Review

Analog Cognition and Consciousness

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Cognition and consciousness may arise from bidirectional interactions between neuronal spiking and rhythmic electric field activity (brain waves). Goal-directed behavior relies on top-down control to coordinate large neural populations into low-dimensional, task-oriented dynamics. Brain waves are well suited for this role, exerting mesoscale influence over neural excitability. They can also support analog computation, shaping activity patterns according to underlying computational principles. Brain waves can flexibly route and organize neural signals, enabling multifunctional neurons to assume context-dependent roles, a hallmark of cognition. In this view, goal-directed thought, action, and unified consciousness emerge from cortex-wide wave dynamics that both reflect and transform spiking into coherent brain states.

Key words: **cognition; consciousness**

Introduction

Cognition is the brain's use of internal representations (e.g., schemas, goals, and memories) to mediate between stimuli and responses. To do so, we evolved top-down feedback mechanisms that filter and modulate feedforward sensory inputs, control actions, and retrieve stored memories. At the highest levels, this includes executive functions that align thought and action with future goals (D'Esposito and Grossman, 1996; Miller and Cohen, 2001; Collette et al., 2006; Banich, 2009; O'Reilly et al., 2010; Diamond, 2013; Botvinick and Braver, 2015; Duncan et al., 2020; Ede and Nobre, 2023). Many top-down processes are unconscious, but they can become conscious to support deliberation, long-term planning, and the inhibition of automatic yet counterproductive impulses. This kind of flexible, self-directed neural processing requires a control system that can coordinate hundreds of millions of neurons within fractions of a second.

This is hard to reconcile with traditional models that view brain function as arising only from brief electrical impulses ("spikes") transmitted through networks shaped by the synaptic connections between neurons. Spiking and synaptic connections are, of course, critical and fundamental. However, synaptic changes are likely too cumbersome for flexible top-down control. That would require a control system to "know" which synapses and neurons were employed for any given neural representation and selectively coordinate them with subsecond precision, a seemingly implausible computational demand.

A biologically plausible mechanism may involve an emergent level of influence from the brain's oscillatory electrical activity, i.e., brain waves. The same circuits that generate spiking also produce oscillatory dynamics via a natural outcome of recurrent loops at different scales, interacting with subcortical modulatory inputs and sensory drive (Buzsáki, 2006; Singer, 2021). Oscillations give the brain an internal organization beyond simple feedforward reactions to sensory input. They produce waves in electric fields surrounding neurons that reflect activity coordinated over millimeter-to-centimeter scales. These brain waves, in turn, influence local membrane potentials, nudging neurons toward or away from the spiking threshold.

Thus, electric field effects provide a means to control neural activity at an intermediate, mesoscale level. This emergent level varies more smoothly across the cortical surface, making it simpler and more low-dimensional than the full, high-dimensional synaptic circuitry. Synaptic connections store information, and spiking can carry detailed sensory and motor signals, but the lower dimensionality of brain waves may make them particularly well suited for a computationally tractable means for controlling and organizing neural processing.

Evolution could have exploited this by evolving the means to influence oscillatory dynamics, gaining control over neural activity. In this view, synaptic connections and spikes work together with brain waves to coordinate large-scale computation, supporting cognition and consciousness.

The Classical Model of Neural Information Processing

A useful starting point is to contrast our hybrid spike/wave view of cortical function with traditional connectionist models. Classical models emphasize computation and memory through changes in synaptic weights driving spiking activity in specialized neurons. Drawing on logic-gate metaphors from early sensory physiology, they describe hierarchical feedforward circuits in which neurons become tuned to progressively more complex features (Fig. 1). This was thought to result in a modular set of brain networks and areas with discrete, nonoverlapping functions. In this view, each neuron serves a stable, specialized function, i.e.,

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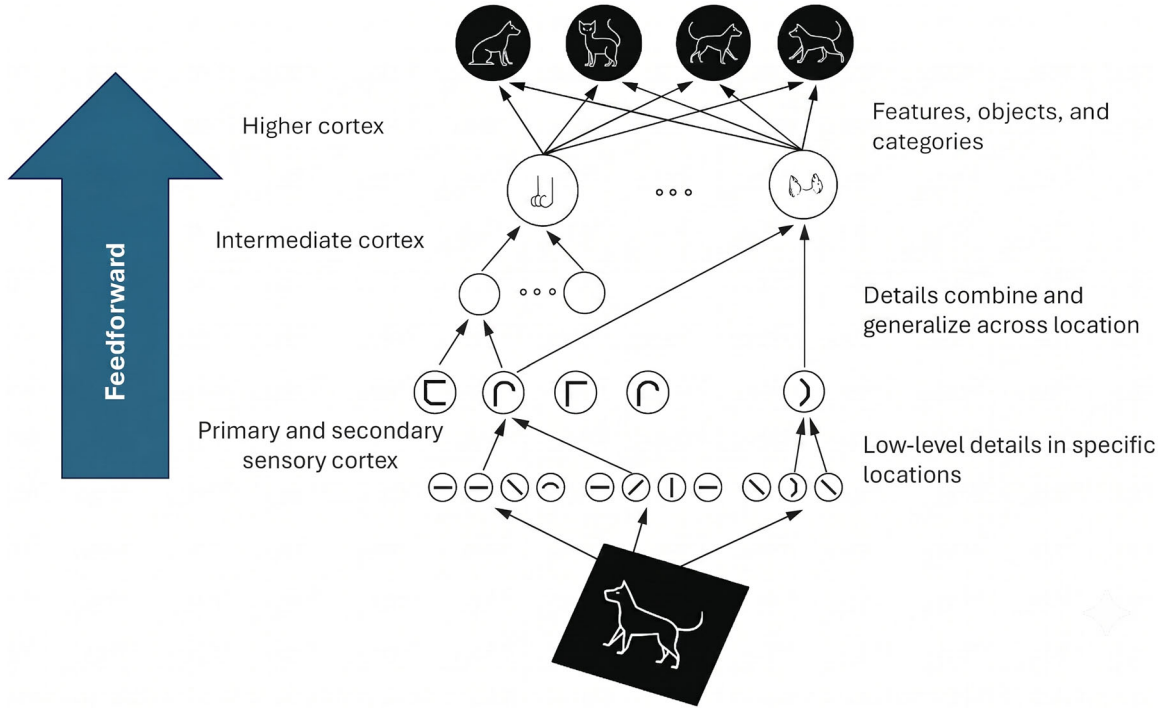

Figure 1. The connectionist view of cortical processing. Lower visual areas detect simple features such as lines and edges and then feed this information forward along the cortical hierarchy, where neurons combine these features into increasingly complex and specialized representations (e.g., limbs, paws, nose, whiskers), until the brain constructs a representation of a holistic category or concept (e.g., cat, dog).

a given neuron's spikes always "mean" the same unique thing. The thought was that if we could decode each neuron's message, their connections, and their collection into a functional patchwork of cortical areas, we could, in principle, understand the brain.

The connectionist approach was foundational and remains a good account of much of feedforward processing in the sensory cortex. But it is incomplete and cannot explain many observations. An early example was the consistent finding that any given task engages around a third of neurons in the prefrontal cortex (Asaad et al., 2000; Freedman et al., 2001; Wallis et al., 2001; Xiang et al., 2025). Under the traditional connectionist model, this would imply that we can only learn about three different cognitive functions before essentially all prefrontal neurons have been "assigned a function," and its computational capacity is saturated. It was proposed instead that many cortical neurons are multifunctional, rather than specialized (Duncan and Miller, 2002, 2013). This was confirmed by observations that the spiking of many cortical (and subcortical) neurons are not organized around single functions and instead multiplex different kinds of information (Asaad et al., 2000; Warden and Miller, 2007; Cromer et al., 2010; Rigotti et al., 2013; Akam and Kullmann, 2014; Ramakrishnan et al., 2017; Lankarany et al., 2019). This phenomenon has come to be called nonlinear "mixed selectivity" (Rigotti et al., 2013; Fusi et al., 2016; Tye et al., 2024).

Mixed Selectivity: Multifunctional Neurons Enable Flexible Cognition

To understand mixed selectivity, consider a task that requires memory for two objects and their order (first vs second; Fig. 2*A*; Warden and Miller, 2007). The traditional connectionist framework would predict neurons that show consistent selectivity in spiking to the same objects, regardless of their order in the sequence (Fig. 2*B*). It would also predict neurons whose sole function was to keep track of order. Some neurons might spike indiscriminately to all objects when they appear first and others to all objects when they appear second.

Instead, many cortical neurons show mixed selectivity that multiplexes information. Their spiking reflects nonlinear combinations of variables, integrating contextual information (like order) with sensory inputs (like objects) and motor actions. In our example, this corresponds to selective spiking to objects that changes depending on the context of their sequence order (Fig. 2*C*), as we observed in many prefrontal neurons (Warden and Miller, 2007; Rigotti et al., 2013). A neuron might spike to Object A, but only when it was seen first, and to Object B, but only when it is seen second (Fig. 2*C*).

These neurons seem to embody the flexible, context-dependent behavior associated with higher cognition (Rigotti et al., 2013; Fusi et al., 2016; Tye et al., 2024). Modeling studies show that nonlinear mixed selectivity neurons greatly expand the brain's computational power by providing a higher-order representational space (Rigotti et al., 2013; Fusi et al., 2016; Tye et al., 2024). Further, they also greatly increase a network's capacity to store information because information is distributed across many multifunctional neurons rather than segregated into specialist neurons (Rigotti et al., 2013). Importantly, mixed selectivity is not merely the "icing on the cake" of cortical processing but instead seems to reflect a core computational principle (Johnston et al., 2020; Tye et al., 2024). They are not only prevalent (30–40% of neurons) in higher areas like prefrontal cortex (Warden and Miller, 2007; Parthasarathy et al., 2017; Dang et al., 2022; Abbass et al., 2025; Mouille et al., 2025) but also in primary sensory and motor cortex (Grunfeld and Likhtik, 2018; Kaufman et al., 2022; Tseng et al., 2022; Kira et al., 2023; Tye et al., 2024).

Mixed selectivity thus shows that the cortex is not a mosaic of specialized neurons, circuits, and areas. The neurons show

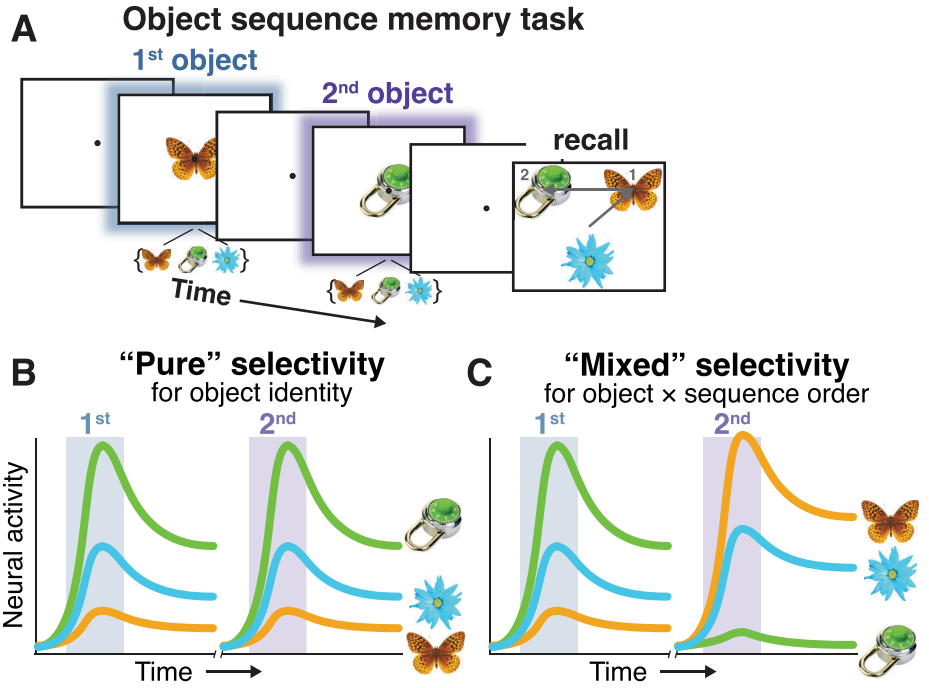

Figure 2. Schematic illustration of pure versus mixed selectivity in an example task. ***A***, Task structure. Subjects were required to briefly remember the identity and order of a sequence of two objects and then reproduce the sequence from memory. ***B***, A neuron with "pure" selectivity for object identity would show the same responses to objects, regardless of their order. ***C***, A neuron with nonlinear mixed selectivity might show different object preferences, depending on the context of the objects' sequential order.

context-dependent spiking, which means they are inherently multifunctional, sending different signals in different situations. Thus, cortical neurons participate in multiple functional networks, shifting membership in different contexts as needed.

This flexibility presents a major challenge from a control perspective. A control system has the challenge of dynamically routing signals through a dense web of overlapping networks, allowing the same neurons to contribute to different computations in different contexts. Such flexible routing is difficult to reconcile with a purely connectionist framework based solely on changing synaptic weights. A more computationally tractable mechanism for controlling and organizing neural processing seems to be needed. Neural oscillations, i.e., brain waves, could serve that role.

Brain Waves Organize Neural Information

Neural oscillations are rhythmic fluctuations in extracellular potential that reflect coordinated neural activity over a mesoscale range of millimeters to centimeters (Buzsáki, 2006). Their phases reflect alternating periods of relative neural excitation and inhibition and thus change the electric field environment in the tissue surrounding neurons. This can be measured within the brain as local field potentials (LFPs) or externally as the EEG.

A wide variety of evidence has associated oscillations with roles in organizing information, routing it between circuits, and coordinating memory and control processes (Buzsáki, 2006; Sejnowski and Paulsen, 2006; Miller et al., 2024; Baker and Cariani, 2025; Singer and Effenberger, 2025). For example, in the cortex and hippocampus, information can be organized by segregating spiking to different phases of local oscillations (Skaggs et al., 1996; Siegel et al., 2009; Lisman and Jensen, 2013). Oscillations can act as a brief "handshake" signal that connects different circuits to flexibly route information (Brincat et al., 2021; Odean et al., 2023). They can facilitate cortical communication by coordinating brief time windows when sending and receiving populations are alternately more or less receptive to inputs (Womelsdorf et al., 2007; Fries, 2015).

In all of these cases, brain waves both reflect and instantiate a coordination of large populations of spiking neurons. This makes brain waves well suited for a role in top-down control because, as we will see next, they can have direct, nearly instantaneous influence on neuronal activity via extra-synaptic means.

Brain Waves Directly Influence Activity via Ephaptic Coupling

Oscillatory fluctuations in extracellular electric fields have direct field effects on neurons via ephaptic coupling. These are effects on the intracellular potentials and spiking activity of nearby neurons that are not mediated by synapses or gap junctions. For example, cerebellar Purkinje cell spikes generate extracellular potentials that are large enough to drive synchrony in nearby cells, even when chemical synapses and gap junctions are blocked (Han et al., 2018). Experimental and modeling studies show that endogenous LFPs and externally applied weak fields modulate spiking, especially in tightly packed cortical and hippocampal circuits where the extracellular space is narrow and resistive (Radman et al., 2007; Fröhlich and McCormick, 2010; Anastassiou and Koch, 2015; Ruffini et al., 2020; Pinotsis and Miller, 2023, 2026). Endogenous electric fields have been shown to modulate spike timing, synchronize local neurons, and alter synaptic efficacy (Radman et al., 2007; Fröhlich and McCormick, 2010; Anastassiou et al., 2011; Jæger and Tveito, 2026).

Ephaptic coupling can have a large influence because many cortical neurons spend much of their time with membrane potentials fluctuating near the spike threshold, i.e., "teetering"

on the edge of spiking (Shifman and Lewis, 2019; Pinotsis and Miller, 2023, 2026). Thus, even weak oscillatory extracellular fields can induce subthreshold voltage changes that significantly modulate both spiking probability and spike timing in local populations of neurons (Francis et al., 2003; Buzsáki and Draguhn, 2004; Radman et al., 2007; Ladenbauer and Obermayer, 2019). Local ephaptic effects, when synchronized and summed across neurons, create effects large enough to shape and coordinate neuron spiking at the mesoscale (Goldwyn and Rinzel, 2016; Cunha et al., 2024). This feedback of electric field effects onto spiking activity can thus recruit neurons into an activated population, as well as spatially and temporally coordinate their activity (Muller et al., 2018; Zhang et al., 2018; Ye et al., 2026). Synaptic and ephaptic interactions form a tightly coupled interactive loop with ephaptic mechanisms augmenting and helping coordinate spiking and synaptic transmission.

Synaptic currents in spiking neurons play a major role in producing the electric field dynamics that drive ephaptic effects, but emerging evidence suggests that another major contribution comes from another type of cell. Astrocytes participate in cognitive functions and have electrical properties that contribute to local electric field effects (Lee et al., 2014; Drummond et al., 2024). However, they do not spike, so their reaction and contribution to wave dynamics are in the absence of spike-triggered synaptic currents (Van Horn et al., 2021). Astrocytes are abundant in the cortex with a 1:3 ratio to neurons in mice but rising to a 1:1.4 ratio to neurons in humans (Degl'Innocenti and Dell'Anno, 2023). This substantial proportion of cortical cells, especially in higher animals, suggests that cortical and higher cognitive function may include electrical mechanisms beyond spike-triggered synaptic transmission.

Neural organization and communication via electric fields potentially offers key advantages over traditional spiking and synaptic mechanisms. While spiking activity is itself very localized, the electric fields it helps create can spread across millimeters or more, due to correlated activity (Xing et al., 2009; Łęski et al., 2013). This could coordinate large cortical neighborhoods simultaneously. Individual spikes are brief, and cortical firing is sparse in space and time, with most neurons firing only a few spikes per second on average in brief bursts followed by longer periods of no spiking (Levenstein and Okun, 2023). In contrast, electric fields are continuous population activity and influence essentially all neurons within a local volume (Anastassiou and Koch, 2015). Further, the speed of spike-based synaptic signaling is limited by conduction along axons and transmission across synapses. In contrast, changes in electric fields arise essentially concurrently with the underlying transmembrane currents and spread through the local tissue at the speed of electromagnetic propagation, making them effectively instantaneous on neuronal timescales (Han et al., 2008; Teleńczuk et al., 2017; Schmidt et al., 2021). This speed makes electric fields well suited for rapidly coordinating local activity. Beyond effects at the level of spiking activity, electric field oscillations may also tune neural circuitry at a molecular level, improving network efficiency (Pinotsis et al., 2023). For example, microtubules align to external electrical fields (Kim et al., 2007). Thus, fields might induce cytoskeletal alterations that could affect neuronal resonance properties by altering dendritic morphology to change input resistance/capacitance (Hutcheon and Yarom, 2000; Laudanski et al., 2014; Stark et al., 2022; Pinotsis et al., 2023).

These properties make oscillatory electric fields excellent candidates for flexible, large-scale control. They can align spike timing, activate or suppress ensembles, and route information across overlapping networks to support adaptive top-down control (Hunt and MacIver, 2026). Key to this concept is that spikes and waves are not separate phenomena. They are part of the same electrical system of bidirectional influences whose activity has different mechanistic and functional impacts at different levels of integration and emergence. One consequence is this saves energy. Electric field oscillations can extend the spatial and temporal reach of spiking, allowing signals to propagate further with less spiking, thus reducing energy demands (Fernández-Ruiz and Herreras, 2013; Jia et al., 2013; Myers et al., 2022). Later, we will consider another potential energy saving mechanism, wave-based analog computation (see Analog Computation with Waves).

Spatial Computing: Brain Wave Control of Neural Information

The "spatial computing" model proposes how spatially structured oscillations can exert flexible executive control over neural computation (Lundqvist et al., 2023). It builds on observations of a push–pull anti-correlation between gamma (~30–80 Hz) versus alpha and beta (~13–30 Hz) rhythms in cortex. Gamma rhythms reflect higher excitation and more spiking while alpha/beta rhythms reflect lower excitation and less spiking (Ray and Maunsell, 2011; Buzsáki and Wang, 2012; Lundqvist et al., 2016; Pellegrino et al., 2021; Headley et al., 2026).

Gamma rhythms subserve feedforward signaling, carrying bottom-up (sensory) inputs and motor outputs (Schoffelen et al., 2005; Gregoriou et al., 2009; Bosman et al., 2012; Rohenkohl et al., 2018). In contrast, alpha/beta rhythms carry feedback signals from higher cortical areas and subserve top-down control functions (Buschman and Miller, 2007; Bastos et al., 2012; Michalareas et al., 2016). Alpha/beta seems to function as an inhibitory mechanism that acts like a brake or filter on gamma excitation (Klimesch et al., 2007; Weisz et al., 2011; Klimesch, 2012; Lundqvist et al., 2016, 2018; Pellegrino et al., 2021; Headley et al., 2026). In the motor cortex, beta power is higher during stable postures and when movements are withheld. It decreases prior to and during movement execution and rebounds after movement cessation (Gilbertson et al., 2005; Khanna and Carmena, 2017; Barone and Rossiter, 2021). This mechanism for controlling motor actions appears to have evolved into a general mechanism for top-down control. Similar dynamics are observed in cognitive functions such as attention and working memory (Buschman and Miller, 2007; Van Kerkoerle et al., 2014; Bastos et al., 2015; Lundqvist et al., 2016; Michalareas et al., 2016). For example, when information is read out of working memory or recalled from long-term memory, there is a decrease in alpha/beta power followed by an increase in gamma and spiking carrying the memories (Lundqvist et al., 2018; Griffiths et al., 2019). This inhibitory dynamic can play a role in maintaining the "status quo" of the system, stabilizing existing sensorimotor or cognitive states (Engel and Fries, 2010). In the cortex, there is a gradual increase of the frequency of oscillations up the cortical hierarchy, from posterior to anterior cortex (Lundqvist et al., 2020). As a result, in the posterior (sensory) cortex, analogous roles are played by oscillations at slightly lower alpha (8–13 Hz) frequencies. There, alpha rhythms play an inhibitory role in visual attention, suppressing bottom-up gamma and spiking to ignored inputs (Klimesch, 2012; de Graaf et al., 2013; Richter et al., 2017; Peylo et al., 2021; Jensen and Bonnefond, 2026).

This cross-frequency dynamic may be a fundamental computational motif embedded in cortical circuitry. In line with their roles in bottom-up versus top-down signaling, gamma power is higher in the superficial cortical layers that send feedforward sensory signals, whereas alpha/beta power is higher in the deep cortical layers carrying feedback signals (Maier et al., 2010; Spaak et al., 2012; Bonaiuto et al., 2018; Bastos et al., 2012, 2020; Mendoza-Halliday et al., 2024). The ubiquity of this spectrolaminar motif points to a central role in cortical function. It has been observed in mouse, marmoset, macaque, and human cortex, and across more than a dozen cortical regions (Mendoza-Halliday et al., 2024).

Spatial computing theory (Fig. 3) proposes that alpha/beta rhythms convey cortical feedback signals generated within higher-level frontoparietal cortex whose spatial patterning reflects top-down information (Fig. 3*A*). They function as temporary inhibitory "stencils" across the surface of cortex. This regulates gamma and spiking in the feedforward and local recurrent circuits that carry sensory-related cognitive contents (Fig. 3*B*) and drive actions. Alpha/beta rhythms thus dampen or suppress gamma and associated spiking in targeted locations, determining where feedforward signals are suppressed. Feedforward signals are then permitted to emerge in the remaining "open" regions, where alpha/beta is weaker. Where spiking is expressed thus depends on the interaction between spatially localized feedforward inputs and more broadly spatially patterned alpha/beta suppression (Fig. 3*C*).

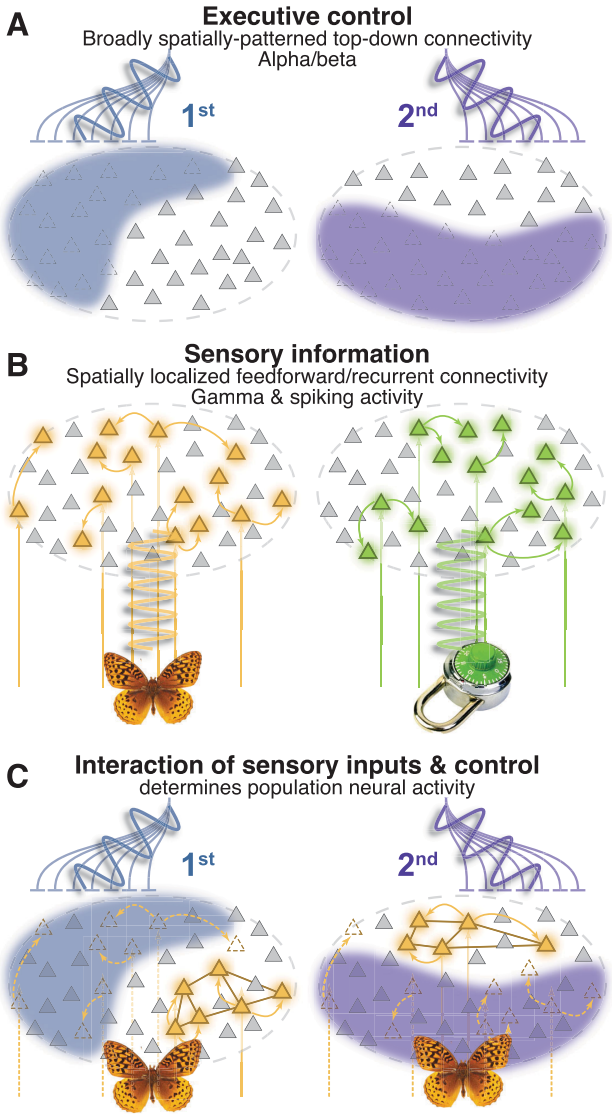

Figure 3. Schematic illustration of spatial computing theory. ***A***, Broad patterns of alpha/beta oscillations reflect information about context, goals, rules, etc. for control. Here, the blue and purple regions represent spatial locations of strong alpha/beta reflecting the contextual sequential order of objects in our example task. ***B***, Detailed feedforward and recurrent connections (columnar in sensory cortex, spatially random in higher cortex) convey the sensory "contents" of cognition via gamma oscillations and spiking. Activation (colored "neurons") induced by two object stimuli is illustrated. ***C***, The interaction of these two signals determines where information is expressed in neural activity. Here, the same object induces two different spatial patterns of population response, depending on the sculpting effects of alpha/beta.

This scheme allows for flexible control over the neural expression of information in spiking, without the control system needing to know the precise neurons and synapses employed for any specific information (Badre et al., 2021; MacDowell et al., 2022; Chandrasekaran et al., 2025). It also allows for compositional reuse of the same control signals for any arbitrary information. Conversely, the same neuronal population can be reused for any arbitrary task demands, simply by changing the control "stencil" imposed on it (Xie et al., 2022; Tafazoli et al., 2026). This flexible push–pull interaction between alpha/beta and gamma/spiking signals provides a mechanism by which control systems can dynamically organize and shape thought and action.

We recently confirmed several key predictions of spatial computing theory by examining prefrontal cortex activity in nonhuman primates during complex cognitive tasks (Chen et al., 2026). Alpha/beta rhythms organized into largely distinct spatial patterns across the cortical surface that reflected learned, internally generated contextual information, such as order within a sequence, the mode of task behavioral report, and learned category structure. These patterns inversely mirrored the spatial distribution of sensory information in spiking activity and predicted behavioral errors through mismatches in contextual representation.

Why the alpha/beta frequency range for top-down control? The spatial scale of influence of waves broadly covaries with temporal frequency (Łęski et al., 2013) and can thus act at different spatial scales (Alexander and Dugué, 2026). Gamma is higher frequency and thus often has a finer spatial scale. This is well suited for forming smaller-scale ensembles that carry detailed feedforward information (Liu and Newsome, 2006; Berens et al., 2008). Lower frequency (delta, 1–4 Hz and theta, 4–8 Hz) oscillations can extend over a scale of several millimeters to centimeters, often close to the scale of a cortical area. These lower frequencies thus may be involved in interarea cortical communication and larger-scale organization of activity (Liebe et al., 2012; Nácher et al., 2013; Womelsdorf and Everling, 2015; Bonnefond et al., 2017; Adams et al., 2019). Theta, for example, often couples with gamma (with multiple gamma cycles within a theta cycle) and is thought to organize gamma over larger spatial scales (Lisman and Jensen, 2013; Spyropoulos et al., 2018; Zhang et al., 2018; Ursino and Pirazzini, 2024; Aguilera et al., 2026). In general, theta seems to act like a master timer for higher frequencies. Attentional focus waxes and wanes at theta frequencies (Fiebelkorn and Kastner, 2019). Theta waves seem to "drag" coupled beta and gamma (in different theta phases) across the surface of the cortex, influencing readout of information from working memory (Han et al., 2026) and long-term memory (Mohan et al., 2024). Frequencies in the lower delta range are more associated with state changes like sleep (Uygun and Basheer, 2022) and loss of consciousness due to anesthesia (Bastos et al., 2021; Redinbaugh et al., 2022; Bardon et al., 2025; Helfrich et al., 2026).

It may be that oscillations in the intermediate alpha/beta range, which extend over a range of a few millimeters, might

be just the right intermediate spatial scale for control of local circuitry (Miller et al., 2024). Further, the timescale of alpha/beta oscillations may be optimal for the temporal accumulation of sensory evidence to generate top-down predictions (Bastos et al., 2012; Samaha et al., 2015).

Explaining Mixed Selectivity with Brain Waves

Spatial computing theory provides a straightforward, concrete way for nonlinear mixed selectivity to emerge from wave-based control acting on a large multifunctional population of neurons. Each goal or context creates a unique, temporary alpha/beta "stencil" that suppresses gamma and spiking in some locations while sparing others (e.g., first versus second sequence order in our example; Fig. 3*A*). Because the neurons have overlapping connectivity, the same neuron may receive many different sensory signals and may lie inside the inhibitory stencil in one context and outside it in another. This context-dependent gating can make a neuron effectively change its selectivity, producing the nonlinear mixed selectivity observed by many studies (Fig. 4*A*). This account predicts that prefrontal cortex neurons should exhibit spatial organization for goals and contexts, as suggested by recent work (Fang et al., 2025).

In this view, there is no requirement for specialized "context neurons" or "object neurons" with fixed tuning predicted by classic connectionist views of cortex. Instead, mixed selectivity arises from the interaction between broadly responsive neurons and mesoscale wave patterns that control when and where spiking is expressed. Synaptic connectivity provides a rich representational space, while alpha/beta versus gamma dynamics determine which subpopulations are active under each condition, enabling flexible computation.

Explaining Subspace Coding with Brain Waves

Mixed selectivity means that single neurons have access to a rich, high-dimensional set of nonlinear features. This information is spread across a population of neurons whose activity is not independent but instead exhibits structured patterns of coordination. As a result, population spiking tends to occupy a lower-dimensional "subspace" or "manifold" within the high-dimensional space defined by all possible population activity patterns (Ebitz and Hayden, 2021). Note that neural coding can be both low-dimensional compared with the high-dimensional code implied by independent activity and high-dimensional compared with the low-dimensional code implied by "pure" unmixed selectivity. This is consistent with broad anatomical gradients in the cortex, which compress signals to create functional equivalences, establishing the anatomical substrate for low dimension representations distributed across a wide population of mixed selectivity neurons (Barrett and Miller, 2026).

Structuring activity via subspace coding is thought to organize information processing, for example, by segregating different computations into independent (orthogonal) subspaces to minimize interference (Fig. 4*B*; Kaufman et al., 2014; Tang et al., 2020; Yoo and Hayden, 2020; Libby and Buschman, 2021; Panichello and Buschman, 2021; Maggi and Humphries, 2022; Xie et al., 2022; Johnston et al., 2023; Weber et al., 2023; Genkin et al., 2025). Spatial computing theory also provides a potential neural mechanism for subspace coding. Alpha/beta control signals segregate spiking activity into partially overlapping active subsets, each of which exhibits structured patterns of correlation (Fig. 4*A*). This is essentially a description of the organization of spiking activity into orthogonal activation subspaces (Fig. 4*B*).

Notably, over short timescales, population spiking traces smooth trajectories through its activity subspace, consistent with the temporal evolution of a dynamical system (Churchland et al., 2012; Vyas et al., 2020; Ebitz and Hayden, 2021). Different sensory stimuli, cognitive operations, and behaviors follow distinct paths. Distractions may briefly nudge trajectories off course, but the population state usually returns smoothly, such that cortical neurons move together according to shared dynamics. As elaborated below (see Traveling Waves

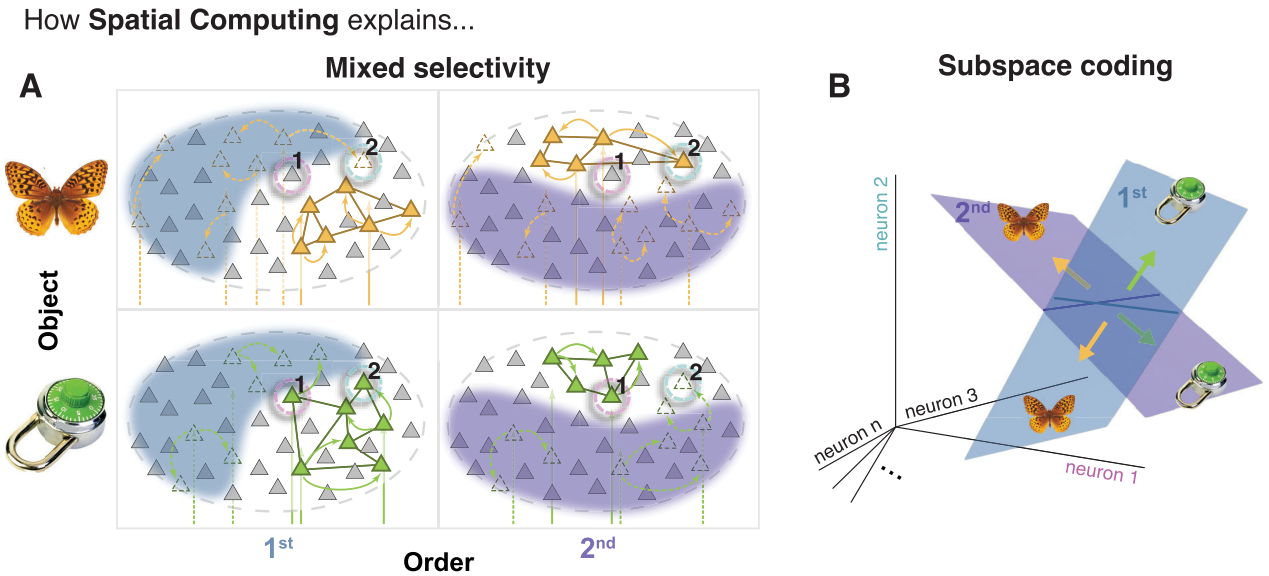

Figure 4. Spatial computing offers mechanistic explanations for mixed selectivity and subspace coding. ***A***, Schematic of spatial computing for two objects (rows) × two sequential contexts (columns). The neuron labeled "1" lies outside of the suppressive alpha/beta "stencil" in both contexts, resulting in "pure" context-independent object selectivity, as in Figure 1*B*. Neuron "2" receives signals for both objects, which are differentially affected in the two contexts, resulting in the context-dependent mixed selectivity in Figure 1*C*. ***B***, Under this scheme, oscillations induce structure in population activity, which is distinct for different contexts. This may also underlie the segregation of different types of information, such as distinct contexts, into orthogonal population activity subspaces.

and Representational Change), these smooth population trajectories are consistent with wave dynamics. As traveling waves sweep continuously over the cortex, they may "pull" population spiking activity along, creating repeatable smooth trajectories (Batabyal et al., 2026).

This framework reconciles two observations: Single neurons are noisy and context dependent, yet populations exhibit structured, low-dimensional behavior. Rather than independent units driven solely by local, specialized connections, cortical populations behave like a coordinated flock governed by shared dynamics. Brain waves offer a tractable mechanism for this coordination. Low-dimensional spiking trajectories in subspace can be seen as the spiking-level expression of broader wave-based control signals that impose global structure on neural activity.

Traveling Waves and Representational Change

Brain waves typically sweep across the cortical surface, tracing complex, but highly organized, spatiotemporal patterns referred to as traveling waves (Ermentrout and Kleinfeld, 2001; Sato et al., 2012; Muller et al., 2018; Bhattacharya et al., 2022; Ye et al., 2026). Traveling waves have been observed at temporal frequencies ranging from the delta to gamma bands (~1–80 Hz). Waves travel with a speed consistent with synaptic propagation and often follow horizontal connections in the superficial layers of cortex (Bringuier et al., 1999; Davis et al., 2021; Ye et al., 2026), but ephaptic effects also contribute to their propagation (Chiang et al., 2019). While the waves may travel across the cortex at slower speeds, their local influence can spread nearly instantaneously via ephaptic influences.

As traveling waves pass across the cortex, they naturally modulate local neuronal excitability. For example, in the visual and frontal cortex, the wave phase at a retinotopic location influences detection of visual targets at that location, as if excitability is sweeping across cortical and visual space like radar (Davis et al., 2020; Han et al., 2026). Traveling waves seem to play a role in a variety of functions, including perception (Muller et al., 2014; Townsend et al., 2017; Davis et al., 2020; Aggarwal et al., 2022), attention (Alamia et al., 2023; Han et al., 2026), memory (Patel et al., 2012; Zhang and Jacobs, 2015; Mohan et al., 2024), sensorimotor, and motor planning/execution (Rubino et al., 2006; Zanos et al., 2015; Best et al., 2016; Balasubramanian et al., 2020). This, importantly, includes plasticity. During sleep, waves that rotate across cortex can coordinate spiking within the narrow time window needed to induce spike timing-dependent plasticity and thus memory consolidation (Muller et al., 2016). Although here we emphasize the role of waves in top-down control, traveling waves are also a prominent feature of stimulus-evoked population responses, including in early visual cortex (Muller et al., 2014; Ye et al., 2026). Thus, both sensory induced and internal dynamics shape wave patterns. Bottom-up inputs trigger waves that shape the spatiotemporal pattern of local spiking, while these same waves are continuously modulated by ongoing activity driven by top-down influences.

We propose that one role of traveling waves, particularly in the alpha/beta band, may be in instantiating state changes in neural coding (McKenna et al., 1994). That is, by moving patterns of inhibition versus excitation across the surface of cortex, alpha/beta waves can alter which subsets of neurons are permitted to spike and their correlational structure. Beta waves are prominent after sensory stimuli and prior to movement (Rubino et al., 2006; Best et al., 2016; Balasubramanian et al., 2020). In the prefrontal cortex, they also increase when sensory information is loaded into working memory (Bhattacharya et al., 2022). These are also times, not coincidentally we suggest, when prefrontal population spiking activity forms new representations (stimulus and movement onset) or transforms representations into different coding subspaces (sensory to memory transformation; Stokes et al., 2013; Parthasarathy et al., 2017).

We propose that alpha/beta waves may constitute a control mechanism that transitions cortical population activity from one subspace to another. This can be thought of as a dynamic, spatiotemporal extension of spatial computing theory, spatial computing in motion. For example, we suggest traveling waves might be involved in transitioning activity between the orthogonal subspaces used to represent sensory stimuli versus their trace in working memory (Fig. 5).

This hypothesis is complementary to the view of static beta oscillations as having a role in maintaining the status quo of stable neural representations (Engel and Fries, 2010). This is usually taken to imply that the inverse situation, representational change, correlates with an overall reduction of beta rhythms. We suggest that this process, when viewed across a larger spatial region, is better characterized as a shift of beta from one spatial pattern to another and that shift is a spatiotemporal traveling wave.

Analog Computation with Waves

Here, we consider another function of traveling waves in not just organizing neural activity, but in performing actual computation to create new brain states.

Analog computing uses continuous physical quantities, such as voltages or mechanical motion, to directly represent input variables and solves mathematical problems through their dynamic interactions over time (Bournez and Pouly, 2018; Hughes et al., 2019; Tzarouchis et al., 2025). Unlike digital systems that rely on binary on/off signals, analog systems combine information continuously. When waves meet, they naturally add together, cancel out, or form new patterns through their superposition and interference. As a simple illustrative example, consider two input variables that are encoded as sinusoidal waves with varying relative phase (Fig. 6). At each point in space, the sum of the two waves yields a unique resultant amplitude that reflects the relative phases of both variables together. The mapping from variables to wave geometry thus specifies the "program" being computed. Their interaction is the computation.

Simple examples like overlapping sine waves show how addition, subtraction, and thus generation of complex activation landscapes can emerge directly from wave physics. But analog computation with waves can do more than add and subtract, they perform complex math. Early analog machines such as mechanical tide predictors and differential analyzers used wheels and disks to even solve complex 18-variable differential equations. Electromagnetic waves can compute using the same

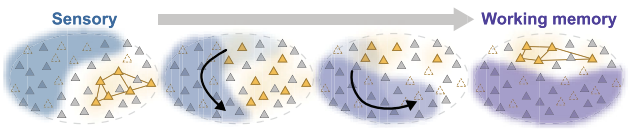

Figure 5. Spatiotemporal computing theory suggests traveling waves instantiate coding dynamics. Depicted is the hypothesized transition between alpha/beta control "stencils" for encoding a sensory object versus storing the same object in working memory and the resulting changes in the neural code for a given object. We propose this shift may be driven by alpha/beta traveling waves transitioning from one static pattern to the other.

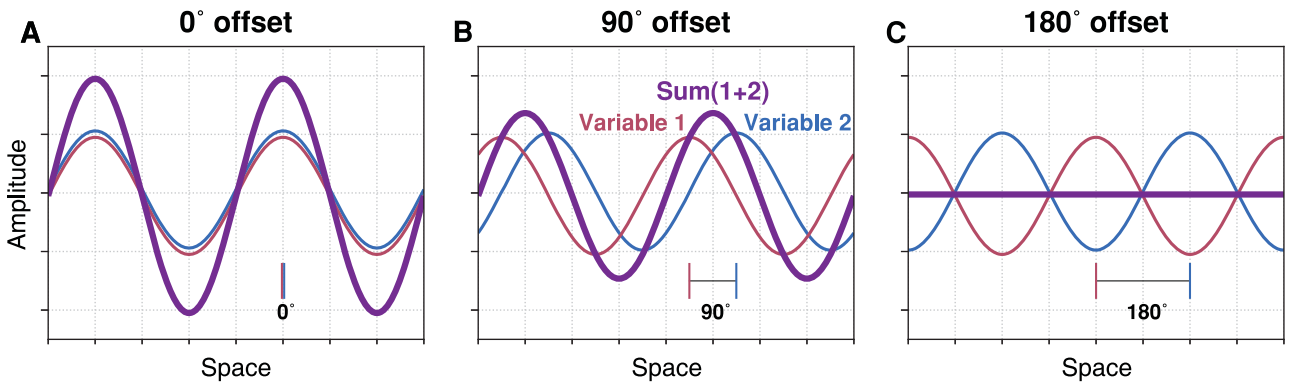

Figure 6. Simple illustration of analog computing with two sine waves. Two input variables are encoded as sinusoidal waves (red and blue lines) with varying relative phase: 0° (***A***), 90° (***B***), and 180° (***C***). The sum of the two sine waves (thick purple lines) depends on their relative phase, producing different resultant values at each point. This simple example illustrates how analog computation can compute interactions between continuously encoded variables in parallel.

principles (Tzarouchis et al., 2025), including in neural networks (Muller et al., 2018; Hughes et al., 2019; Singer and Effenberger, 2025).

Importantly, analog computing is efficient. Analog computing is inherently parallel. In an analog system, the physical medium itself evolves all at once. How the waves interact (e.g., their geometry, frequencies, and phase relationships) model the equation. The variables are all encoded as a continuous physical quantity in different phases of the wave. Because the wave interactions occur everywhere simultaneously, the computation is inherently parallel. An analog system does not loop through variables but settles into a solution as a whole. Parallel computing is more computationally and energy efficient than digital computing, which is inherently sequential and solves problems one step at a time. The fact that analog neuromorphic hardware achieves order-of-magnitude energy savings over digital systems supports the plausibility of wave-based computation contributing to the brain's energy efficiency (Ambrogio et al., 2023; Ye et al., 2025). Human brains perform vast amounts of computation while consuming only ~20 W, roughly the power of a dim light bulb (Kováč, 2010). In contrast, modern digital AI systems require enormous energy.

In the cortex, oscillating electric fields provide a similar medium. Waves of different frequencies move in different directions and at different speeds across the cortical sheet. As they overlap, their interactions can result in temporary excitation of some neuron groups and suppression of others. Waves can thus essentially act as dynamic spatiotemporal basis functions that can synthesize any spatial landscape of local electric fields. This might be employed to route and shape neural activity. Slower rhythms can also modulate faster ones, allowing multiple interacting streams of information at once (see below).

As a simple concrete example, consider an extension to the previous task that requires combining control signals reflecting two distinct types of task context (Fig. 7*A*): (1) the sequential order of objects to be remembered (first vs second) and (2) the mode of their eventual behavioral report (sequence matching or cued recall of the sequence). Thus, subjects are required to maintain two independent types of contexts during task trials, both of which have been shown to robustly modulate the encoding of objects into spiking activity (Warden and Miller, 2010; Rigotti et al., 2013). We propose this task may be solved by generating two sets of waves to represent these two input variables. One signals whether the item is first or second in the sequence (Fig. 7*B*, blue vs purple). The other signals the response mode (matching vs cued recall; Fig. 7*B*, brown vs lavender). When these two control patterns add together, they produce four distinct space-time activation patterns, one for each combination (first/match, second/match, first/recall, second/recall). The key idea is that the summation of different wave patterns would essentially compute an intersection of constraints, routing neural activation for the same sensory input into different subpopulations purely by changing these control waves, without altering the underlying synaptic wiring.

This idea is not restricted to only simple combinations of control signals reflecting categorical variables. Waves might also be used to represent continuous physical quantities (e.g. speed, distance, spatial relationships) or mental constructs (e.g. value, emotion, social relationships). Their interactions might be used for neural computations underlying such complex cognitive functions as spatial causal reasoning or evaluating interpersonal relationships. Similar analog computations might also occur between the radially spreading waves generated in the sensory cortex by sensory stimulation (Nauhaus et al., 2009; Sato et al., 2012; Zanos et al., 2015; Muller et al., 2014, 2018). For example, the intersection of waves induced by an object's contours in the visual cortex might compute a "grassfire transform" (Blum, 1973) that can identify the medial axes of an object (Kovács and Julesz, 1994).

In this view, synapses define the network's structure, but moment to moment computation can be carried out by evolving wave patterns rather than by spikes alone. The brain could rely heavily on efficient, parallel, wave-based computation layered on top of synaptic mechanisms that store long-term information and perform some level of computation. Wave patterns are patterns of different levels of neural excitation. Analog wave dynamics can thus create new patterns of excitation in a computationally principled fashion. This could be key to the mesoscale organization needed for cognition and the unified neural representations needed for consciousness.

Altered Brain Waves and Unconsciousness

General anesthesia further supports a central role for brain waves in cognition and consciousness. Anesthetics do not simply shut off the cortex. Instead, they profoundly alter wave dynamics (Redinbaugh et al., 2020; Bastos et al., 2021).

Despite acting on different molecular targets, different anesthetic agents, such as propofol (GABAergic), ketamine (NMDAergic), and dexmedetomidine (alpha-2 adrenergic), all

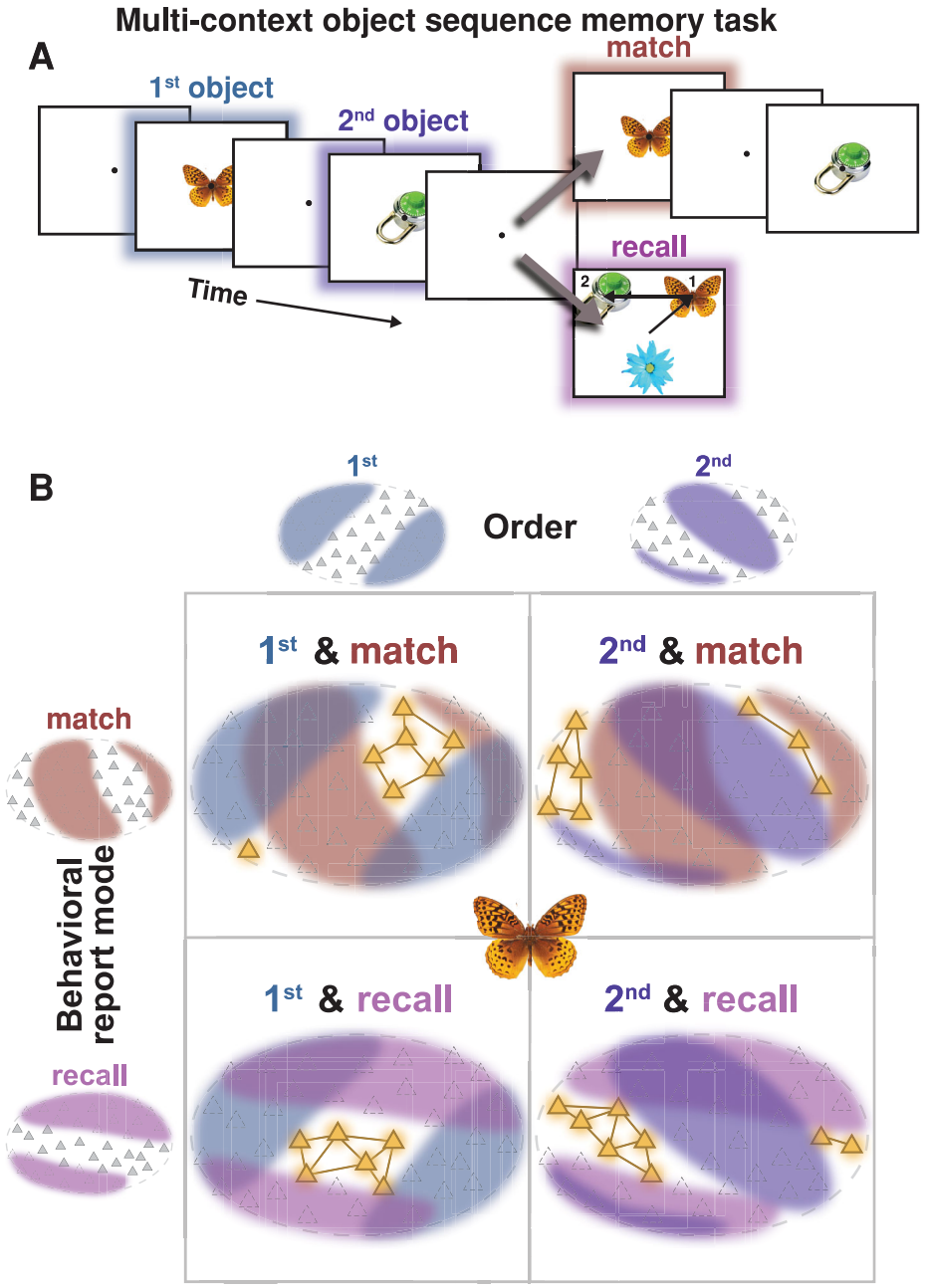

Figure 7. Schematic illustration of analog computing in a cognitive task. ***A***, Extension of example task requiring combination of two distinct types of contextual signals: sequential order (first vs second) and mode of behavioral report (cued recall vs matching). ***B***, Each context is proposed to instantiate a specific spatiotemporal wave as a control signal (grid margins). The summation of these waves (grid rows/columns) constrains neural activity to a specific pattern unique to each combination of contexts.

converge on similar large-scale electrical effects in the cortex (Bardon et al., 2025; Eisen et al., 2026). The mixed, low-amplitude higher-frequency activity of wakefulness transitions to high-power slow delta (~1–4 Hz) oscillations across frontal, parietal, and sensory regions. These slow waves are often temporally misaligned, disrupting coordinated communication. The result may be a destabilized, fragmented cortex.

The main point here is that different pharmacological routes of different drugs nonetheless converge on the same systems-level outcome: slow, desynchronized cortical waves. This suggests that consciousness depends less on specific receptors or cell types and more on the integrity of large-scale wave organization. In our framework, general anesthesia disrupts the organized wave patterns that normally coordinate cortical computation, leaving synaptic circuitry largely intact but unable to express coherent, large-scale brain states.

A Hybrid Synapse/Wave Theory for Cognition and Consciousness

In our framework, synaptic transmission and electric fields are components of a single, bidirectionally coupled dynamical system whose functional impact depends on scale. At the mesoscale, their interaction generates brain waves, spatiotemporal patterns of neural excitation, that interact according to principles of analog computation. Through spatial computing, these wave

patterns organize cortical activity, shaping spiking, modifying synaptic strengths, and even driving structural changes at the microscopic level.

The idea is that synapses and brain waves have complementary roles (Fig. 8). Synaptic connections, shaped by experience, store long-term information and define potential activity patterns. When neurons fire spikes, they generate electric fields that influence nearby neurons through ephaptic coupling, i.e., electrical interaction without direct synaptic contact. This creates a feedback loop: synapses shape spiking, spiking contributes to brain waves, and waves shape spiking (Singer, 2021). Spikes and gamma, by virtue of their higher frequency, represent higher-resolution (smaller-spatial scale) sensory and motor information. Lower-frequency rhythms such as alpha/beta and theta instead exert larger-scale control, organizing where sensory and motor spiking/gamma occur according to top-down schemas, goals, plans, and memories.

Experience "bakes" information about the world into synaptic wiring (Barrett and Miller, 2026). When neurons spike in response to sensory input or internally generated activity, they interact with ongoing wave dynamics, producing brain states that reflect both current inputs and stored knowledge encoded in synaptic connectivity. This stored information is the source of top-down signals. It is initially expressed through spiking activity and then propagated and organized by wave patterns that structure cortical excitation. Through principles of analog computation, wave interactions combine and transform wave patterns to generate new brain states, new goals, plans, and insights, which can in turn be written back into synaptic weights via spike-dependent plasticity.

Moment-to-moment coordination underlying cognition and consciousness is dominated by brain waves rather than rapid synaptic changes. Different wave frequencies organize activity across scales: slower waves gate spiking across regions, effectively routing information. Synapses store representations, while wave dynamics determine which representations are active at any given time. Because these dynamics are shaped by synaptically stored knowledge, brain waves carry top-down information that filters and structures perception and thought according to internal models. By dynamically linking distributed activity, they help solve the binding problem (Hunt and Schooler, 2019). Through their interactions, they generate new brain states that can update those models via spike-dependent plasticity.

Comparison to Other Theories of Cognitive Control and Consciousness

Our analog theory shares key themes with major theories but diverges in its mechanism.

It connects with neural theories of cognitive ("executive") control that posits the influence that top-down signals from the frontoparietal cortex and anterior cingulate exert on sensory cortex (Desimone and Duncan, 1995; Miller and Cohen, 2001; Botvinick et al., 2004; Banich, 2009; Rossi et al., 2009; Funahashi and Andreau, 2013). The influences have been

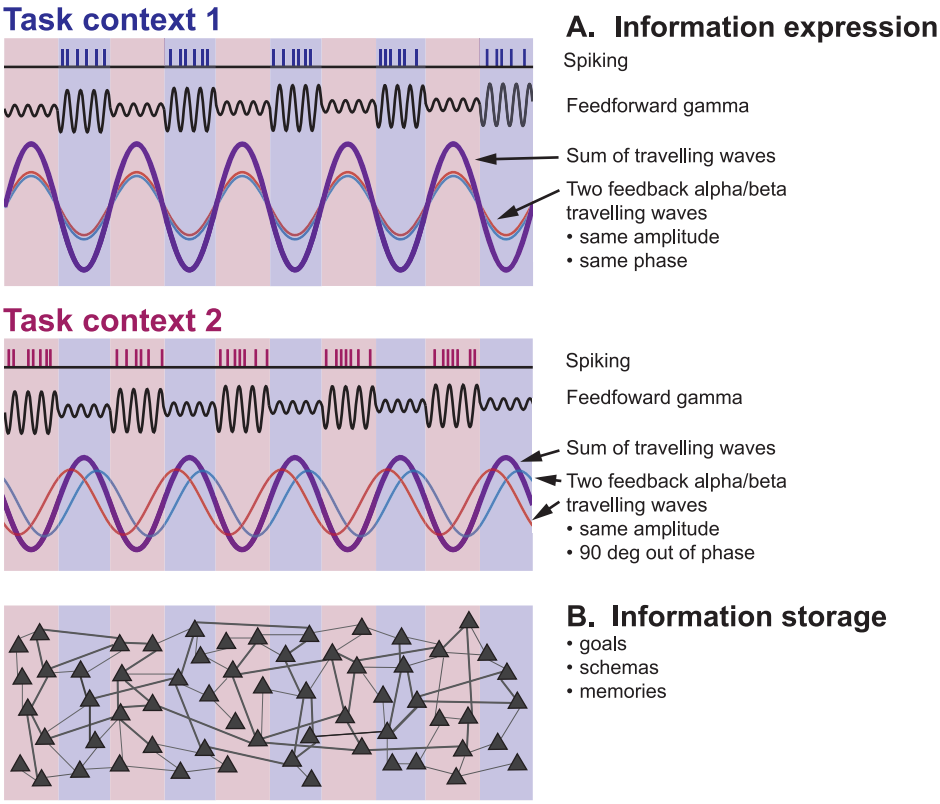

Figure 8. A hybrid system of synapses, spikes, and waves. Schematic illustrating our proposed framework. Synapses define a network's structure and thus its set of possible activity patterns. This structure stores information reflecting environmental regularities and memories, acquired through development and experience (***B***). Different contexts and goals instantiate distinct patterns of traveling waves across cortex, which interact via wave summation. The resulting pattern, combined with feedforward/recurrent drive conveyed via synapses, determines moment-to-moment what information is actually expressed in high-frequency gamma and spiking activity and thus communicated to downstream regions (***A***). The pink and light-blue shaded columns going through all panels can represent either time and/or cortical space.

thought to involve excitatory influences transmitted via spiking and synaptic connectivity that selects neural representations via winner-take-all dynamics (Desimone and Duncan, 1995; Miller and Cohen, 2001). In this new framework, we instead place emphasis on top-down influences exerted by wave dynamics. In this way, our theory grounds the higher-order, top-down architecture of cognition in a specific physical mechanism, analog wave computation and the organizing influence of wave dynamics across the cortex.

Like the Global Workspace (GW) and Global Neuronal Workspace Theory (GNWT) of consciousness, our theory holds that a distributed cortical network supports flexible, global integration (Baars, 1997; Dehaene et al., 1998; Mashour et al., 2020). We, however, emphasize how this integration occurs via dynamic field interactions rather than broadcasting of information (GW) and spikes alone (GWNT). Similarly, our theory resembles Integrated Information Theory (IIT) in treating organization and self-influence as essential to consciousness (Tononi et al., 2016). However, we locate its mechanisms not in a "hot zone," but in the large-scale wave dynamics that organize cortical computation.

Our theory aligns with Higher-Order Theories (HOTs) of consciousness that stress top-down model or schema influences in which a brain state becomes conscious when it is the target of a higher-order representation, an internal model likely formed in frontal cortex (Rosenthal, 2005; Lau and Rosenthal, 2011; Michel and Morales, 2020; Graziano, 2022; LeDoux, 2023; Riddle and Schooler, 2024). As such, it also aligns with predictive coding theories of cortical function and perceptual awareness (Friston and Kiebel, 2009; Bastos et al., 2012; Seth et al., 2012; Bastos et al., 2020). We conceptualize consciousness as emerging naturally when higher-order predictive models, implemented through oscillatory wave patterns, impose organized structure on lower-level cortical processes. This is similar to the nested observer model in which oscillatory dynamics impose a hierarchy of consciousness (Riddle and Schooler, 2024). Rather than a separate observer system making representations "conscious," we emphasize the very act of top-down organization in generating conscious integration.

Conclusion

Our theory shares with others the general idea that cognition and consciousness involve mesoscale coordination and thus top-down control across the brain. But instead of describing function mainly in terms of information exchange between discrete neurons, circuits, and regions, we emphasize brain-wide wave dynamics as an organizing principle.

In this view, rhythmic electric fields help unify and structure cortical activity, allowing analog computation to take place across space and time. These wave interactions not only bind distributed neural populations into coherent states but also carry out computations that support flexible thought and control. Consciousness, then, emerges when these dynamic wave patterns bring the cortex into an organized, globally integrated state, one that naturally links and influences widespread activity.

This theory is not only conceptually plausible but biologically feasible. Cortical circuits naturally generate oscillatory dynamics and propagate waves through recurrent connectivity and horizontal cortical connections across multiple scales. The dynamics we emphasize thus require no special machinery. These waves are energetically efficient, leveraging continuous field interactions rather than metabolically costly, all-or-none spiking at every step. In this sense, the brain exploits its own physics: Electric field dynamics offer a low-overhead substrate for organizing and coordinating information across cortical networks. Given strong evolutionary pressure to maximize computation per unit energy, it would be surprising if evolution did not exploit such a built-in analog computing substrate.

References

Abbass M, Corrigan B, Johnston R, Gulli R, Sachs A, Lau JC, Martinez-Trujillo J (2025) Prefrontal cortex neuronal ensembles dynamically encode task features during associative memory and virtual navigation. Cell Rep 44:115124.

Adams NE, Teige C, Mollo G, Karapanagiotidis T, Cornelissen PL, Smallwood J, Traub RD, Jefferies E, Whittington MA (2019) Theta/delta coupling across cortical laminae contributes to semantic cognition. J Neurophysiol 121:1150–1161.

Aggarwal A, Brennan C, Luo J, Chung H, Contreras D, Kelz MB, Proekt A (2022) Visual evoked feedforward–feedback traveling waves organize neural activity across the cortical hierarchy in mice. Nat Commun 13:4754.

Aguilera A, Espinosa N, Caneo M, Lazcano G, Lara-Vasquez A, Fuentealba P (2026) Cross-frequency coordination in a hippocampo–cortical circuit during probabilistic reversal learning. Commun Biol.

Akam T, Kullmann DM (2014) Oscillatory multiplexing of population codes for selective communication in the mammalian brain. Nat Rev Neurosci 15:111–122.

Alamia A, Terral L, D'ambra MR, VanRullen R (2023) Distinct roles of forward and backward alpha-band waves in spatial visual attention. Elife 12:e85035.

Alexander DM, Dugué L (2026) The dominance of large-scale phase dynamics in human cortex, from delta to gamma. Elife 13:RP100674.

Ambrogio S, et al. (2023) An analog-AI chip for energy-efficient speech recognition and transcription. Nature 620:768–775.

Anastassiou CA, Perin R, Markram H, Koch C (2011) Ephaptic coupling of cortical neurons. Nat Neurosci 14:217–223.

Anastassiou CA, Koch C (2015) Ephaptic coupling to endogenous electric field activity: why bother? Curr Opin Neurobiol 31:95–103.

Asaad WF, Rainer G, Miller EK (2000) Task-specific neural activity in the primate prefrontal cortex. J Neurophysiol 84:451–459.

Baars BJ (1997) In the theatre of consciousness. Global workspace theory, a rigorous scientific theory of consciousness. J Conscious Stud 4:292–309.

Badre D, Bhandari A, Keglovits H, Kikumoto A (2021) The dimensionality of neural representations for control. Comput Cogn Neurosci 38:20–28.

Baker JMM, Cariani P (2025) Time-domain brain: temporal mechanisms for brain functions using time-delay nets, holographic processes, radio communications, and emergent oscillatory sequences. Front Comput Neurosci 19:1540532.

Balasubramanian K, Papadourakis V, Liang W, Takahashi K, Best MD, Suminski AJ, Hatsopoulos NG (2020) Propagating motor cortical dynamics facilitate movement initiation. Neuron 106:526–536.e4.

Banich MT (2009) Executive function: the search for an integrated account. Curr Dir Psychol Sci 18:89–94.

Bardon AG, Ballesteros JJ, Brincat SL, Roy JE, Mahnke MK, Ishizawa Y, Brown EN, Miller EK (2025) Convergent effects of different anesthetics on changes in phase alignment of cortical oscillations. Cell Rep 44:115685.

Barone J, Rossiter HE (2021) Understanding the role of sensorimotor beta oscillations. Front Syst Neurosci 15:655886.

Barrett LF, Miller EK (2026) Categorization is "baked" into the brain. Nat Rev Neurosci 27:435–456.

Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ (2012) Canonical microcircuits for predictive coding. Neuron 76:695–711.

Bastos AM, Vezoli J, Bosman CA, Schoffelen J-M, Oostenveld R, Dowdall JR, De Weerd P, Kennedy H, Fries P (2015) Visual areas exert feedforward and feedback influences through distinct frequency channels. Neuron 85:390–401.

Bastos AM, Lundqvist M, Waite AS, Kopell N, Miller EK (2020) Layer and rhythm specificity for predictive routing. Proc Natl Acad Sci U S A 117:31459–31469.

Bastos AM, et al. (2021) Neural effects of propofol-induced unconsciousness and its reversal using thalamic stimulation. Elife 10:e60824.

Batabyal T, Brincat SL, Donoghue JA, Lundqvist M, Mahnke MK, Miller EK (2026) State–space trajectories and traveling waves following distraction. J Cogn Neurosci 38:695–715.

Berens P, Keliris GA, Ecker AS, Logothetis NK, Tolias AS (2008) Feature selectivity of the gamma-band of the local field potential in primate primary visual cortex. Front Neurosci 2:199–207.
Best MD, Suminski AJ, Takahashi K, Brown KA, Hatsopoulos NG (2016) Spatio-temporal patterning in primary motor cortex at movement onset. Cereb Cortex 27:1491–1500.
Bhattacharya S, Brincat SL, Lundqvist M, Miller EK (2022) Traveling waves in the prefrontal cortex during working memory. PLoS Comput Biol 18: e1009827.
Blum H (1973) Biological shape and visual science (part I). J Theor Biol 38: 205–287.
Bonaiuto JJ, Meyer SS, Little S, Rossiter H, Callaghan MF, Dick F, Barnes GR, Bestmann S (2018) Lamina-specific cortical dynamics in human visual and sensorimotor cortices. Elife 7:e33977.
Bonnefond M, Kastner S, Jensen O (2017) Communication between brain areas based on nested oscillations. eNeuro 4:ENEURO.0153-16.2017.
Bosman CA, Schoffelen J-M, Brunet N, Oostenveld R, Bastos AM, Womelsdorf T, Rubehn B, Stieglitz T, De Weerd P, Fries P (2012) Attentional stimulus selection through selective synchronization between monkey visual areas. Neuron 75:875–888.
Botvinick M, Braver T (2015) Motivation and cognitive control: from behavior to neural mechanism. Annu Rev Psychol 66:83–113.
Botvinick MM, Cohen JD, Carter CS (2004) Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn Sci 8:539–546.
Bournez O, Pouly A (2018) A Survey on Analog Models of Computation.
Brincat SL, Donoghue JA, Mahnke MK, Kornblith S, Lundqvist M, Miller EK (2021) Interhemispheric transfer of working memories. Neuron 109: 1055–1066.e4.
Bringuier V, Chavane F, Glaeser L, Frégnac Y (1999) Horizontal propagation of visual activity in the synaptic integration field of area 17 neurons. Science 283:695–699.
Buschman TJ, Miller EK (2007) Top-Down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science 315: 1860–1862.
Buzsáki G (2006) *Rhythms of the brain*. Oxford: Oxford University Press.
Buzsáki G, Draguhn A (2004) Neuronal oscillations in cortical networks. Science 304:1926–1929.
Buzsáki G, Wang X-J (2012) Mechanisms of gamma oscillations. Annu Rev Neurosci 35:203–225.
Chandrasekaran C, Gupta D, Javadzadeh M, Wang T, Vivar-Lazo M, Engel T, Cisek P, Fetsch CR (2025) No central executive? Decision formation through multi-area population dynamics. J Neurosci 45: e1633252025.
Chen Z, Brincat SL, Lundqvist M, Loonis RF, Warden MR, Miller EK (2026) Oscillatory control of cortical space as a computational dimension. Curr Biol 36:402–414.e5.
Chiang C-C, Shivacharan RS, Wei X, Gonzalez-Reyes LE, Durand DM (2019) Slow periodic activity in the longitudinal hippocampal slice can self-propagate non-synaptically by a mechanism consistent with ephaptic coupling. J Physiol 597:249–269.
Churchland MM, Cunningham JP, Kaufman MT, Foster JD, Nuyujukian P, Ryu SI, Shenoy KV (2012) Neural population dynamics during reaching. Nature 487:51–56.
Collette F, Hogge M, Salmon E, Van der Linden M (2006) Exploration of the neural substrates of executive functioning by functional neuroimaging. Neuroscience 139:209–221.
Cromer JA, Roy JE, Miller EK (2010) Representation of multiple, independent categories in the primate prefrontal cortex. Neuron 66:796–807.
Cunha GM, Corso G, Sousa MPB, Lima GZ (2024) Can ephapticity contribute to brain complexity? PLoS One 19:e0310640.
Dang W, Li S, Pu S, Qi X-L, Constantinidis C (2022) More prominent nonlinear mixed selectivity in the dorsolateral prefrontal than posterior parietal cortex. eNeuro 9:ENEURO.0517-21.2022.
Davis ZW, Muller L, Martinez-Trujillo J, Sejnowski T, Reynolds JH (2020) Spontaneous travelling cortical waves gate perception in behaving primates. Nature 587:432–436.
Davis ZW, Benigno GB, Fletterman C, Desbordes T, Steward C, Sejnowski TJ, Reynolds JH, Muller L (2021) Spontaneous traveling waves naturally emerge from horizontal fiber time delays and travel through locally asynchronous-irregular states. Nat Commun 12:6057.
Degl'Innocenti E, Dell'Anno MT (2023) Human and mouse cortical astrocytes: a comparative view from development to morphological and functional characterization. Front Neuroanat 17:1130729.
de Graaf TA, Gross J, Paterson G, Rusch T, Sack AT, Thut G (2013) Alpha-band rhythms in visual task performance: phase-locking by rhythmic sensory stimulation. PLoS One 8:e60035.
Dehaene S, Kerszberg M, Changeux J-P (1998) A neuronal model of a global workspace in effortful cognitive tasks. Proc Natl Acad Sci U S A 95:14529–14534.
Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193–222.
D'Esposito M, Grossman M (1996) The physiological basis of executive function and working memory. Neuroscientist 2:345–352.
Diamond A (2013) Executive functions. Annu Rev Psychol 64:135–168.
Drummond GT, et al. (2024) Cortical norepinephrine-astrocyte signaling critically mediates learned behavior.
Duncan J, Assem M, Shashidhara S (2020) Integrated intelligence from distributed brain activity. Trends Cogn Sci 24:838–852.
Duncan J, Miller EK (2002) *Cognitive focus through adaptive neural coding, principles of frontal lobe function*. Oxford: Oxford University Press.
Duncan J, Miller EK (2013) *Adaptive neural coding in frontal and parietal cortex, Second. Ed. principles of frontal lobe function*. Oxford: OUP.
Ebitz RB, Hayden BY (2021) The population doctrine in cognitive neuroscience. Neuron 109:3055–3068.
Ede F, Nobre AC (2023) Turning attention inside out: how working memory serves behavior. Annu Rev Psychol 74:137–165.
Eisen AJ, et al. (2026) Similar destabilization of neural dynamics under different general anesthetics. Cell Rep 45:117048.
Engel AK, Fries P (2010) Beta-band oscillations — signalling the status quo? Curr Opin Neurobiol 20:156–165.
Ermentrout GB, Kleinfeld D (2001) Traveling electrical waves in cortex. Neuron 29:33–44.
Fang W, Jiang X, Chen J, Zhang C, Wang L (2025) Oscillatory control over representational geometry of sequence working memory in macaque frontal cortex. Curr Biol 35:1495–1507.e5.
Fernández-Ruiz A, Herreras O (2013) Identifying the synaptic origin of ongoing neuronal oscillations through spatial discrimination of electric fields. Front Comput Neurosci 7:5.
Fiebelkorn IC, Kastner S (2019) A rhythmic theory of attention. Trends Cogn Sci 23:87–101.
Francis JT, Gluckman BJ, Schiff SJ (2003) Sensitivity of neurons to weak electric fields. J Neurosci 23:7255–7261.
Freedman DJ, Riesenhuber M, Poggio T, Miller EK (2001) Categorical representation of visual stimuli in the primate prefrontal cortex. Science 291: 312–316.
Fries P (2015) Rhythms for cognition: communication through coherence. Neuron 88:220–235.
Friston K, Kiebel S (2009) Predictive coding under the free-energy principle. Philos Trans R Soc B Biol Sci 364:1211–1221.
Fröhlich F, McCormick DA (2010) Endogenous electric fields may guide neocortical network activity. Neuron 67:129–143.
Funahashi S, Andreau JM (2013) Prefrontal cortex and neural mechanisms of executive function. J Physiol Paris 107:471–482.
Fusi S, Miller EK, Rigotti M (2016) Why neurons mix: high dimensionality for higher cognition. Curr Opin Neurobiol 37:66–74.
Genkin M, Shenoy KV, Chandrasekaran C, Engel TA (2025) The dynamics and geometry of choice in the premotor cortex. Nature 645:168–176.
Gilbertson T, Lalo E, Doyle L, Di Lazzaro V, Cioni B, Brown P (2005) Existing motor state is favored at the expense of new movement during 13-35 Hz oscillatory synchrony in the human corticospinal system. J Neurosci 25: 7771–7779.
Goldwyn JH, Rinzel J (2016) Neuronal coupling by endogenous electric fields: cable theory and applications to coincidence detector neurons in the auditory brain stem. J Neurophysiol 115:2033–2051.
Graziano MSA (2022) A conceptual framework for consciousness. Proc Natl Acad Sci U S A 119:e2116933119.
Gregoriou GG, Gotts SJ, Zhou H, Desimone R (2009) High-frequency, long-range coupling between prefrontal and visual cortex during attention. Science 324:1207–1210.
Griffiths BJ, Mayhew SD, Mullinger KJ, Jorge J, Charest I, Wimber M, Hanslmayr S (2019) Alpha/beta power decreases track the fidelity of stimulus-specific information. Elife 8:e49562.
Grunfeld I, Likhtik E (2018) Mixed selectivity encoding and action selection in the prefrontal cortex during threat assessment. Curr Opin Neurobiol 49:108–115.
Han F, Caporale N, Dan Y (2008) Reverberation of recent visual experience in spontaneous cortical waves. Neuron 60:321–327.

Han H-B, Brincat SL, Buschman TJ, Miller EK (2026) Working memory readout varies with frontal theta rhythms. Neuron 114:159–166.e2.
Han K-S, Guo C, Chen CH, Witter L, Osorno T, Regehr WG (2018) Ephaptic coupling promotes synchronous firing of cerebellar Purkinje cells. Neuron 100:564–578.e3.
Headley DB, Latimer B, Aberbach A, Nair SS (2026) Spatially targeted inhibitory rhythms differentially affect neuronal integration. Elife 13:RP95562.
Helfrich JD, Szaflarski J, Nævra MCJ, Romunstad L, Walker MP, Mander BA, Knight RT, Larsson PG, Helfrich RF (2026) Spectral mapping reveals a resemblance of the anesthetic brain state to both sleep and coma. Proc Natl Acad Sci U S A 123:e2514098123.
Hughes TW, Williamson IAD, Minkov M, Fan S (2019) Wave physics as an analog recurrent neural network. Sci Adv 5:eaay6946.
Hunt T, MacIver MB (2026) A historical review of ephaptic field research: from early foundations through contemporary renaissance. Front Hum Neurosci 20:1747899.
Hunt T, Schooler JW (2019) The easy part of the hard problem: a resonance theory of consciousness. Front Hum Neurosci 13:378.
Hutcheon B, Yarom Y (2000) Resonance, oscillation and the intrinsic frequency preferences of neurons. Trends Neurosci 23:216–222.
Jensen O, Bonnefond M (2026) The alpha rhythm: from physiology to behaviour. Physiol Rev 106:1123–1159.
Jæger KH, Tveito A (2026) Extracellular stimulation and ephaptic coupling of neurons in a fully coupled finite element-based extracellular—membrane—intracellular (EMI) model. Front Comput Neurosci 20:1755548.
Jia X, Tanabe S, Kohn A (2013) Gamma and the coordination of spiking activity in early visual cortex. Neuron 77:762–774.
Johnston WJ, Palmer SE, Freedman DJ (2020) Nonlinear mixed selectivity supports reliable neural computation. PLoS Comput Biol 16: e1007544.
Johnston WJ, Fine JM, Yoo SBM, Ebitz RB, Hayden BY (2023) Subspace orthogonalization as a mechanism for binding values to space.
Kaufman MT, Churchland MM, Ryu SI, Shenoy KV (2014) Cortical activity in the null space: permitting preparation without movement. Nat Neurosci 17:440–448.
Kaufman MT, Benna MK, Rigotti M, Stefanini F, Fusi S, Churchland AK (2022) The implications of categorical and category-free mixed selectivity on representational geometries. Curr Opin Neurobiol 77:102644.
Khanna P, Carmena JM (2017) Beta band oscillations in motor cortex reflect neural population signals that delay movement onset. Elife 6: e24573.
Kim T, Kao M-T, Hasselbrink EF, Meyhöfer E (2007) Active alignment of microtubules with electric fields. Nano Lett 7:211–217.
Kira S, Safaai H, Morcos AS, Panzeri S, Harvey CD (2023) A distributed and efficient population code of mixed selectivity neurons for flexible navigation decisions. Nat Commun 14:2121.
Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition-timing hypothesis. Brain Res Rev 53:63–88.
Klimesch W (2012) Alpha-band oscillations, attention, and controlled access to stored information. Trends Cogn Sci 16:606–617.
Kováč L (2010) The 20W sleep-walkers. EMBO Rep 11:2–2.
Kovács I, Julesz B (1994) Perceptual sensitivity maps within globally defined visual shapes. Nature 370:644–646.
Ladenbauer J, Obermayer K (2019) Weak electric fields promote resonance in neuronal spiking activity: analytical results from two-compartment cell and network models. PLoS Comput Biol 15:e1006974.
Lankarany M, Al-Basha D, Ratté S, Prescott SA (2019) Differentially synchronized spiking enables multiplexed neural coding. Proc Natl Acad Sci U S A 116:10097–10102.
Lau H, Rosenthal D (2011) Empirical support for higher-order theories of conscious awareness. Trends Cogn Sci 15:365–373.
Laudanski J, Torben-Nielsen B, Segev I, Shamma S (2014) Spatially distributed dendritic resonance selectively filters synaptic input. PLoS Comput Biol 10:e1003775.
LeDoux J (2023) The deep history of ourselves: the four-billion-year story of how we got conscious brains. Philos Psychol 36:704–715.
Lee HS, et al. (2014) Astrocytes contribute to gamma oscillations and recognition memory. Proc Natl Acad Sci U S A 111:E3343–E3352.
Łęski S, Lindén H, Tetzlaff T, Pettersen KH, Einevoll GT (2013) Frequency dependence of signal power and spatial reach of the local field potential. PLoS Comput Biol 9:e1003137.
Levenstein D, Okun M (2023) Logarithmically scaled, gamma distributed neuronal spiking. J Physiol 601:3055–3069.
Libby A, Buschman TJ (2021) Rotational dynamics reduce interference between sensory and memory representations. Nat Neurosci 24:715–726.
Liebe S, Hoerzer GM, Logothetis NK, Rainer G (2012) Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. Nat Neurosci 15:456–462.
Lisman JE, Jensen O (2013) The theta-gamma neural code. Neuron 77:1002–1016.
Liu J, Newsome WT (2006) Local field potential in cortical area MT: stimulus tuning and behavioral correlations. J Neurosci 26:7779–7790.
Lundqvist M, Rose J, Herman P, Brincat SL, Buschman TJ, Miller EK (2016) Gamma and beta bursts underlie working memory. Neuron 90:152–164.
Lundqvist M, Herman P, Warden MR, Brincat SL, Miller EK (2018) Gamma and beta bursts during working memory readout suggest roles in its volitional control. Nat Commun 9:394.
Lundqvist M, Bastos AM, Miller EK (2020) Preservation and changes in oscillatory dynamics across the cortical hierarchy. J Cogn Neurosci 32:2024–2035.
Lundqvist M, Brincat SL, Rose J, Warden MR, Buschman TJ, Miller EK, Herman P (2023) Working memory control dynamics follow principles of spatial computing. Nat Commun 14:1429.
MacDowell CJ, Tafazoli S, Buschman TJ (2022) A Goldilocks theory of cognitive control: balancing precision and efficiency with low-dimensional control states. Curr Opin Neurobiol 76:102606.
Maggi S, Humphries MD (2022) Activity subspaces in medial prefrontal cortex distinguish states of the world. J Neurosci 42:4131–4146.
Maier A, Adams GK, Aura C, Leopold DA (2010) Distinct superficial and deep laminar domains of activity in the visual cortex during rest and stimulation. Front Syst Neurosci 4:31.
Mashour GA, Roelfsema P, Changeux J-P, Dehaene S (2020) Conscious processing and the global neuronal workspace hypothesis. Neuron 105:776–798.
McKenna TM, McMullen TA, Shlesinger MF (1994) The brain as a dynamic physical system. Neuroscience 60:587–605.
Mendoza-Halliday D, et al. (2024) A ubiquitous spectrolaminar motif of local field potential power across the primate cortex. Nat Neurosci 27:547–560.
Michalareas G, Vezoli J, van Pelt S, Schoffelen J-M, Kennedy H, Fries P (2016) Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. Neuron 89:384–397.
Michel M, Morales J (2020) Minority reports: consciousness and the prefrontal cortex. Mind Lang 35:493–513.
Miller EK, Brincat SL, Roy JE (2024) Cognition is an emergent property. Curr Opin Behav Sci 57:101388.
Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167–202.
Mohan UR, Zhang H, Ermentrout B, Jacobs J (2024) The direction of theta and alpha travelling waves modulates human memory processing. Nat Hum Behav 8:1124–1135.
Mouille A, Gaillard C, Astrand E, Wardak C, Amengual JL, Hamed SB (2025) The prefrontal cortex encodes task-identity information and flexibly adjusts its sensory processes as a function of the specific ongoing task. PLoS Biol 23:e3003353.
Muller L, Reynaud A, Chavane F, Destexhe A (2014) The stimulus-evoked population response in visual cortex of awake monkey is a propagating wave. Nat Commun 5:3675.
Muller L, Piantoni G, Koller D, Cash SS, Halgren E, Sejnowski TJ (2016) Rotating waves during human sleep spindles organize global patterns of activity that repeat precisely through the night. Elife 5:e17267.
Muller L, Chavane F, Reynolds J, Sejnowski TJ (2018) Cortical travelling waves: mechanisms and computational principles. Nat Rev Neurosci 19: 255–268.
Myers JC, Smith EH, Leszczynski M, O'Sullivan J, Yates MJ, McKhann G, Mesgarani N, Schroeder C, Schevon C, Sheth SA (2022) The spatial reach of neuronal coherence and spike-field coupling across the human neocortex. J Neurosci 42:6285–6294.
Nácher V, Ledberg A, Deco G, Romo R (2013) Coherent delta-band oscillations between cortical areas correlate with decision making. Proc Natl Acad Sci U S A 110:15085–15090.
Nauhaus I, Busse L, Carandini M, Ringach DL (2009) Stimulus contrast modulates functional connectivity in visual cortex. Nat Neurosci 12: 70–76.
Odean NN, Sanayei M, Shadlen MN (2023) Transient oscillations of neural firing rate associated with routing of evidence in a perceptual decision. J Neurosci 43:6369–6383.

O'Reilly RC, Herd SA, Pauli WM (2010) Computational models of cognitive control. Curr Opin Neurobiol 20:257–261.
Panichello MF, Buschman TJ (2021) Shared mechanisms underlie the control of working memory and attention. Nature 592:601–605.
Parthasarathy A, Herikstad R, Bong JH, Medina FS, Libedinsky C, Yen S-C (2017) Mixed selectivity morphs population codes in prefrontal cortex. Nat Neurosci 20:1770–1779.
Patel J, Fujisawa S, Berényi A, Royer S, Buzsáki G (2012) Traveling theta waves along the entire septotemporal axis of the hippocampus. Neuron 75:410–417.
Pellegrino G, Hedrich T, Sziklas V, Lina J-M, Grova C, Kobayashi E (2021) How cerebral cortex protects itself from interictal spikes: the alpha/beta inhibition mechanism. Hum Brain Mapp 42:3352–3365.
Peylo C, Hilla Y, Sauseng P (2021) Cause or consequence? Alpha oscillations in visuospatial attention. Trends Neurosci 44:705–713.
Pinotsis DA, Fridman G, Miller EK (2023) Cytoelectric coupling: electric fields sculpt neural activity and "tune" the brain's infrastructure. Prog Neurobiol 226:102465.
Pinotsis DA, Miller EK (2023) In vivo ephaptic coupling allows memory network formation. Cereb Cortex 1991:bhad251.
Pinotsis DA, Miller EK (2026) Ephaptic coupling can explain variability in neural activity. Cereb Cortex 36:bhag098.
Radman T, Su Y, An JH, Parra LC, Bikson M (2007) Spike timing amplifies the effect of electric fields on neurons: implications for endogenous field effects. J Neurosci 27:3030–3036.
Ramakrishnan A, Byun YW, Rand K, Pedersen CE, Lebedev MA, Nicolelis MAL (2017) Cortical neurons multiplex reward-related signals along with sensory and motor information. Proc Natl Acad Sci U S A 114: E4841–E4850.
Ray S, Maunsell JHR (2011) Different origins of gamma rhythm and high-gamma activity in macaque visual cortex. PLoS Biol 9:e1000610.
Redinbaugh MJ, Phillips JM, Kambi NA, Mohanta S, Andryk S, Dooley GL, Afrasiabi M, Raz A, Saalmann YB (2020) Thalamus modulates consciousness via layer-specific control of cortex. Neuron 106:66–75.e12.
Redinbaugh MJ, Afrasiabi M, Phillips JM, Kambi NA, Mohanta S, Raz A, Saalmann YB (2022) Thalamic deep brain stimulation paradigm to reduce consciousness: cortico-striatal dynamics implicated in mechanisms of consciousness. PLoS Comput Biol 18:e1010294.
Richter CG, Thompson WH, Bosman CA, Fries P (2017) Top-down beta enhances bottom-up gamma. J Neurosci 37:6698–6711.
Riddle J, Schooler JW (2024) Hierarchical consciousness: the nested observer windows model. Neurosci Conscious 2024:niae010.
Rigotti M, Barak O, Warden MR, Wang X-J, Daw ND, Miller EK, Fusi S (2013) The importance of mixed selectivity in complex cognitive tasks. Nature 497:585–590.
Rohenkohl G, Bosman CA, Fries P (2018) Gamma synchronization between V1 and V4 improves behavioral performance. Neuron 100:953–963.e3.
Rosenthal D (2005) *Consciousness and mind*. Oxford: Clarendon Press.
Rossi AF, Pessoa L, Desimone R, Ungerleider LG (2009) The prefrontal cortex and the executive control of attention. Exp Brain Res 192:489–497.
Rubino D, Robbins KA, Hatsopoulos NG (2006) Propagating waves mediate information transfer in the motor cortex. Nat Neurosci 9: 1549–1557.
Ruffini G, Salvador R, Tadayon E, Sanchez-Todo R, Pascual-Leone A, Santarnecchi E (2020) Realistic modeling of mesoscopic ephaptic coupling in the human brain. PLoS Comput Biol 16:e1007923.
Samaha J, Bauer P, Cimaroli S, Postle BR (2015) Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. Proc Natl Acad Sci U S A 112:8439–8444.
Sato TK, Nauhaus I, Carandini M (2012) Traveling waves in visual cortex. Neuron 75:218–229.
Schmidt H, Hahn G, Deco G, Knösche TR (2021) Ephaptic coupling in white matter fibre bundles modulates axonal transmission delays. PLoS Comput Biol 17:e1007858.
Schoffelen J-M, Oostenveld R, Fries P (2005) Neuronal coherence as a mechanism of effective corticospinal interaction. Science 308:111–113.
Sejnowski TJ, Paulsen O (2006) Network oscillations: emerging computational principles. J Neurosci 26:1673–1676.
Seth AK, Suzuki K, Critchley HD (2012) An interoceptive predictive coding model of conscious presence. Front Psychol 2:395.
Shifman AR, Lewis JE (2019) ELFENN: a generalized platform for modeling ephaptic coupling in spiking neuron models. Front Neuroinformatics 13:35.
Siegel M, Warden MR, Miller EK (2009) Phase-dependent neuronal coding of objects in short-term memory. Proc Natl Acad Sci U S A 106:21341–21346.
Singer W (2021) Recurrent dynamics in the cerebral cortex: integration of sensory evidence with stored knowledge. Proc Natl Acad Sci U S A 118: e2101043118.
Singer W, Effenberger F (2025) Oscillations in natural neuronal networks; An epiphenomenon or a fundamental computational mechanism? Hum Arenas 8:846–868.
Skaggs WE, McNaughton BL, Wilson MA, Barnes CA (1996) Theta phase precession in hippocampal neuronal populations and the compression of temporal sequences. Hippocampus 6:149–172.
Spaak E, Bonnefond M, Maier A, Leopold DA, Jensen O (2012) Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Curr Biol 22:2313–2318.
Spyropoulos G, Bosman CA, Fries P (2018) A theta rhythm in macaque visual cortex and its attentional modulation. Proc Natl Acad Sci U S A 115: E5614.
Stark E, Levi A, Rotstein HG (2022) Network resonance can be generated independently at distinct levels of neuronal organization. PLoS Comput Biol 18:e1010364.
Stokes MG, Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J (2013) Dynamic coding for cognitive control in prefrontal cortex. Neuron 78: 364–375.
Tafazoli S, Bouchacourt FM, Ardalan A, Markov NT, Uchimura M, Mattar MG, Daw ND, Buschman TJ (2026) Building compositional tasks with shared neural subspaces. Nature 650:164–172.
Tang C, Herikstad R, Parthasarathy A, Libedinsky C, Yen S-C (2020) Minimally dependent activity subspaces for working memory and motor preparation in the lateral prefrontal cortex. Elife 9:e58154.
Teleńczuk B, Dehghani N, Le Van Quyen M, Cash SS, Halgren E, Hatsopoulos NG, Destexhe A (2017) Local field potentials primarily reflect inhibitory neuron activity in human and monkey cortex. Sci Rep 7:40211.
Tononi G, Boly M, Massimini M, Koch C (2016) Integrated information theory: from consciousness to its physical substrate. Nat Rev Neurosci 17: 450–461.
Townsend RG, Solomon SS, Martin PR, Solomon SG, Gong P (2017) Visual motion discrimination by propagating patterns in primate cerebral cortex. J Neurosci 37:10074–10084.
Tseng S-Y, Chettih SN, Arlt C, Barroso-Luque R, Harvey CD (2022) Shared and specialized coding across posterior cortical areas for dynamic navigation decisions. Neuron 110:2484–2502.e16.
Tye KM, Miller EK, Taschbach FH, Benna MK, Rigotti M, Fusi S (2024) Mixed selectivity: cellular computations for complexity. Neuron 112: 2289–2303.
Tzarouchis DC, Edwards B, Engheta N (2025) Programmable wave-based analog computing machine: a metastructure that designs metastructures. Nat Commun 16:908.
Ursino M, Pirazzini G (2024) Theta–gamma coupling as a ubiquitous brain mechanism: implications for memory, attention, dreaming, imagination, and consciousness. Curr Opin Behav Sci 59:101433.
Uygun DS, Basheer R (2022) Circuits and components of delta wave regulation. Brain Res Bull 188:223–232.
Van Horn MR, Benfey NJ, Shikany C, Severs LJ, Deemyad T (2021) Neuron-astrocyte networking: astrocytes orchestrate and respond to changes in neuronal network activity across brain states and behaviors. J Neurophysiol 126:627–636.
Van Kerkoerle T, Self MW, Dagnino B, Gariel-Mathis M-A, Poort J, Van Der Togt C, Roelfsema PR (2014) Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. Proc Natl Acad Sci U S A 111:14332–14341.
Vyas S, Golub MD, Sussillo D, Shenoy KV (2020) Computation through neural population dynamics. Annu Rev Neurosci 43:249–275.
Wallis JD, Anderson KC, Miller EK (2001) Single neurons in prefrontal cortex encode abstract rules. Nature 411:953–956.
Warden MR, Miller EK (2007) The representation of multiple objects in prefrontal neuronal delay activity. Cereb Cortex 17:i41–i50.
Warden MR, Miller EK (2010) Task-Dependent changes in short-term memory in the prefrontal cortex. J Neurosci 30:15801–15810.
Weber J, Iwama G, Solbakk A-K, Blenkmann AO, Larsson PG, Ivanovic J, Knight RT, Endestad T, Helfrich R (2023) Subspace partitioning in the human prefrontal cortex resolves cognitive interference. Proc Natl Acad Sci U S A 120:e2220523120.

Weisz N, Hartmann T, Müller N, Lorenz I, Obleser J (2011) Alpha rhythms in audition: cognitive and clinical perspectives. Front Psychol 2:73.
Womelsdorf T, Schoffelen J-M, Oostenveld R, Singer W, Desimone R, Engel AK, Fries P (2007) Modulation of neuronal interactions through neuronal synchronization. Science 316:1609–1612.
Womelsdorf T, Everling S (2015) Long-range attention networks: circuit motifs underlying endogenously controlled stimulus selection. Trends Neurosci 38:682–700.
Xiang JD, Martinez-Trujillo JC, Schmitz TW, Mur M (2025) Toward task mapping of primate prefrontal cortex. Neuropsychologia 219:109234.
Xie Y, et al. (2022) Geometry of sequence working memory in macaque prefrontal cortex. Science 375:632–639.
Xing D, Yeh C-I, Shapley RM (2009) Spatial spread of the local field potential and its laminar variation in visual cortex. J Neurosci 29:11540–11549.
Ye J, Wang W, Shi C, Cui X, Qu W, Lin P, Yu X, Cheng R, Wu H, Chen B (2025) An overhead-reduced, efficient, fully analog neural-network computing hardware. Sci Adv 11:eadv7555.
Ye Z, et al. (2026) Brain-wide topographic coordination of rotating waves. Science 392:eadx1369.
Yoo SBM, Hayden BY (2020) The transition from evaluation to selection involves neural subspace reorganization in core reward regions. Neuron 105:712–724.e4.
Zanos TP, Mineault PJ, Nasiotis KT, Guitton D, Pack CC (2015) A sensorimotor role for traveling waves in primate visual cortex. Neuron 85:615–627.
Zhang H, Jacobs J (2015) Traveling theta waves in the human hippocampus. J Neurosci 35:12477–12487.
Zhang H, Watrous AJ, Patel A, Jacobs J (2018) Theta and alpha oscillations are traveling waves in the human neocortex. Neuron 98:1269–1281.e4.