19,20]. In fact, experiments have shown that externally induced EFs with amplitudes similar to endogenous fields can entrain spike times [18] and boost network-level 'Up' states [17]. Ephaptic coupling of EFs can be very useful. Traditional synaptic connectivity is limited by the speed of axonal conduction and synaptic transmission. In contrast, because EFs have a direct effect on intracellular potential, they spread at the speed of an electric field in neural tissue, nearly instantaneously. This seems ideal for rapidly coordinating local neural activity. They may even influence the brain's infrastructure on the molecular level, 'tuning' networks to make them function more efficiently [21].

Next, we consider examples of how the brain uses these dynamics in the flexible control of cognition.

Figure 1



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Bidirectional influence of EFs on neural activity. **(a)** Synchronous, rhythmic neural spiking activity (filled triangles) induces localized oscillatory EFs (measured as LFPs or EEG). **(b)** EFs have sufficient field strength to influence the intracellular potential of nearby neurons. This 'ephaptic coupling' can recruit additional neurons and temporally entrain their spiking activity.

Spatial computing controls expression of neural engrams

An emerging theory of neural computation stems from observations that throughout the cortex, alpha/beta (12–30 Hz) and gamma (> 30 Hz) oscillations tend to be anticorrelated [9,22,23] (though they can be dissociated in some cases [24]). Gamma is associated with activated neurons and higher spiking rates [25]. This mechanism could regulate computation by controlling the spatial expression of spiking, and thus information, within cortical networks.

Spatial computing [26] proposes that mesoscale patterns of alpha/beta activity carry top-down control signals, which reflect information about the current context and goals. These alpha/beta patterns are inhibitory and spatially constrain the bottom-up gamma power associated with content-related spiking at a microscale level. In essence, alpha/beta patterns act as stencils, allowing content (microscale gamma/spiking) to be expressed in areas where alpha/beta is absent. These stencils represent different cognitive states or task operations. This is in line with observations that power and coupling in gamma versus alpha/beta are respectively associated with bottom-up processing versus top-down control [9,10,22,23,27–30].

For example, consider a task to remember a sequence of two objects in order of their appearance (Figure 2a,b) [31]. The idea is that bottom-up inputs from the visual cortex convey selectivity for each object to a random subset of neurons in the higher-level (e.g. prefrontal) cortex (Figure 2c,d). Top-down inputs (recurrent or feedback connections) convey inhibitory influences via alpha/beta oscillations and have a unique spatial pattern across the cortical surface for each 'slot' in the sequence. Spiking activity reflects the integration of both types of inputs — neurons that would have been activated by an object are suppressed by the top-down contextual inputs, leaving a spatially-restricted subset of active neurons. In short, network spatial arrangement is used as an encoding dimension, one that adds context to spiking activity.

This theory could explain a wide range of seemingly unrelated phenomena, including 'mixed selectivity' [31–33]. Many cortical neurons show spiking that is highly dependent on context. For example, in tasks like the one in Figure 2, neurons in the prefrontal cortex show complex responses reflecting both object identity and order (e.g. spiking only to 'butterfly' when it is first). This kind of 'nonlinear mixed selectivity' allows for flexible read-out of arbitrary functions of input signals, exactly the type of flexibility needed for higher-level cognition [32,33]. The exact combinations of factors activating these neurons were originally thought to be random, similar to 'hidden units' in a neural network model. Spatial computing posits a guiding principle: alpha/beta patterns carrying control signals that constrain and sculpt spiking. Similar principles may underlie contextual modulation and mixed selectivity in other cognitive domains and brain regions [34–36].

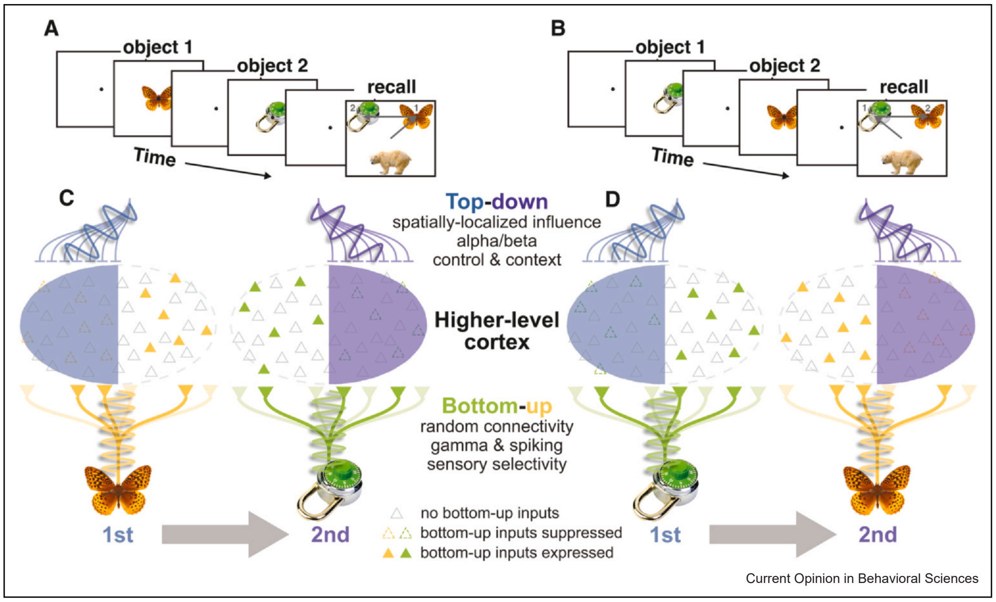
This separation of content (gamma/spiking) and control (alpha/beta) into different spatial scales endows generalization and flexibility. It enables the brain to perform top-down operations without 'knowing' the specifics of the underlying ensembles carrying content. This allows the brain to instantly generalize control to new content. Contrast this with standard neural network models, where all information — content and control — is encoded at the same level, synaptic connectivity. As a result, a standard network model learning a task with one set of objects needs retraining to perform with a new set of objects. Your brain does not need retraining to instantly generalize.

Importantly, emergent organization is not just evident at the EF level. It can also be seen in the spiking of neurons, in subspace coding.

Subspace coding organizes neural computation and communication

Activity in a population of neurons can be understood as existing in a high-dimensional 'state space', one dimension for each neuron. Any particular condition (sensation, action, and/or cognitive state) is represented by a specific pattern of activity across the neural population (Figure 3a). This corresponds to a specific point in neural 'state space' (Figure 3b). Different conditions elicit different population patterns, corresponding to distinct points in state space.

Figure 2



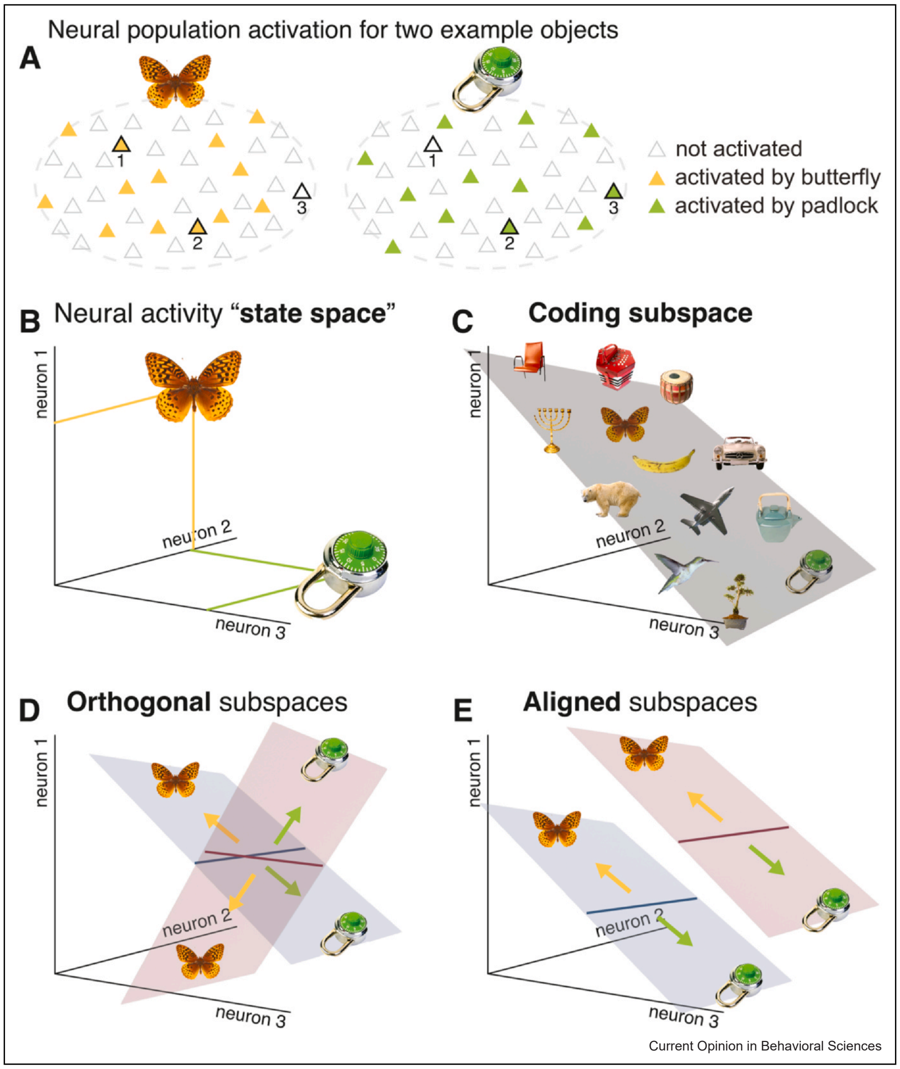
Spatial computing creates mixed selectivity. **(a,b)** Two trials of a task to remember the identity and order (cf. a vs b) of two sequentially presented objects, then recall them after a brief delay. Prefrontal neurons exhibit ‘nonlinear mixed selectivity’ — activity for specific objects in specific order ‘slots’. **(c,d)** Spatial computing model of nonlinear mixed selectivity in the two corresponding trials. Orange/green lines represent bottom-up connections, which distribute sensory selectivity for the objects over a random subset of neurons (orange/green triangles). Blue/purple lines represent top-down alpha/beta signals, which contribute spatially localized inhibition (shaded regions) that reflects control and context (e.g. the sequential order of the two objects). These signals constrain where bottom-up signals are expressed (white regions), resulting in patches of activated neurons (filled orange/green triangles) that reflect both object identity and their sequential order, that is, mixed selectivity.

However, it turns out that neural activity does not fully sample all possible states. Instead, population spiking activity is restricted to a low-dimensional subspace of the full high-dimensional population space (Figure 3c) [37–40]. This reflects the fact that the activity of individual neurons is not completely independent of one another. Rather, their activity covaries in complex, but structured ways (e.g. in Figure 3c, when neuron 1’s activity increases, neuron 3 decreases).

A key benefit of such subspace coding is the organization of neural processing. When multiple pieces of information must be held simultaneously in memory [41] or compared [42], they are often stored in approximately orthogonal subspaces (Figure 3d). That is, the spiking patterns reflecting one item are independent of those for the other item, minimizing interference between them. Similarly, as incoming sensory information is encoded into working memory, it is rotated from a ‘sensory’ subspace to an orthogonal ‘memory’ subspace, protecting it from interference from further sensory inputs [43]. Thus, subspace coding allows distinct information to be stored and operated on independently [44]. On the other hand, when distinct information must be mapped onto a common behavioral response, subspaces reflecting different types of information may be rotated into alignment (Figure 3e), so that behavior could be driven by a single linear read-out [41]. Thus, the organization of neural responses into subspaces can both segregate and integrate information.

In addition to local within-region processing, subspace coding can also organize communication between brain regions. When trial-to-trial fluctuations of population activity are compared between connected cortical areas, only a small subset of activity patterns in each area exhibit correlations between areas. This has been interpreted to mean that only a restricted subspace of population activity in one area, a ‘communication subspace’, drives activity in another [44,45]. Different communication subspaces are used within the same area for feedforward and feedback communication [46]. These results suggest that information flow across the cortex might be organized by restricting activity patterns to — or excluding them from — specific subspaces, analogous to a lock-and-key mechanism. During motor preparation, cortical activity evolves within dimensions that avoid the subspaces that, during motor execution, drive downstream motor cortex or muscles [47]. This suggests that ‘subspace exclusion’ may be a mechanism for the cortex to perform internal computations without prematurely transmitting output signals.

Figure 3



Subspace coding. **(a)** Example of patterns of neural population activity for two different conditions (in this case, visual objects). **(b)** Population activity patterns can be thought of as points in a high-dimensional 'state-space', with one dimension for each neuron (three are shown, corresponding to the three labeled neurons in part **(a)**, but actual experiments sample hundreds from an underlying population of millions). **(c)** Activity for different conditions is typically restricted to a much lower-dimensional subspace (represented by a 2D plane). **(d)** Information that must be kept separate is often encoded in orthogonal subspaces, so it can be read out independently. **(e)** When information must be mapped onto a common behavioral response, it is often encoded into aligned subspaces, so behavior can be driven by a single linear read-out.

Critically, distinct subspaces tend to be composed of largely overlapping populations of neurons [41–43,47,48]. That is, they reflect distinct patterns of activity across a single neural population, not distinct subpopulations of neurons. Thus, subspace coding allows multiplexing of different functions, while obviating the need to segregate every computation into separate subpopulations or regions. This implies that the activity of individual neurons is ambiguous and can only be fully understood in the context of population patterns, that is, as an emergent property.

Conclusion and future directions

One set of emergent properties — organization of coding and communication in subspaces — is observed at the local spiking level. Another set of properties — oscillations that can bidirectionally influence spikes and organize cortical information flow — is observed at the mesoscale network level. A key question for future research is understanding the relationship between these emergent phenomena. One possibility is that they are causally related. Spatially structured oscillations may control not only the expression of spiking activity but also its subspace organization. Further, spatial dynamics of oscillations, as seen in traveling waves [49], may control shifts from one subspace organization to another.

Studying individual neural components in isolation — individual neurons and synapses — has made enormous contributions to our understanding of the brain and remains important. However, it is becoming increasingly clear that, to fully capture the brain's complexity, those components must be analyzed in concert to identify, study, and relate their emergent properties. This is especially critical as many neurological and psychiatric disorders, such as schizophrenia, epilepsy, and Parkinson's, involve disruption of emergent properties like neural synchrony [50]. We anticipate that understanding how to interpret and interface with these emergent properties will be critical for developing effective treatments [51] as well as understanding cognition.

CRediT authorship contribution statement

Earl K. Miller: Writing – original draft. **Scott L. Brincat:** Writing – original draft. **Jefferson E. Roy:** Writing – review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors report no conflict of interest.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest.

1. In *The Oxford Companion To Philosophy*. Edited by Honderich T. new edn 2, Oxford University Press; 2005.
2. Buzsáki G, Vöröslakos M: **Brain rhythms have come of age**. *Neuron* 2023, **111**:922-926, https://doi.org/10.1016/j.neuron.2023.03.018
3. Singer W: **Neuronal oscillations: unavoidable and useful?** *Eur J Neurosci* 2018, **48**:2389-2398, https://doi.org/10.1111/ejn.13796
4. Miller EK, Cohen JD: **An integrative theory of prefrontal cortex function**. *Ann Rev Neurosci* 2001, **24**:167-202, https://doi.org/10.1146/annurev.neuro.24.1.167
5. Gazzaley A, Nobre AC: **Top-down modulation: bridging selective attention and working memory**. *Trends Cogn Sci* 2012, **16**:129-135, https://doi.org/10.1016/j.tics.2011.11.014
6. Vyas S, Golub MD, Sussillo D, Shenoy KV: **Computation through neural population dynamics**. *Ann Rev Neurosci* 2020, **43**:249-275, https://doi.org/10.1146/annurev-neuro-092619-094115
7. Buschman TJ, Denovellis EL, Diogo C, Bullock D, Miller EK: **Synchronous oscillatory neural ensembles for rules in the prefrontal cortex**. *Neuron* 2012, **76**:838-846, https://doi.org/10.1016/j.neuron.2012.09.029
8. Antzoulatos EG, Miller EK: **Increases in functional connectivity between prefrontal cortex and striatum during category learning**. *Neuron* 2014, **83**:216-225, https://doi.org/10.1016/j.neuron.2014.05.005
9. Bastos AM, Lundqvist M, Waite AS, Kopell N, Miller EK: **Layer and rhythm specificity for predictive routing**. *Proc Natl Acad Sci USA* 2020, **117**:31459-31469, https://doi.org/10.1073/pnas.2014868117
10. Fiebelkorn IC, Kastner S: **A rhythmic theory of attention**. *Trends Cogn Sci* 2019, **23**:87-101, https://doi.org/10.1016/j.tics.2018.11.009
11. Buschman TJ, Miller EK: **Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations**. *Neuron* 2009, **63**:386-396, https://doi.org/10.1016/j.neuron.2009.06.020
12. Fries P, Reynolds JH, Rorie AE, Desimone R: **Modulation of oscillatory neuronal synchronization by selective visual attention**. *Science* 2001, **291**:1560-1563, https://doi.org/10.1126/science.1055465
13. Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE: **Entrainment of neuronal oscillations as a mechanism of attentional selection**. *Science* 2008, **320**:110-113, https://doi.org/10.1126/science.1154735
14. Pinotsis DA, Miller EK: **Beyond dimension reduction: stable electric fields emerge from and allow representational drift**. *Neuroimage* 2022, **253**:119058, https://doi.org/10.1016/j.neuroimage.2022.119058
15. Cunha GM, Corso G, Miranda JGV, Dos Santos Lima GZ: **Ephaptic entrainment in hybrid neuronal model**. *Sci Rep* 2022, **12**:1629, https://doi.org/10.1038/s41598-022-05343-3
16. Van Horn JD, Jacokes Z, Newman B, Henry T: **Editorial: is now the time for foundational theory of brain connectivity?** *Neuroinform* 2023, **21**:633-635, https://doi.org/10.1007/s12021-023-09641-7
17. Fröhlich F, McCormick DA: **Endogenous electric fields may guide neocortical network activity**. *Neuron* 2010, **67**:129-143, https://doi.org/10.1016/j.neuron.2010.06.005
18. Anastassiou CA, Perin R, Markram H, Koch C: **Ephaptic coupling of cortical neurons**. *Nat Neurosci* 2011, **14**:217-223, https://doi.org/10.1038/nn.2727
19. Anastassiou CA, Koch C: **Ephaptic coupling to endogenous electric field activity: why bother?** *Curr Opin Neurobiol* 2015, **31**:95-103, https://doi.org/10.1016/j.conb.2014.09.002
20. Schmidt H, Hahn G, Deco G, Knösche TR: **Ephaptic coupling in white matter fibre bundles modulates axonal transmission delays**. *PLoS Comput Biol* 2021, **17**:e1007858, https://doi.org/10.1371/journal.pcbi.1007858
21. Pinotsis DA, Fridman G, Miller EK: **Cytoelectric coupling: electric fields sculpt neural activity and "tune" the brain's infrastructure**. *Prog Neurobiol* 2023, **226**:102465, https://doi.org/10.1016/j.pneurobio.2023.102465
22. Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ: **Canonical microcircuits for predictive coding**. *Neuron* 2012, **76**:695-711, https://doi.org/10.1016/j.neuron.2012.10.038
23. van Kerkoerle T, Self MW, Dagnino B, Gariel-Mathis M-A, 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 USA* 2014, **111**:14332-14341, https://doi.org/10.1073/pnas.1402773111
24. Fellner M-C, Gollwitzer S, Rampp S, Kreiselmeyr G, Bush D, Diehl B, Axmacher N, Hamer H, Hanslmayr S: **Spectral fingerprints or spectral tilt? Evidence for distinct oscillatory signatures of**

memory formation. *PLoS Biol* 2019, **17**:e3000403, https://doi.org/10.1371/journal.pbio.3000403

25. Fries P, Nikolić D, Singer W: **The gamma cycle**. *Trends Neurosci* 2007, **30**:309-316, https://doi.org/10.1016/j.tins.2007.05.005

26. •• Lundqvist M, Brincat SL, Rose J, Warden MR, Buschman TJ, Miller EK, Herman P: **Working memory control dynamics follow principles of spatial computing**. *Nat Commun* 2023, **14**:1429, https://doi.org/10.1038/s41467-023-36555-4.

This paper introduced the theory of spatial computing, that top-down control is exerted through spatial patterns of suppressive alpha/beta oscillations that constrain the expression of bottom-up sensory information in spiking. Results from multiple studies consistent with the theory are presented.

27. Buschman TJ, Miller EK: **Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices**. *Science* 2007, **315**:1860-1862, https://doi.org/10.1126/science.1138071

28. Saalmann YB, Kastner S: **Cognitive and perceptual functions of the visual thalamus**. *Neuron* 2011, **71**:209-223, https://doi.org/10.1016/j.neuron.2011.06.027

29. 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 USA* 2011, **108**:11262.

30. Riddle J, Scimeca JM, Cellier D, Dhanani S, D'Esposito M: **Causal evidence for a role of theta and alpha oscillations in the control of working memory**. *Curr Biol* 2020, **30**:1748-1754.e4, https://doi.org/10.1016/j.cub.2020.02.065

31. Warden MR, Miller EK: **Task-dependent changes in short-term memory in the prefrontal cortex**. *J Neurosci* 2010, **30**:15801-15810, https://doi.org/10.1523/JNEUROSCI.1569-10.2010

32. Rigotti M, Barak O, Warden MR, Wang X-J, Daw ND, Miller EK, Fusi S: **The importance of mixed selectivity in complex cognitive tasks**. *Nature* 2013, **497**:585-590, https://doi.org/10.1038/nature12160

33. Fusi S, Miller EK, Rigotti M: **Why neurons mix: high dimensionality for higher cognition**. *Curr Opin Neurobiol* 2016, **37**:66-74, https://doi.org/10.1016/j.conb.2016.01.010

34. Kolibius LD, Roux F, Parish G, Ter Wal M, Van Der Plas M, Chelvarajah R, Sawlani V, Rollings DT, Lang JD, Gollwitzer S, Walther K, Hopfengärtner R, Kreiselmeyer G, Hamer H, Staresina BP, Wimber M, Bowman H, Hanslmayr S: **Hippocampal neurons code individual episodic memories in humans**. *Nat Hum Behav* 2023, **7**:1968-1979, https://doi.org/10.1038/s41562-023-01706-6

35. Zhang CY, Aflalo T, Revechkis B, Rosario ER, Ouellette D, Pouratian N, Andersen RA: **Partially mixed selectivity in human posterior parietal association cortex**. *Neuron* 2017, **95**:697-708.e4, https://doi.org/10.1016/j.neuron.2017.06.040

36. Mao D: **Neural correlates of spatial navigation in primate hippocampus**. *Neurosci Bull* 2023, **39**:315-327, https://doi.org/10.1007/s12264-022-00968-w

37. •• Ebitz RB, Hayden BY: **The population doctrine in cognitive neuroscience**. *Neuron* 2021, **109**:3055-3068, https://doi.org/10.1016/j.neuron.2021.07.011.

An excellent introductory review of current ideas around population-level neural information processing, particularly for understanding cognition.

38. Urai AE, Doiron B, Leifer AM, Churchland AK: **Large-scale neural recordings call for new insights to link brain and behavior**. *Nat Neurosci* 2022, **25**:11-19, https://doi.org/10.1038/s41593-021-00980-9

39. Sapountzis P, Paneri S, Papadopoulos S, Gregoriou GG: **Dynamic and stable population coding of attentional instructions coexist in the prefrontal cortex**. *Proc Natl Acad Sci USA* 2022, **119**:e2202564119, https://doi.org/10.1073/pnas.2202564119

40. Badre D, Bhandari A, Keglovits H, Kikumoto A: **The dimensionality of neural representations for control**. *Curr Opin Behav Sci* 2021, **38**:20-28, https://doi.org/10.1016/j.cobeha.2020.07.002

41. •• Panichello MF, Buschman TJ: **Shared mechanisms underlie the control of working memory and attention**. *Nature* 2021, **592**:601-605, https://doi.org/10.1038/s41586-021-03390-w.

This study compared prefrontal cortex subspaces for colors of two items in different locations held in working memory. It found that the two items' subspaces were kept roughly orthogonal until subjects were instructed to select one. Then, the subspace for the selected item was transformed such that it was aligned regardless of the item's initial location.

42. Yoo SBM, Hayden BY: **The transition from evaluation to selection involves neural subspace reorganization in core reward regions**. *Neuron* 2020, **105**:712-724.e4, https://doi.org/10.1016/j.neuron.2019.11.013

43. Libby A, Buschman TJ: **Rotational dynamics reduce interference between sensory and memory representations**. *Nat Neurosci* 2021, **24**:715-726, https://doi.org/10.1038/s41593-021-00821-9

44. MacDowell CJ, Libby A, Jahn CI, Tafazoli S, Buschman TJ **:** Multiplexed Subspaces Route Neural Activity Across Brain-wide Networks; 2023:2023.02.08.527772. https://doi.org/10.1101/2023.02.08.527772.

45. Semedo JD, Zandvakili A, Machens CK, Yu BM, Kohn A: **Cortical areas interact through a communication subspace**. *Neuron* 2019, **102**:249-259.e4, https://doi.org/10.1016/j.neuron.2019.01.026

46. • Semedo JD, Jasper AI, Zandvakili A, Krishna A, Aschner A, Machens CK, Kohn A, Yu BM: **Feedforward and feedback interactions between visual cortical areas use different population activity patterns**. *Nat Commun* 2022, **13**:1099, https://doi.org/10.1038/s41467-022-28552-w.

This study used a novel method for measuring directional (feedforward vs feedback) 'communication subspaces' between cortical areas. Subspaces estimated for one direction generalized poorly to the other, suggesting feedforward and feedback communication use distinct subspace 'channels'.

47. Kaufman MT, Churchland MM, Ryu SI, Shenoy KV: **Cortical activity in the null space: permitting preparation without movement**. *Nat Neurosci* 2014, **17**:440-448, https://doi.org/10.1038/nn.3643

48. Raposo D, Kaufman MT, Churchland AK: **A category-free neural population supports evolving demands during decision-making**. *Nat Neurosci* 2014, **17**:1784-1792, https://doi.org/10.1038/nn.3865

49. Batabyal T, Brincat SL, Donoghue JA, Lundqvist M, Mahnke MK, Miller EK: **Stability from subspace rotations and traveling waves**. *bioRxiv* 2024, https://doi.org/10.1101/2024.02.19.581020 2024.02.19.581020.

50. Uhlhaas PJ, Singer W: **Neural synchrony in brain disorders: relevance for cognitive dysfunctions and pathophysiology**. *Neuron* 2006, **52**:155-168, https://doi.org/10.1016/j.neuron.2006.09.020:

51. Widge AS, Miller EK: **Targeting cognition and networks through neural oscillations: next-generation clinical brain stimulation**. *JAMA Psychiatry* 2019, **76**:671-672, https://doi.org/10.1001/jamapsychiatry.2019.0740