Journal of Integrative Neuroscience

J. Integr. Neurosci. **2026**; 25(11): 53958
https://doi.org/10.31083/JIN53958

Review

Functional Neural Ensembles and the Development of Cognition: A Developmental Framework

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Academic Editor: Bettina Platt
Submitted: 17 May 2026 Revised: 18 August 2026 Accepted: 1 September 2026 Published: 16 November 2026

Abstract

Functional neural ensembles, temporally coordinated groups of neurons or neural populations whose activity supports specific computations and behaviors, are increasingly recognized as important intermediate units linking local circuit dynamics to large-scale brain function. Most studies, however, have focused on their role in the mature nervous system, with relatively little consideration of how ensemble organization emerges across development. In this review, we propose a developmental framework in which functional neural ensembles are conceptualized as progressively assembled and refined substrates of cognition from prenatal life through adulthood. We synthesize evidence from developmental neuroscience, electrophysiology, neuroimaging, and systems neuroscience concerning spontaneous neural activity, sensorimotor coupling, thalamocortical development, oscillatory coordination, and large-scale network maturation. Current evidence suggests that coordinated neural activity emerges prenatally through intrinsically generated activity patterns that contribute to early functional organization. Following birth, sensorimotor interactions, activity-dependent plasticity, and environmental engagement refine and stabilize these patterns, promoting increasing specificity and efficiency. Across childhood and adolescence, ensembles become progressively specialized and integrated through oscillatory synchronization, hemispheric differentiation, and the maturation of long-range connectivity. Mature cognition is proposed to depend upon the flexible recruitment and coordination of ensembles across distributed neural systems. We argue that functional neural ensembles should be viewed not solely as products of mature brain organization but as developmentally constructed entities shaped by interactions among intrinsic activity, experience-dependent processes, and environmental constraints. The developmental ensemble framework advanced here provides a conceptual model linking early neural activity to later cognitive function while generating testable predictions regarding typical and atypical neurodevelopment. Framing cognition in terms of the developmental assembly, refinement, and coordination of neural ensembles offers a unifying perspective for understanding how complex cognitive functions emerge across the lifespan.

Keywords: brain development; cognition; neural networks (physiology); synaptic plasticity; motor activity; cognitive neuroscience

1. Introduction

Functional neural ensembles, coordinated groups of neurons that transiently or stably co-activate, are increasingly recognized as fundamental units of neural computation underlying perception, action, memory, and cognition. Across electrophysiological, imaging, and computational studies, ensembles have been identified as the substrates through which information is represented, transformed, and integrated within neural systems. These coordinated patterns of activity are not reducible to individual neurons nor fully captured by large-scale network descriptions alone; rather, they constitute an intermediate level of organization linking local circuit dynamics to distributed brain function [1].

Defining Functional Neural Ensembles

A central concept throughout this review is that of the functional neural ensemble. The term is used here to describe a temporally coordinated pattern of activity among neurons or neural populations that participate in a shared functional process. Functional neural ensembles differ from several related concepts commonly used in neuroscience. Unlike individual neurons, ensembles represent collective patterns of coordinated activity. Unlike microcircuits, which refer primarily to anatomically defined local networks, ensembles are defined functionally and may extend across multiple anatomical regions. Ensembles also differ from large-scale functional networks such as the default mode, salience, or frontoparietal systems. Whereas large-scale networks describe broad patterns of connectivity among brain regions, ensembles are proposed to represent the intermediate level at which coordinated neural activity gives rise to specific perceptual, motor, or cognitive functions. The concept overlaps with Hebb's notion of cell assemblies but places greater emphasis on dynamic coordination, temporal synchronization, developmental plasticity, and context-dependent recruitment [2].

Functional neural ensembles occupy a conceptual level between individual neurons and large-scale functional networks. Unlike neural populations, which may be defined anatomically or statistically, ensembles are characterized by temporally coordinated activity associated with a

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specific computational or behavioral function. They differ from classical cell assemblies in that ensemble membership may be transient and context-dependent, and from large-scale functional networks in that they represent the dynamic coordinating units through which network-level functions are implemented. Throughout this review, the term "functional neural ensemble" refers to coordinated groups of neurons or neuronal populations whose temporally organized activity contributes to a specific functional outcome.

Despite growing interest in ensemble-based accounts of neural processing, most work has focused on their role in the mature brain. Ensembles are typically examined as relatively stable or task-dependent configurations supporting coding, decision-making, and behavioral output, with limited attention to how such coordinated structures arise. As a result, a central question remains insufficiently addressed: how do functional neural ensembles emerge, stabilize, and become integrated across development to support cognition?

Addressing this question requires a developmental perspective. Neural systems are not born fully organized but are constructed through temporally structured processes that begin before birth and extend into early adulthood. Across this period, the brain undergoes continuous transformation driven by spontaneous neural activity [3,4], sensorimotor interaction, circuit refinement, and large-scale integration. These processes are not independent; they interact across spatial and temporal scales to shape the organization and coordination of neural activity. Within the developmental framework proposed here, functional neural ensembles are conceptualized not simply as outputs of mature systems but as progressively assembled units whose properties reflect the cumulative history of these interactions.

Converging evidence from developmental neuroscience supports this view. Patterns of spontaneous neural activity [3,4] are observable in the fetal brain and contribute to the establishment of early functional architecture before extensive sensory experience. Following birth, sensorimotor interactions, particularly those driven by self-generated movement, calibrate and refine these activity patterns through continuous coupling between action and sensory feedback. Concurrently, thalamocortical pathways [5] structure cortical dynamics, while oscillatory processes provide a temporal framework for coordination within and between neural populations. Across infancy, childhood, and adolescence, these interacting processes give rise to increasing specificity, stability, and integration of neural activity, culminating in the flexible recruitment of distributed systems that characterize mature cognition.

However, these processes are typically examined in isolation. Spontaneous activity, sensorimotor coupling, thalamocortical development, and network maturation are often treated as separate domains, limiting the development of a unified account of how coordinated neural activity evolves across the lifespan. This fragmentation obscures the role of functional neural ensembles as the organizing link between early neural activity and higher-order cognitive function. Alternative developmental accounts have emphasized network maturation, modular specialization, predictive processing, neuroconstructivism, or embodied approaches as primary explanatory frameworks. The present review does not reject these perspectives but instead proposes that ensemble dynamics may provide an intermediate level of organization through which many of these developmental processes are expressed [5,6].

We further propose the concept of proto-ensembles, defined as transient and developmentally immature patterns of coordinated neural activity that exhibit statistical regularities but lack the stability, specialization, and context sensitivity characteristic of mature functional ensembles. The term is used here as a heuristic construct intended to describe early forms of neural coordination observed during prenatal development.

The present review addresses this gap by advancing a developmental framework in which functional neural ensembles are proposed as an intermediate organizational level linking early neural activity to the emergence of cognition. Ensemble organization is proposed to unfold through interrelated processes in which early intrinsic activity establishes initial coordination, sensorimotor interaction refines and calibrates these patterns, and subsequent specialization and integration enable the emergence of flexible cognitive systems. Development is thus understood not as a simple increase in connectivity or complexity, but as a process of progressive stabilization, coordination, and integration of neural ensembles across scales. Fig. 1 (Ref. [3,4,5,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25]) provides a schematic overview of this developmental trajectory [1,26]. The framework also generates a series of empirically testable predictions concerning the developmental emergence, refinement, and integration of ensemble dynamics across the lifespan.

By synthesizing advances from developmental neuroscience, systems neuroscience, and functional neuroimaging, this review provides a structured account of how functional neural ensembles emerge from fetal stages through brain maturity. In doing so, it establishes a conceptual bridge between early neural activity and higher-order cognition, with implications for both typical development and conditions in which these processes are altered.

2. Prenatal Foundations of Ensemble Formation

Neural development begins not with fully formed circuits, but with dynamically evolving patterns of activity that precede mature connectivity and behavioral output. These early processes, unfolding during fetal life, establish the foundational conditions under which functional neural ensembles can emerge. Rather than viewing prenatal neural activity as immature or epiphenomenal, converging evi-

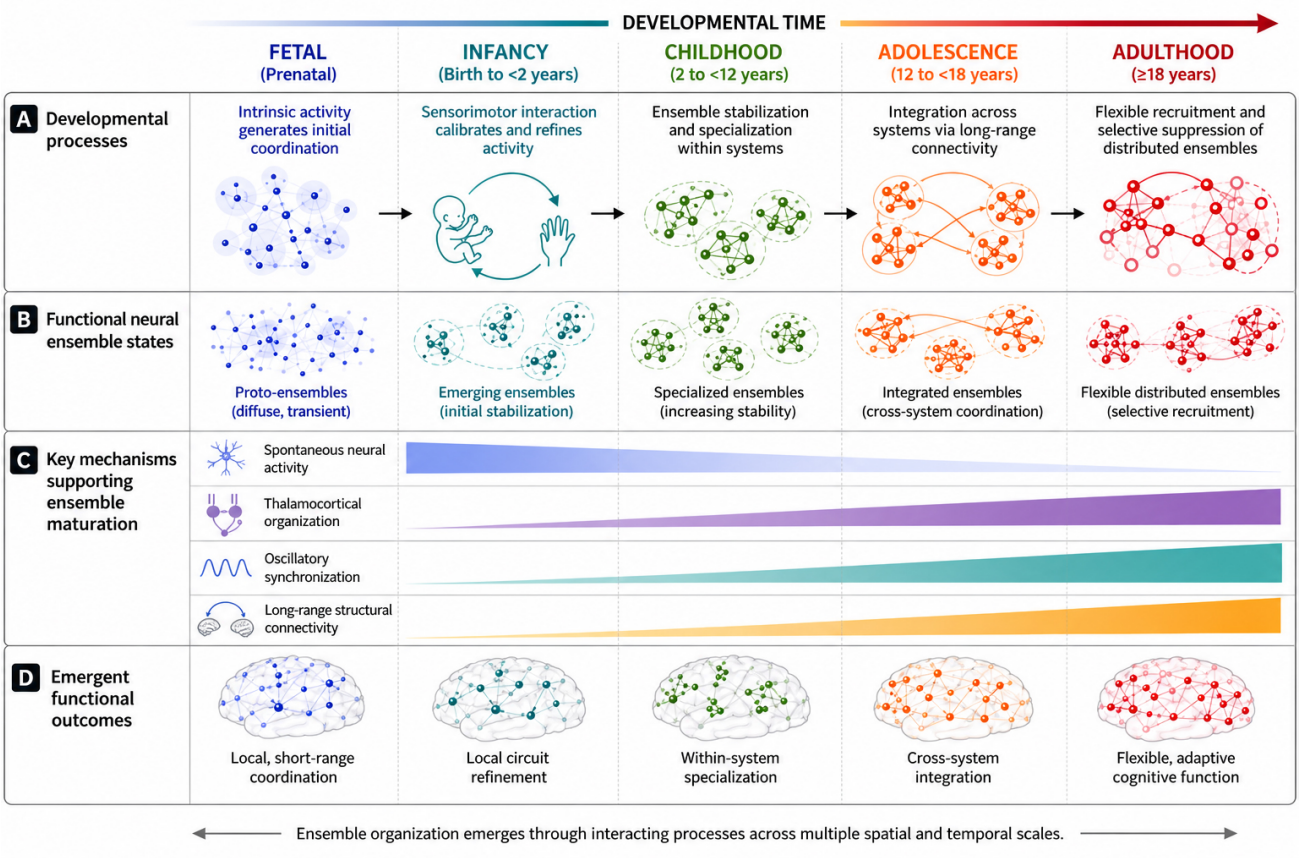


Fig. 1. Developmental framework of functional neural ensemble assembly across the lifespan. This schematic illustrates the developmental framework proposed in this review, depicting how functional neural ensembles may emerge, stabilize, specialize, and become integrated from prenatal development through adulthood. The figure is organized into four complementary panels spanning developmental time from the fetal period to adulthood. (A) Developmental processes. Intrinsic neural activity provides an initial substrate for coordinated activity during fetal development [3,4,7]. Following birth, sensorimotor interactions are proposed to refine neural activity through continuous action–perception feedback loops [10,11,12,13,14,15,16,17]. Across childhood, repeated activation and activity-dependent refinement promote ensemble stabilization and specialization [14,15,16,17,21,22], while adolescence and adulthood are characterized by increasing integration across distributed systems supported by long-range connectivity and network maturation [18,19,20]. (B) Functional neural ensemble states. Diffuse and transient proto-ensembles are proposed to represent early forms of coordinated neural activity during prenatal development. Within the framework advanced here, these immature configurations progressively evolve into emerging ensembles, specialized ensembles, integrated ensembles, and ultimately flexible distributed ensembles capable of context-dependent recruitment and selective suppression. The concept of proto-ensembles is introduced as a developmental heuristic rather than a directly established neural category. (C) Key mechanisms supporting ensemble maturation. Major mechanisms contributing to ensemble development include spontaneous neural activity [3,4], thalamocortical organization [5], oscillatory synchronization and temporal coordination [8,9,23], and the maturation of long-range structural and functional connectivity [18,19,24]. The relative contribution of these mechanisms is schematic and intended to illustrate developmental trends rather than quantitative relationships. (D) Emergent functional outcomes. Increasing ensemble organization is associated with a progression from local short-range coordination and local circuit refinement toward within-system specialization, cross-system integration, and flexible adaptive cognition [12,20,22,24,25]. These developmental outcomes reflect increasing coordination across spatial and temporal scales rather than the maturation of isolated neural regions. The figure summarizes a conceptual and heuristic developmental model linking early neural activity to mature cognitive function. Developmental trajectories are schematic and do not imply a strictly linear, deterministic, or causally established sequence. Rather, the figure is intended to illustrate how empirical findings from developmental neuroscience may be integrated within an ensemble-based framework of cognitive emergence.

dence suggests that it plays an active role in organizing the structure and coordination of future brain function [7,27].

During gestation, the developing brain undergoes rapid neurogenesis, migration, and differentiation, giving

rise to the basic anatomical architecture of the central nervous system. By the second trimester, key structures, including the thalamus, cortex, and early association pathways, are sufficiently developed to support coordinated neural signaling. Importantly, these anatomical developments are accompanied by the emergence of spontaneous neural activity [3,4], which is not random noise but exhibits structured, temporally patterned dynamics. Such activity has been observed across multiple species and is increasingly documented in the human fetus using advanced imaging and electrophysiological techniques. Although important species differences exist in developmental timing and cortical maturation, comparative findings suggest that spontaneous activity serves broadly conserved organizational functions across mammalian development.

This spontaneous activity provides an initial substrate for coordination across neuronal populations. Even in the absence of fully developed sensory systems, neurons engage in synchronous firing patterns that reflect early forms of network organization. These coordinated patterns are hypothesized to support the emergence of proto-ensembles, a term used here to describe transient and developmentally immature patterns of coordinated neural activity whose co-activation may establish statistical regularities relevant for later functional specialization. Within the framework proposed here, intrinsically generated activity is hypothesized to provide an early scaffold for later ensemble formation before extensive sensory experience.

The importance of these early dynamics is reinforced by evidence that learning-related processes begin prenatally. Fetal exposure to sensory stimuli, including auditory and vestibular inputs, leads to measurable changes in neural responsiveness and behavioral reactivity. By approximately 24–28 weeks of gestation, fetuses demonstrate the capacity to encode and retain information, as indicated by habituation and recognition responses. These findings suggest that rudimentary forms of learning and memory are already detectable during fetal life and may reflect the operation of developing neural systems capable of encoding and retaining simple sensory regularities [7,28].

Crucially, these early learning processes occur within a neural environment that is still undergoing rapid structural reorganization. Synaptogenesis accelerates during the third trimester, leading to a dramatic increase in the number of synaptic connections. This proliferation is followed by activity-dependent refinement, in which patterns of neural activation influence which connections are stabilized and which are eliminated. Such processes imply that coordinated activity, rather than mere anatomical proximity, drives the selection and consolidation of neural circuits, further supporting the emergence of functional ensembles [29,30].

The mechanisms underlying this refinement are thought to include activity-dependent synaptic plasticity, competitive stabilization of co-active pathways, early inhibitory circuit maturation, and synaptic pruning. Repeated patterns of coordinated activation may strengthen specific connections through Hebbian-like processes, while less consistently active pathways are weakened or eliminated. Although these mechanisms have been studied most extensively in animal models, converging evidence suggests that activity-dependent refinement plays a central role in shaping the functional architecture of developing neural systems. Within the present framework, such processes are proposed to contribute to the transition from transient proto-ensemble states toward increasingly stable and specialized patterns of neural coordination [31,32].

A central component of this early coordination is the development of thalamocortical connectivity. The thalamus acts as a hub that organizes and relays information to the cortex, contributing to the synchronization of neural activity across distributed regions. Thalamocortical pathways begin to establish functional connectivity during mid-gestation, providing a structural and functional framework for large-scale coordination. These pathways are critical for integrating internally generated activity with incoming sensory signals, enabling the transition from diffuse activation patterns to more structured and regionally differentiated ensembles.

Parallel to these developments, early forms of oscillatory activity [8,9] emerge, providing a temporal framework for neural coordination. Fetal and neonatal recordings reveal discontinuous patterns of neural activity that gradually evolve into more continuous and organized rhythms. These oscillations are not merely epiphenomenal; they play a functional role in synchronizing neuronal firing, thereby enabling the temporal binding necessary for ensemble formation. As oscillatory dynamics become more stable and coherent, they support increasingly precise coordination across neural populations.

Importantly, prenatal neural organization is not solely driven by intrinsic processes. Even before birth, the fetus engages in sensorimotor activity, including spontaneous movements that generate proprioceptive and vestibular feedback. These movements exhibit increasing complexity over gestation and contribute to the calibration of neural circuits. Sensorimotor contingencies established in utero provide a critical link between action and perception, enabling the developing brain to begin organizing activity patterns in relation to the body and environment [10].

This perspective challenges traditional views that place the origins of cognition exclusively in postnatal experience. Instead, developmental evidence indicates that key elements of neural organization, including coordination, synchronization, and early learning, are already in place before birth. These processes do not constitute fully formed cognitive functions, but they establish the operational principles upon which later cognition depends.

The implications of this framework extend to theoretical accounts of early cognition. Models that assume the

presence of mature perceptual or conceptual mechanisms at birth fail to account for the developmental processes that precede them. Evidence from fetal neural organization and early behavioral responses suggests that cognition emerges through a process of progressive reorganization, in which early activity patterns are reshaped by both intrinsic dynamics and environmental interaction. Within the framework advanced here, functional neural ensembles are proposed as an intermediate level of organization emerging through this reorganization, linking early neural activity to later cognitive capabilities. Fig. 2 (Ref. [3,4,5,7,8,9]) illustrates the prenatal emergence of coordinated neural activity, emphasizing the progressive organization of neural ensembles through intrinsic dynamics and early structural connectivity.

Within the developmental framework proposed in this review, the prenatal period may be viewed as a phase of proto-ensemble formation in which spontaneous activity, thalamocortical organization, oscillatory dynamics, and early sensorimotor engagement interact to establish conditions favorable for later coordinated neural function. These early patterns are not yet specialized or stable functional ensembles but may provide developmental scaffolding upon which subsequent processes of stabilization, specialization, and integration can build.

3. Sensorimotor Calibration and Early Postnatal Refinement of Neural Ensembles

The transition from prenatal to postnatal life introduces a fundamental shift in the conditions under which neural activity is generated and organized. While prenatal development is characterized by intrinsically driven and scaffolded patterns of coordination, the postnatal period is marked by the rapid expansion of sensorimotor interaction, through which neural activity becomes increasingly calibrated to the external environment. This transition does not replace earlier processes but rather builds upon them, transforming proto-ensembles into more stable, functionally meaningful configurations, and is hypothesized to contribute to the transformation of transient proto-ensemble states into more stable and functionally differentiated patterns of neural coordination.

At birth, the brain is already equipped with a partially organized architecture, including established thalamocortical pathways [5,7], emerging oscillatory dynamics, and rudimentary patterns of coordinated activity. However, these early structures remain highly plastic and require calibration through interaction with sensory input and motor output. It is within this context that sensorimotor coupling is increasingly recognized as an important contributor to neural organization, shaping the refinement and stabilization of functional neural ensembles.

Movement is a central driver in this process. Neonatal and early infant behavior is characterized by frequent, variable, and often self-generated motor activity, including spontaneous limb movements, reflexive actions, and exploratory behaviors. These movements generate continuous streams of proprioceptive, tactile, and vestibular feedback, providing the developing brain with temporally structured information about the relationship between action and sensation. Through repeated cycles of movement and feedback, neural systems begin to encode the statistical regularities of the environment, enabling the progressive alignment of internal activity patterns with external contingencies.

This developmental perspective also converges with active inference accounts of brain function, which emphasize that perception and action develop through continuous reciprocal interactions between the organism and its environment [33]. Within the present framework, however, the primary emphasis is developmental. Rather than focusing on inferential computations alone, the present model proposes that repeated cycles of spontaneous activity, sensorimotor experience, and environmental interaction progressively assemble, stabilize, and refine functional neural ensembles that subsequently support higher cognitive function. Fig. 3 (Ref. [8,9,10,11,12,13,14,15,16,17,18,19,21,23,34,35]) illustrates these proposed processes of sensorimotor calibration and developmental ensemble refinement.

This process constitutes sensorimotor calibration, in which neural ensembles are actively constructed through continuous interaction between internally generated activity and externally derived sensory feedback. Movement is not merely an output of neural processing but a mechanism for generating the input necessary for its own organization. At the cellular and circuit levels, sensorimotor calibration is thought to influence neural development through activity-dependent synaptic plasticity, selective strengthening of co-active pathways, and broader processes of circuit refinement and stabilization [16,21,34]. These processes provide biologically plausible mechanisms through which repeated sensorimotor experiences may contribute to the stabilization and specialization of coordinated neural activity patterns.

Empirical evidence supports this view across multiple domains of development. Early motor activity has been shown [11,12] to influence synaptic plasticity, myelination, and the maturation of large-scale functional networks. Several studies have reported associations between greater opportunities for varied motor experience and subsequent development in domains including attention, memory, and executive function [11,12,14,16]. These relationships are not coincidental; they reflect underlying neurobiological processes through which movement contributes to the refinement of neural circuits and the coordination of distributed activity patterns.

Variability in early movement is a critical driver of neural organization. Infant motor behavior is characterized by a high degree of fluctuation and redundancy, which may appear inefficient from a mature perspective but serves a

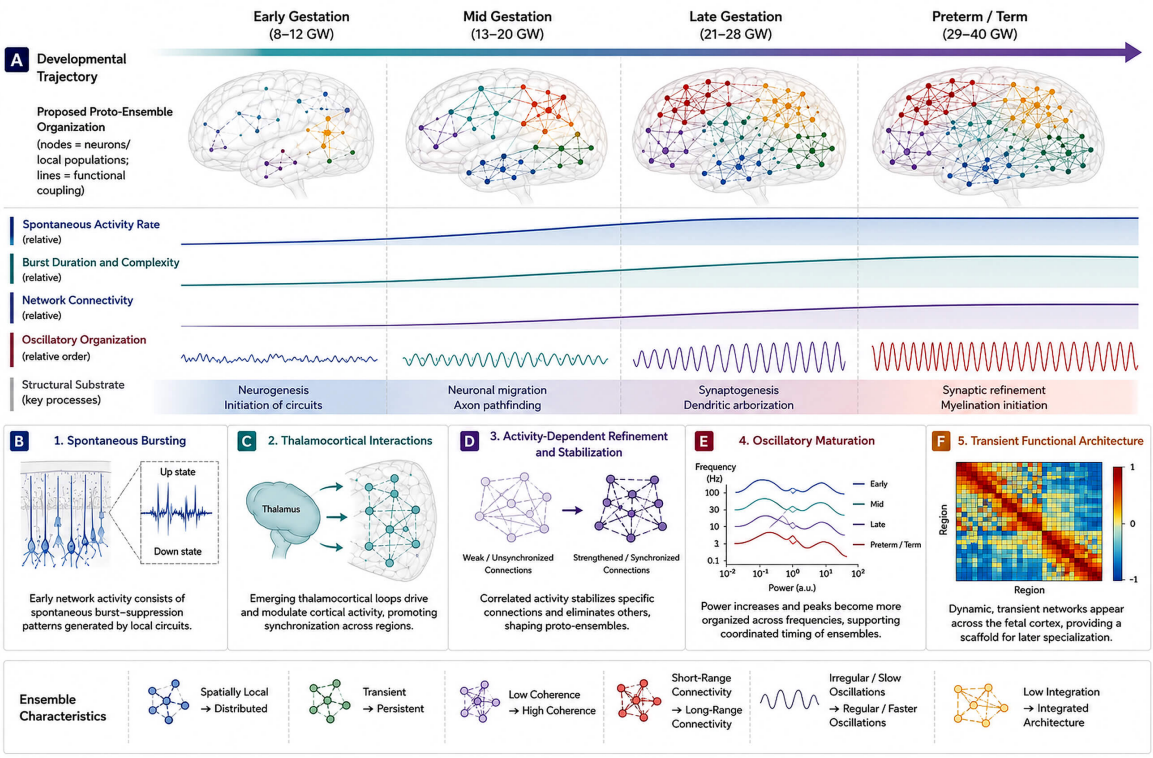


Fig. 2. Prenatal foundations of functional neural ensemble formation. This figure is a schematic summary of the developmental processes and mechanisms proposed to contribute to the emergence of functional neural ensembles during fetal development. The schematic is organized into six complementary panels spanning early gestation through the preterm/term period. (A) Developmental trajectory. Across gestation, intrinsically generated neural activity provides an initial substrate for coordinated signaling within local neuronal populations [3,4,7]. Progressive increases in spontaneous activity, burst complexity, network connectivity, and oscillatory organization occur alongside major structural events, including neurogenesis, neuronal migration, synaptogenesis, dendritic arborization, and the onset of myelination. Within the framework proposed here, these processes may support the emergence of increasingly coordinated proto-ensemble organization prior to extensive sensory experience. (B) Spontaneous bursting. Early fetal neural activity is characterized by spontaneous burst–suppression-like patterns generated within immature local circuits [3,4]. These coordinated bursts are thought to contribute to the establishment of early functional relationships among neuronal populations. (C) Thalamocortical interactions. The progressive establishment of thalamocortical pathways [5] contributes to the synchronization and spatial organization of cortical activity. Emerging thalamocortical loops may facilitate coordination across distributed regions, supporting increasing integration of neural signaling. (D) Activity-dependent refinement and stabilization. Repeated patterns of coordinated activation promote selective strengthening of some neural connections while less consistently active pathways are weakened or eliminated. Such activity-dependent processes are proposed to contribute to the refinement and stabilization of emerging proto-ensemble organization. (E) Oscillatory maturation. Fetal oscillatory activity evolves from irregular and discontinuous patterns toward increasingly organized rhythmic activity [8,9]. Progressive maturation of oscillatory dynamics provides a temporal framework for synchronization within and between neural populations, supporting increasingly precise coordination. (F) Transient functional architecture. As gestation progresses, transient patterns of functional connectivity become increasingly structured and distributed. Although these early architectures remain dynamic and developmentally constrained, they may provide a scaffold for later specialization and large-scale network organization observed after birth. The lower panel summarizes proposed developmental changes in ensemble characteristics, including transitions from local to distributed organization, transient to more persistent coordination, low to higher coherence, short-range to longer-range connectivity, irregular to more organized oscillatory activity, and relatively weak integration toward increasingly coordinated functional architecture. The figure presents a conceptual and heuristic model integrating empirical findings from fetal neurodevelopment. Developmental trajectories are schematic and do not imply a strictly linear or causally established sequence. Rather, the figure illustrates how spontaneous activity, thalamocortical organization, activity-dependent refinement, and oscillatory maturation may interact to support the prenatal foundations of functional neural ensemble formation. GW, Gestational Weeks.

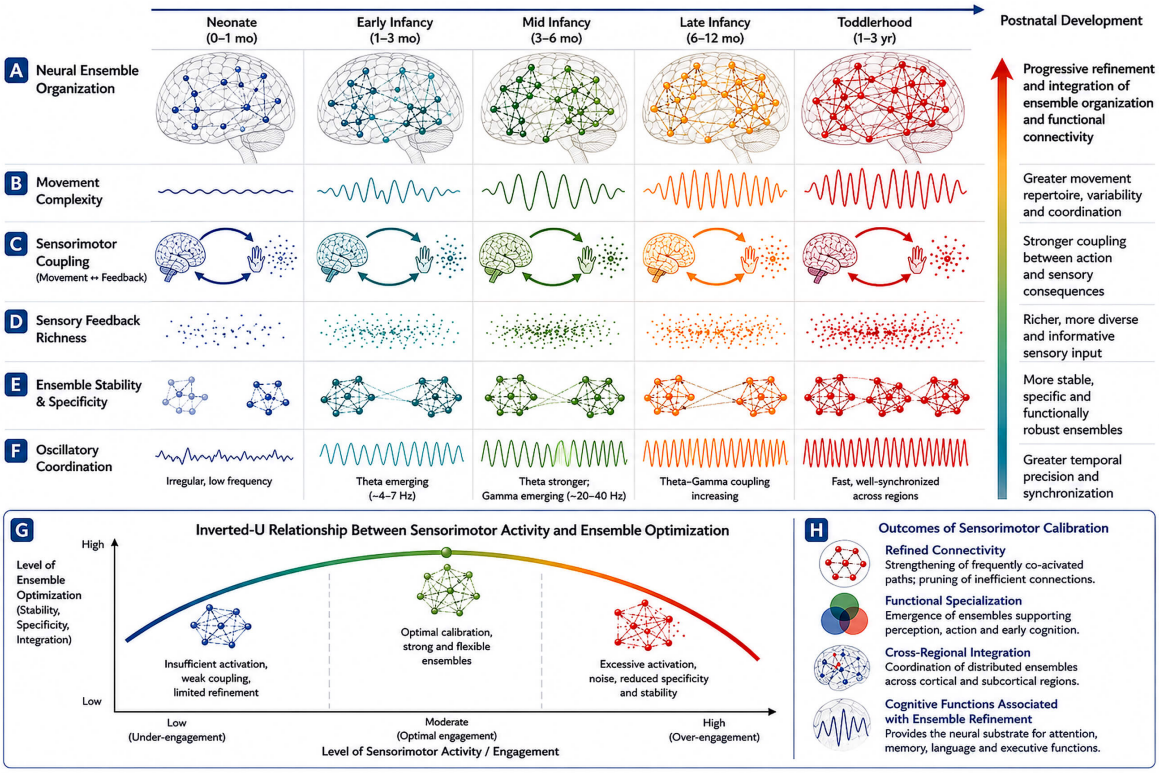


Fig. 3. Sensorimotor calibration and refinement of functional neural ensembles during early postnatal development. This figure summarizes the developmental framework proposed in this review, illustrating how sensorimotor interaction may contribute to the refinement, stabilization, and integration of functional neural ensembles from the neonatal period through toddlerhood. The figure is organized into eight complementary panels. (A) Neural ensemble organization. Across early postnatal development, patterns of coordinated neural activity become increasingly organized and distributed. Within the present framework, ensemble organization is proposed to progress from relatively diffuse and weakly coordinated activity toward increasingly integrated patterns of functional connectivity. (B) Movement complexity. Early motor behavior progresses from relatively simple and repetitive movements toward increasingly variable, coordinated, and goal-directed actions. This expansion of the motor repertoire provides a growing range of sensorimotor experiences that may contribute to neural refinement [11,12,13,14]. (C) Sensorimotor coupling. Self-generated movement produces continuous sensory consequences, creating reciprocal interactions between action and perception. Repeated movement–feedback cycles provide structured information through which the developing nervous system may calibrate neural activity to environmental contingencies [10,14,17]. (D) Sensory feedback richness. Increasing movement complexity generates increasingly diverse proprioceptive, tactile, vestibular, and visual feedback. The resulting expansion of sensory information provides opportunities for the refinement of coordinated neural activity patterns [14,17]. (E) Ensemble stability and specificity. Repeated patterns of co-activation are proposed to contribute to the stabilization of some neural relationships while less consistent interactions are reduced. Through activity-dependent refinement, coordinated activity patterns may become increasingly stable, differentiated, and functionally specific [14,15,16,21,34]. (F) Oscillatory coordination. Early irregular and discontinuous neural activity progressively evolves into more organized oscillatory patterns [8,9,23,35]. Increasing synchronization across frequencies may provide a temporal framework supporting more precise coordination within and between neural populations. (G) Inverted-U relationship between sensorimotor activity and ensemble optimization. The lower panel illustrates a conceptual non-linear relationship between sensorimotor engagement and ensemble refinement. Insufficient activity may limit coordination and refinement, whereas excessive or poorly regulated activity may reduce specificity and stability. Moderate, variable, and context-sensitive engagement is hypothesized to provide conditions favorable for the development of stable, flexible, and integrated ensemble organization [12]. (H) Outcomes of sensorimotor calibration. Proposed consequences of ensemble refinement include increased connectivity efficiency, functional specialization, cross-regional integration, and the emergence of neural architectures associated with later cognitive functions, including attention, memory, language, and executive control [11,12,16,18,19]. The figure integrates findings from developmental neuroscience, motor development, oscillatory physiology, and functional connectivity research. Developmental trajectories are schematic and do not imply a strictly linear or causally established sequence. Rather, the figure illustrates how sensorimotor experience may contribute to the progressive refinement of coordinated neural activity within the developmental ensemble framework advanced in this review. mo, months; yr, years.

critical developmental function. This variability allows the nervous system to explore a wide range of sensorimotor contingencies, facilitating the selection and stabilization of effective coordination patterns. From the perspective of ensemble formation, such variability facilitates the differentiation of neural activity patterns, potentially promoting the emergence of increasingly differentiated coordinated neural activity patterns [13].

As development progresses, these initially variable patterns become increasingly structured. Repeated sensorimotor experiences strengthen specific neural pathways and suppress less relevant connections, resulting in more efficient and reliable coordination. This process mirrors the broader principles of activity-dependent refinement observed in synaptic pruning but operates at the level of coordinated neural populations. Within the framework proposed here, functional ensembles are hypothesized to evolve from loosely organized, transient groupings into increasingly stable and context-sensitive patterns of coordinated activity [14,15,16].

Activity- and experience-dependent refinement of emerging neural ensembles may also be influenced by reinforcement processes operating throughout development. Patterns of coordinated neural activity that repeatedly support successful interactions with the physical and social environment may become more likely to be re-engaged, contributing to the progressive stabilization and functional specialization of neural ensembles. Within the present developmental framework, reinforcement is conceptualized broadly as the strengthening of adaptive perception–action relationships rather than exclusively as hedonic reward. Repeated reinforcement may therefore increase the probability that effective ensemble configurations are reactivated and consolidated, while less adaptive patterns are modified or eliminated through ongoing activity-dependent plasticity. Together, these processes may contribute to the increasing stability, flexibility, and functional specificity of neural ensembles supporting cognitive development.

Concurrently, the maturation of oscillatory dynamics enhances the temporal precision of neural coordination. Early postnatal brain activity is characterized by discontinuous patterns that gradually transition into more continuous and rhythmically organized oscillations. These oscillatory patterns facilitate synchronization both within and between neural ensembles, enabling more precise timing of neuronal firing. The emergence of coordinated oscillatory activity [8,9] supports the integration of information across spatially distributed regions, contributing to the formation of increasingly complex functional networks.

Evidence for these developmental processes has been obtained through converging methodologies, including longitudinal behavioral studies, electroencephalography (EEG), magnetoencephalography (MEG), developmental magnetic resonance imaging (MRI), and analyses of functional connectivity [9,18,19,35,36,37]. Although direct observation of functional neural ensemble dynamics in human infants remains challenging, these approaches provide indirect measures of increasing neural coordination, specialization, oscillatory organization, and large-scale integration across development [20,22,24].

Sensorimotor calibration also plays a critical role in the development of multisensory integration. Early in life, sensory modalities are only loosely coordinated, with visual, auditory, and somatosensory systems operating with limited alignment [17]. Through repeated interactions with the environment, the brain learns to associate signals across modalities, leading to the formation of integrated representations. These processes depend on the coordinated activation of neural populations across different sensory systems, consistent with the proposal that functional neural ensembles may serve as integrative units of processing across sensory systems [17].

The refinement of neural ensembles during this period is not uniform across brain regions. Primary sensorimotor areas tend to mature earlier, reflecting their direct involvement in processing movement-related information. In contrast, higher-order association areas, including prefrontal regions, develop more gradually, relying on the progressive integration of sensorimotor and perceptual information [18,19]. This differential timing contributes to the hierarchical organization of neural systems, in which lower-level sensorimotor systems are thought to provide a developmental foundation for the emergence of more complex cognitive functions. This developmental gradient is consistent with broader neuroconstructivist accounts in which higher-order cognitive functions emerge through the progressive reorganization and integration of lower-level sensorimotor systems [16,18,19].

From a developmental perspective, the interaction between movement and neural organization can be understood within a broader framework of optimal regulation. Several developmental models have proposed non-linear relationships between activity levels and functional outcomes [12], suggesting that both insufficient and excessive stimulation may be associated with less optimal developmental trajectories. Moderate, variable, and context-sensitive movement appears to provide the most effective conditions for neural development, supporting the balanced refinement of ensembles across systems. This principle extends across the lifespan but is particularly critical during early development, when neural systems are most sensitive to environmental input.

The consequences of disrupted sensorimotor calibration further underscore its importance. Conditions that limit movement or alter sensory feedback, such as prematurity, neurological injury, or developmental disorders, are associated with atypical patterns of neural connectivity and coordination. These alterations can lead to persistent differences in the organization and function of neural ensembles, affecting cognitive, motor, and social outcomes, al-

though the specific mechanisms linking altered sensorimotor experience to later outcomes remain incompletely understood. Such findings highlight the necessity of early sensorimotor experience for typical neural development and reinforce the view that ensemble formation is fundamentally an experience-dependent process [1].

Within the developmental framework proposed here, the postnatal period may be viewed as a phase of ensemble refinement and stabilization during which early patterns of coordinated neural activity are progressively shaped by sensorimotor experience. Through cycles of movement, feedback, and neural adaptation, functional ensembles become increasingly specialized, temporally coordinated, and integrated within broader network structures. This process transforms the proto-ensembles established during prenatal development into the more stable and flexible configurations required for higher-order cognition.

4. Childhood: Specialization, Plasticity, and Network Formation

Following the early postnatal period of sensorimotor calibration, development enters a phase characterized by increasing selectivity, efficiency, and functional differentiation of neural activity. Childhood is not simply a period of growth but one of progressive stabilization of coordinated neural activity in which functional neural ensembles are proposed to become increasingly tuned to task demands and environmental structure. This transition reflects the cumulative effects of prior developmental processes, including spontaneous activity, sensorimotor interaction, and early oscillatory coordination, now operating within increasingly structured neural systems [20].

A defining feature of this period is the shift from broadly distributed and variable activation patterns toward more selective and reliable ensemble configurations. Early in development, neural responses are often diffuse, with widespread activation across multiple regions. As experience accumulates, activity becomes more focused, reflecting the strengthening of relevant pathways and the suppression of less efficient or redundant connections. This process is supported by ongoing synaptic pruning, myelination, and activity-dependent plasticity, which together contribute to the refinement of neural circuits [16,21,34].

Within the present framework, this refinement is hypothesized to be reflected in increasing specificity of coordinated activity patterns. Ensembles that are repeatedly engaged in similar contexts become more stable and efficient, while those that are less frequently recruited are weakened or eliminated. This selective stabilization enables the emergence of distinct functional systems supporting perception, action, language, and higher-order cognition. Importantly, these systems are not static modules, but dynamic configurations of ensembles that can be flexibly recruited depending on task demands [1].

Abilities such as working memory, inhibitory control, and cognitive flexibility emerge gradually across childhood and are supported by increasing coordination among distributed neural populations, particularly within frontoparietal and cingulo-opercular systems [38,39,40]. Early executive function is characterized by variability and limited stability, reflecting the ongoing maturation of the neural ensembles supporting these processes. Across development, performance improvements correspond to greater consistency and precision of coordinated neural activity as well as more effective integration across distributed brain regions [20,36].

A central mechanism underlying this increasing coordination is the maturation of oscillatory dynamics. During childhood, neural oscillations become increasingly stable, differentiated, and hierarchically organized. Developmental changes in frequency-specific activity, including alpha, theta, and gamma oscillations, are associated with improvements in attention, memory, and cognitive control [9,23,35]. These oscillatory dynamics support the temporal coordination of neural activity, enabling functional ensembles to synchronize across both local and distributed neural networks. As oscillatory coherence and cross-regional coordination increase, the brain becomes progressively more capable of integrating information across spatially distributed systems, facilitating the emergence of increasingly complex cognitive functions [20,23,24,35].

Concurrently, childhood is marked by the progressive development of large-scale network organization. Functional connectivity studies demonstrate increasing segregation of specialized networks alongside enhanced integration among them. Networks supporting attention, executive control, and default-mode processing become increasingly differentiated while retaining the capacity for coordinated interaction. From an ensemble perspective, these networks may be understood as higher-order configurations of interacting neural ensembles rather than as isolated functional units. The maturation of network organization reflects the progressive coordination and integration of ensemble-level activity across multiple spatial and temporal scales [20,22,24,37]. The developmental progression from ensemble specialization to large-scale integration and flexible coordination is summarized in Fig. 4 (Ref. [18,19,20,22,23,24,25,35,38,39,40,41,42,43]).

Evidence for increasing specialization and integration during childhood derives from converging findings obtained through functional MRI, diffusion imaging, EEG, MEG, and large-scale network analyses [18,19,20,22,37]. These approaches reveal developmental increases in network segregation, cross-regional coordination, and hierarchical organization, providing indirect evidence for progressively differentiated and integrated patterns of neural activity. Although direct measurement of functional neural ensembles in developing humans remains limited, these

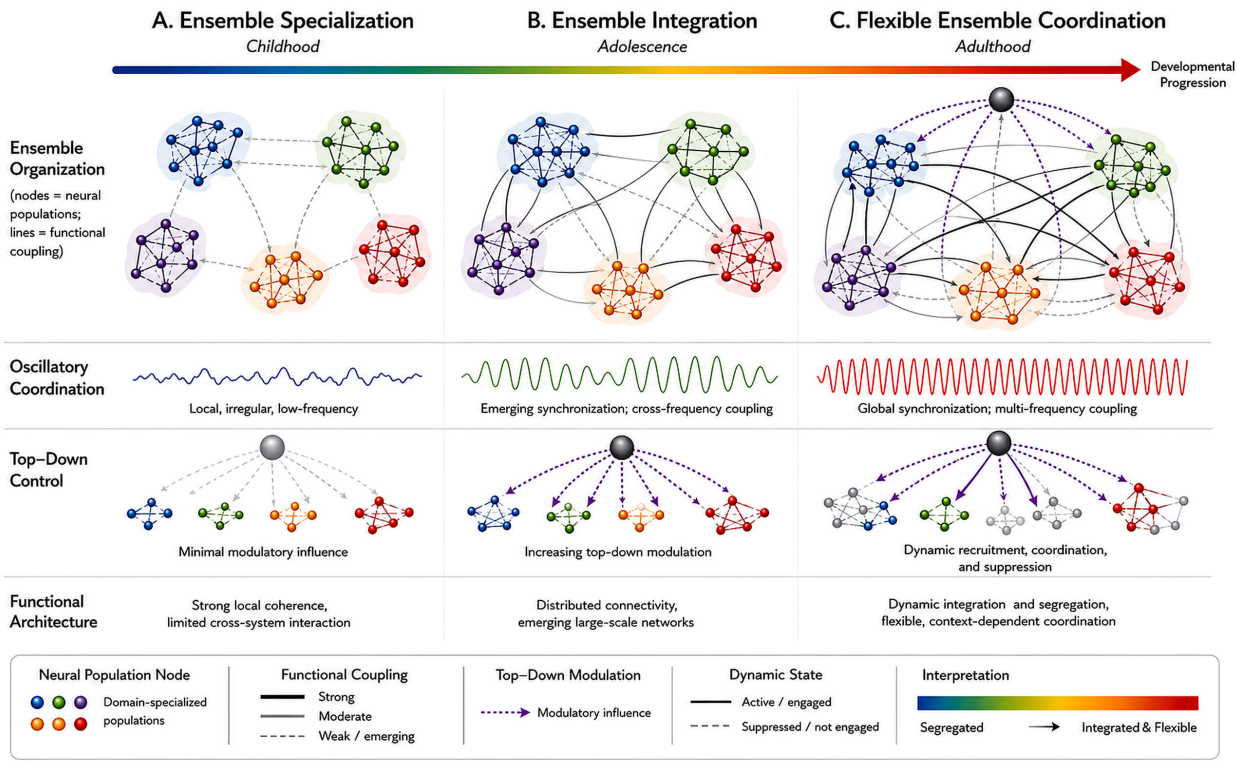


Fig. 4. Hierarchical integration and flexible coordination of functional neural ensembles across development. This figure illustrates the developmental progression from ensemble specialization during childhood to increasing integration during adolescence and flexible coordination in adulthood. The schematic summarizes the framework proposed in this review, depicting how increasingly differentiated patterns of neural activity may become integrated into large-scale systems capable of adaptive and context-dependent cognitive function. (A) Ensemble specialization (childhood). During childhood, coordinated neural activity becomes increasingly differentiated and functionally specialized. Neural populations supporting specific perceptual, motor, attentional, and cognitive processes exhibit strong local coherence and relatively limited interaction across systems. Oscillatory activity remains predominantly local, and top-down modulation is comparatively limited. Functional architecture is characterized by segregation and domain-specific processing [18,19,20,22]. (B) Ensemble integration (adolescence). Across adolescence, maturation of long-range structural and functional connectivity promotes increasing interaction among previously segregated systems [19,20,24]. Oscillatory synchronization becomes more robust and increasingly incorporates cross-frequency coupling [23,35]. Concurrently, top-down modulation strengthens, supporting coordination among distributed neural populations. Functional architecture transitions toward the emergence of large-scale networks integrating information across multiple domains [20,22,24]. (C) Flexible ensemble coordination (adulthood). In mature neural systems, cognitive function depends upon the dynamic recruitment, coordination, and suppression of distributed neural populations according to task demands [25,35,38,39,40,41,42,43]. Oscillatory activity exhibits widespread synchronization across multiple frequency bands, while top-down control systems support context-dependent modulation of neural activity. Functional architecture is characterized by the flexible balance of integration and segregation, enabling adaptive behavior and efficient cognitive control [20,24,39,40,41,42]. The lower rows illustrate developmental changes in oscillatory coordination, top-down modulation, and functional architecture that accompany increasing integration of neural activity across spatial and temporal scales. The progression from segregated to integrated and flexible organization is schematic and does not imply a strictly linear developmental sequence. Rather, the figure summarizes how empirical findings from developmental neuroscience, network neuroscience, and cognitive neuroscience may be interpreted within the ensemble-based framework advanced in this review.

observations are consistent with the ensemble-based framework proposed here.

An additional dimension of this developmental process involves the emergence of hemispheric specialization and temporal asymmetry. Early in life, neural activity is often relatively bilateral and broadly distributed. Across development, increasing functional lateralization emerges, with particular cognitive operations becoming preferentially associated with one hemisphere. This transition reflects not only structural maturation but also developmental changes in the timing and coordination of neural activity across hemispheres. Developmental changes in

timing, connectivity, and interhemispheric communication may contribute to increasingly asymmetric patterns of neural coordination and ensemble activation, supporting more efficient and specialized processing [20,22,24].

The role of experience remains central throughout this developmental period. Learning, education, social interaction, and continued sensorimotor engagement all contribute to the refinement of neural ensembles through activity-dependent plasticity [1,11,16,21,34]. Importantly, the relationship between experience and neural development is not strictly linear. Optimal development appears to depend upon a balance between stability and variability, with moderate and context-sensitive engagement supporting the most adaptive outcomes. Excessive rigidity may constrain exploration and flexibility, whereas excessive variability may impair the stabilization of functional neural patterns. The developing brain operates within a dynamic regime that supports both exploratory adaptation and progressive consolidation of coordinated neural activity [1,11,20,22,34].

The increasing complexity of cognitive behavior during childhood reflects the progressive integration of multiple functional systems. Language acquisition, for example, is thought to involve the coordination of auditory, motor, and semantic processes supported by interacting neural ensembles distributed across temporal, frontal, and parietal regions. Similarly, the development of social cognition is thought to depend on the integration of perceptual, emotional, and executive processes requiring coordinated activity across distributed neural populations. In both cases, cognitive abilities emerge not from isolated brain regions but from the dynamic interaction of specialized yet interconnected neural ensembles operating across multiple spatial and temporal scales [1,20,22,24].

At the same time, this period remains one of significant vulnerability. Disruptions to neural development arising from genetic, environmental, or experiential factors may alter the trajectory of neural ensemble formation and integration across development [1,22]. Conditions such as developmental coordination disorder, attention-deficit/hyperactivity disorder, and autism spectrum conditions have been associated with atypical patterns of neural connectivity, oscillatory coordination, and large-scale network organization [20,22,44,45,46,47,48].

Within the developmental framework advanced here, childhood represents a phase of ensemble specialization and hierarchical organization in which early patterns of coordinated activity are refined into stable, efficient, and functionally differentiated systems. Through processes of selective stabilization, oscillatory synchronization, and network integration, functional neural ensembles are proposed to serve as the building blocks of increasingly complex cognitive functions. This developmental progression sets the stage for the next phase, in which these systems are further integrated and flexibly coordinated to support adaptive behavior.

5. Adolescence to Maturity: Integration and Flexible Control of Neural Ensembles

Adolescence and early adulthood represent a critical phase in which previously established neural systems undergo further integration and functional reorganization. While earlier developmental stages are proposed to establish and specialize patterns of coordinated neural activity, this period is defined by the emergence of flexible coordination across distributed systems, enabling adaptive, goal-directed behavior. The mature brain is thus defined not by increased stability alone, but by its capacity for flexible and context-dependent reconfiguration of neural activity.

A central feature of this transition is the continued maturation of long-range connectivity. Structural and functional connections between distant brain regions, particularly those linking prefrontal, parietal, and subcortical systems, strengthen during adolescence. These changes are supported by ongoing myelination and synaptic refinement, which increase the efficiency and speed of neural communication [12]. From an ensemble perspective, this maturation enables the coordination of activity across spatially distributed neuronal populations, allowing ensembles to operate not only locally but also as components of larger integrated systems.

This expanded coordination underlies the development of cognitive control, including planning, decision-making, and the regulation of attention and behavior. Prefrontal systems play a central role in these processes, acting as hubs that coordinate activity across other brain systems [38]. However, cognitive control does not reside in any single region; rather, it emerges from the dynamic interaction of multiple ensembles across cortical and subcortical networks. The ability to selectively activate, sustain, or suppress specific ensembles allows for flexible adaptation to task demands, supporting complex forms of cognition [41,42].

An essential mechanism supporting this flexibility is the refinement of oscillatory coordination across frequency bands. During adolescence, neural oscillations become increasingly synchronized across regions, with more stable phase relationships and improved cross-frequency coupling [12,35]. These dynamics facilitate the temporal alignment of activity across ensembles, enabling efficient information transfer and integration. For example, interactions between theta and gamma oscillations are associated with working memory and cognitive control, reflecting coordinated activity across prefrontal and hippocampal systems. Such oscillatory mechanisms provide the temporal infrastructure necessary for the rapid reconfiguration of ensemble activity [43].

Another defining characteristic of this stage is the development of network switching and context-sensitive engagement. Functional neuroimaging studies have identified large-scale networks, such as the default mode network (DMN), frontoparietal control network (FPN) [38,39], and

salience network [40], that exhibit coordinated patterns of activation and deactivation depending on cognitive demands [38]. Within the framework proposed here, these networks may be interpreted as higher-order configurations of interacting ensembles rather than independent functional units. The ability to switch between internally oriented processes (e.g., DMN activity) and externally directed tasks (e.g., FPN engagement) depends on the precise coordination and timing of ensemble recruitment and suppression [43].

Evidence for increasing integration and flexible control during adolescence derives from converging findings obtained through functional neuroimaging, electrophysiology, network analyses, and developmental cognitive neuroscience [20,35,38,39,40,41,42,43]. These approaches reveal increasing coordination among distributed systems, enhanced network switching, and more efficient top-down regulation. Although direct observation of large-scale functional ensemble dynamics in humans remains limited, these findings are broadly consistent with the ensemble-based framework advanced here.

The capacity for flexible switching reflects a balance between stability and adaptability. On one hand, ensembles must be sufficiently stable to support reliable representations and learned behaviors. On the other hand, they must remain flexible enough to allow for rapid reorganization in response to novel or changing conditions. This balance is not fixed but dynamically regulated through ongoing interactions between neural systems. The mature brain thus operates within a regime that supports both robustness and plasticity, enabling efficient yet adaptable cognitive function [25,49].

The refinement of inhibitory control mechanisms plays a crucial role in achieving this balance. During adolescence, inhibitory processes become more effective, allowing for the suppression of irrelevant or competing neural activity [50,51]. This selective inhibition is essential for preventing interference between ensembles and for maintaining task-relevant patterns of activation. Dysfunction in these processes can lead to difficulties in attention, impulse control, and behavioral regulation, highlighting their importance for adaptive functioning [50,51].

Importantly, the integration of neural ensembles during this period is influenced by ongoing experience and environmental demands. Education, social interaction, and continued engagement in complex cognitive and motor activities contribute to the refinement of neural coordination. Lifespan perspectives emphasize that the relationship between activity and cognitive function remains non-linear [12], with optimal levels of engagement supporting the maintenance and enhancement of neural function. Even as the brain approaches structural maturity, functional organization continues to be shaped by patterns of use and experience [49,52,53].

Despite these advances, adolescence also represents a period of heightened vulnerability [54]. The ongoing reorganization of neural systems can lead to temporary imbalances in coordination, particularly between limbic and prefrontal regions [54]. These imbalances are associated with increased risk-taking, emotional variability, and susceptibility to environmental influences [55].

By early adulthood, the brain is characterized by increasingly efficient and flexible functional integration [25,53]. Cognitive performance during this period is marked by efficiency, adaptability, and the ability to manage complex, multi-component tasks [53]. However, this state does not represent a fixed endpoint. Rather, it reflects a dynamic equilibrium in which neural systems remain capable of ongoing adaptation and reorganization [49].

This perspective aligns with broader models of lifespan development, in which cognitive function follows nonlinear trajectories influenced by biological, environmental, and experiential factors [12]. Optimal functioning depends not only on structural integrity but also on the dynamic regulation of neural activity, including the ability to recruit and coordinate ensembles effectively across contexts [25]. Thus, the mature brain is best understood not as a static system but as a flexible, dynamically organized network of interacting ensembles [12].

Adolescence to maturity represents a phase of ensemble integration and dynamic control, in which previously specialized systems are coordinated into flexible, adaptive configurations. Through the maturation of long-range connectivity, oscillatory synchronization, and inhibitory regulation, functional neural ensembles are proposed to serve as substrates of higher-order cognition, supporting the complex and context-dependent behaviors that characterize mature brain function.

6. Developmental Disruption and Atypical Ensemble Dynamics

The developmental framework outlined above proposes that cognition depends in part on the successful development and coordination of functional neural ensembles [18]. From this perspective, atypical development can be understood not as the failure of isolated regions or systems but as disruptions in the timing, coordination, and stability of ensemble dynamics across development [54]. Such disruptions may arise through interacting genetic, biological, environmental, and experiential influences operating across multiple developmental timescales. In addition to genetic and neurobiological factors, variations in early-life experience—including caregiver interaction, socioeconomic conditions, stress exposure, sleep quality, nutrition, and environmental enrichment—may influence the refinement of neural activity through their effects on neural plasticity, sensorimotor experience, and learning opportunities. Within the present framework, these influences are viewed

not as independent causes of atypical development but as developmental modifiers capable of shaping the trajectory of ensemble formation.

A central principle emerging from developmental neuroscience is that neural systems are highly sensitive to temporal constraints [18,56]. Processes such as spontaneous activity, sensorimotor calibration, synaptic refinement, and oscillatory synchronization must occur within specific developmental windows [56,57]. Deviations in the timing, sequence, or coordination of these processes can lead to cascading effects, altering the trajectory of ensemble formation [56]. In this context, developmental disorders can be conceptualized as reflecting divergent developmental pathways, in which early perturbations propagate through successive stages of neural organization [18,56].

One domain in which such disruptions have been extensively examined is autism spectrum disorders (ASD) [58]. A growing body of evidence suggests that ASD is associated with atypical patterns of neural connectivity, including altered balance between local and long-range interactions, differences in oscillatory activity [59], and variability in functional coordination across brain regions [60]. From an ensemble perspective, these findings reflect differences in the stability and integration of coordinated neural activity. Within the framework proposed here, early disruptions in spontaneous activity or sensorimotor calibration are hypothesized to contribute to patterns of neural coordination that may be either insufficiently synchronized or excessively rigid, potentially limiting flexible coordination across neural systems [58].

In particular, atypical oscillatory dynamics observed in ASD, including differences in gamma-band activity and reduced cross-frequency coupling, suggest impairments in the temporal coordination of neural populations [59]. Such impairments affect the ability to integrate information across modalities and contexts, contributing to differences in perception, communication, and social interaction [59]. Importantly, these alterations are not confined to specific regions but reflect distributed changes in the coordination of neural activity, consistent with an ensemble-level account [24,59].

Related patterns are observed in conditions involving early disruption of sensorimotor experience, such as prematurity or perinatal brain injury. In these cases, the transition from prenatal to postnatal environments occurs under altered physiological conditions, often accompanied by reduced or atypical movement and sensory input. Given the role of sensorimotor interaction in calibrating neural activity, such disruptions can lead to differences in the refinement of early ensembles. Studies of preterm infants have reported altered functional connectivity [61], delayed maturation of oscillatory activity [8,9], and differences in the organization of large-scale networks [62]. These findings suggest that early deviations in experience-dependent calibration can have lasting effects on ensemble dynamics.

Reduced variability or altered movement patterns in early life can limit the range of sensorimotor contingencies available to the developing brain, potentially constraining the differentiation and stabilization of neural ensembles [14]. Conversely, excessive or poorly regulated activity may lead to inefficient or unstable coordination. These observations are consistent with the principle that optimal development depends on a balance between variability and stability, as reflected in non-linear relationships between activity and cognitive function [12].

Attention-deficit/hyperactivity disorder (ADHD) and related conditions also illustrate alterations in neural coordination, particularly in domains involving inhibitory control, attention, and network regulation. Individuals with ADHD frequently exhibit differences in functional connectivity and oscillatory activity, including alterations in theta- and beta-band rhythms associated with attentional and executive processes [47,63]. From the perspective advanced in this review, such findings may reflect differences in the selective recruitment, coordination, and suppression of neural activity across distributed systems. These alterations may contribute to increased variability and reduced stability of cognitive processing, particularly in tasks requiring sustained attention, inhibitory control, and flexible behavioral regulation [47,63].

Evidence for atypical ensemble-related dynamics is derived from converging methodologies, including EEG, MEG, functional MRI, diffusion imaging, and analyses of functional connectivity [18,20,36,46,47,48,59,60,61,62,63]. Although these approaches do not directly measure functional neural ensembles, they provide indirect indicators of altered coordination, synchronization, oscillatory organization, and large-scale integration. Such observations are broadly consistent with the interpretation that developmental conditions may involve differences in the formation, stabilization, or coordination of neural activity patterns.

Across these conditions, a common theme is that atypical development may involve alterations in the dynamic properties of neural coordination rather than deficits confined to isolated functions. These include changes in the timing of activation, the strength and consistency of co-activation, and the capacity for flexible reconfiguration. Such properties are central to the operation of functional neural ensembles, suggesting that ensemble-level analysis may provide a unifying framework for understanding diverse developmental conditions.

This perspective also highlights the potential for intervention and plasticity. Because functional neural ensembles are shaped by activity and experience, they remain modifiable throughout development. Interventions targeting sensorimotor engagement, environmental enrichment, cognitive training, caregiver interaction, sleep quality, and the reduction of chronic environmental stress may all influence the organization and coordination of neural activ-

ity, thereby supporting more adaptive ensemble dynamics [64,65,66,67,68,69]. Evidence from studies of physical activity, cognitive training, and enriched environments suggests that such interventions can enhance neural plasticity, improve functional connectivity, and support cognitive outcomes even in the presence of early developmental disruption [70]. More broadly, this perspective emphasizes that developmental trajectories emerge through continuous interactions between intrinsic neurobiological processes and the quality of the environments in which development unfolds.

At the same time, the effectiveness of such interventions depends on their alignment with developmental timing [53]. Interventions introduced during periods of heightened plasticity are more likely to influence the trajectory of ensemble formation, whereas later interventions may need to work within more constrained systems [53]. This underscores the importance of early identification and targeted support, particularly in conditions where ensemble dynamics are altered from the outset.

Developmental disorders and atypical trajectories provide critical insight into the mechanisms underlying neural organization. By examining how ensemble dynamics are disrupted, it becomes possible to infer the processes that are essential for typical development. From this perspective, the concept of functional neural ensembles provides a useful framework for understanding both typical developmental organization and variability across the developmental spectrum.

7. Integrative Framework: Functional Neural Ensembles as Developmental Units of Cognition

The preceding sections converge on the proposition that cognition may be understood not primarily as the output of fixed brain regions or static networks, but as the emergent product of developmentally constructed and dynamically coordinated neural ensembles. These ensembles are neither fully specified at birth nor solely shaped by later experience. Rather, they arise through a continuous process of interaction between intrinsic neural dynamics, sensorimotor engagement, and environmental structure, unfolding across multiple temporal and spatial scales. Table 1 (Ref. [3,4,5,7,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25,28,34,35,36,37,38,39,40,41,42,43,44,46,47,48,50,51,52,53,54,55,56,57,58,59,60,61,62,63,70,71,72]) summarizes the principal developmental stages, proposed ensemble characteristics, and associated cognitive outcomes described throughout this review.

7.1 From Activity to Architecture: A Developmental Sequence

We conceptualize the emergence of functional neural ensembles as a developmental sequence of interdependent processes:

(1) Spontaneous Neural Activity (Prenatal Phase)

Intrinsically generated activity establishes initial patterns of coordination across neuronal populations. These patterns form the basis of proto-ensembles, providing the earliest substrate for functional organization.

(2) Sensorimotor Calibration (Early Postnatal Phase)

Self-generated movement and sensory feedback refine early activity patterns, aligning neural dynamics with environmental contingencies. This phase is proposed to contribute to the transformation of diffuse proto-ensemble states.

(3) Selective Stabilization and Specialization (Childhood)

Repeated activation leads to the strengthening of specific co-activation patterns and the pruning of less efficient connections. Patterns of coordinated neural activity become increasingly specialized, supporting distinct perceptual, motor, and cognitive functions.

(4) Integration and Dynamic Coordination (Adolescence to Adulthood)

Long-range connectivity and oscillatory synchronization enable the coordination of ensembles across distributed systems. Mature cognition is proposed to emerge from the flexible recruitment, interaction, and suppression of these ensembles in response to context and task demands.

The proposed developmental sequence, summarized schematically in Fig. 5 (Ref. [3,4,5,7,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25,34,35,36,37,38,39,40,41,42,43,44,45,46,47,48,50,52,53,54,55]), does not represent discrete stages but rather overlapping and recursive processes in which earlier mechanisms continue to influence later development. At each point, the properties of neural ensembles reflect both current conditions and the cumulative history of prior interactions.

7.2 Core Properties of Functional Neural Ensembles

Within this framework, functional neural ensembles are characterized by several core properties:

(1) Coordination: Ensembles are defined by the co-activation of neurons within specific temporal windows, supported by both local circuit dynamics and long-range interactions.

(2) Plasticity: Ensemble structure is shaped by experience through activity-dependent mechanisms, including synaptic modification, pruning, and myelination.

(3) Temporal Organization: Oscillatory dynamics provide the temporal framework for synchronization within and between ensembles, enabling efficient information processing.

(4) Context Sensitivity: Ensembles are not fixed representations but are dynamically recruited and reconfigured depending on task demands and environmental context.

(5) Hierarchical Integration: Ensembles operate across multiple scales, from local circuits to large-scale net-

Table 1. Developmental progression of functional neural ensemble organization.

	Dominant neural processes	Proposed ensemble characteristics	Cognitive/Behavioral outcomes	Representative evidence
Prenatal	Spontaneous neural activity; thalamocortical development; early oscillatory organization	Proto-ensemble organization; diffuse coordination; emerging synchrony	Habituation, sensory responsiveness, early learning capacities	Spontaneous activity, fetal imaging, fetal electrophysiology [3,4,5,7,28,71,72]
Early postnatal	Sensorimotor calibration; activity-dependent plasticity; multisensory integration	Increasing stability; experience-sensitive coordination; refinement of activity patterns	Sensorimotor adaptation, perception-action coupling, early learning	Movement studies, infant EEG, developmental motor research [10,11,12,13,14,15,16,17]
Childhood	Synaptic refinement; myelination; oscillatory maturation; network segregation	Selective stabilization; specialization; increasing efficiency and coherence	Language development, executive function, cognitive flexibility, social cognition	Functional connectivity, developmental neuroimaging, oscillatory studies [18,19,20,21,22,23,24,34,36,37,51]
Adolescence	Long-range connectivity; cross-frequency coupling; inhibitory maturation	Ensemble integration; distributed coordination; increasing flexibility	Cognitive control, decision-making, adaptive behavior	Developmental network neuroscience, electrophysiology [25,35,38,39,40,41,42,43,44,50,52,53,54,55]
Adulthood	Dynamic network switching; top-down modulation; flexible recruitment	Context-dependent coordination; dynamic integration and segregation	Goal-directed cognition, executive regulation, adaptive performance	Network neuroscience, large-scale functional network organization, dynamic neural coordination, and cognitive control studies [25,41,42,43]
Atypical development	Altered timing, connectivity, oscillatory coordination, or sensorimotor calibration	Reduced stability, altered synchronization, impaired flexibility, atypical integration	ASD, ADHD, prematurity-associated differences, developmental variability	Clinical neurodevelopmental studies [46,47,48,56,57,58,59,60,61,62,63,70]

ASD, autism spectrum disorders; ADHD, attention-deficit/hyperactivity disorder; EEG, electroencephalography.

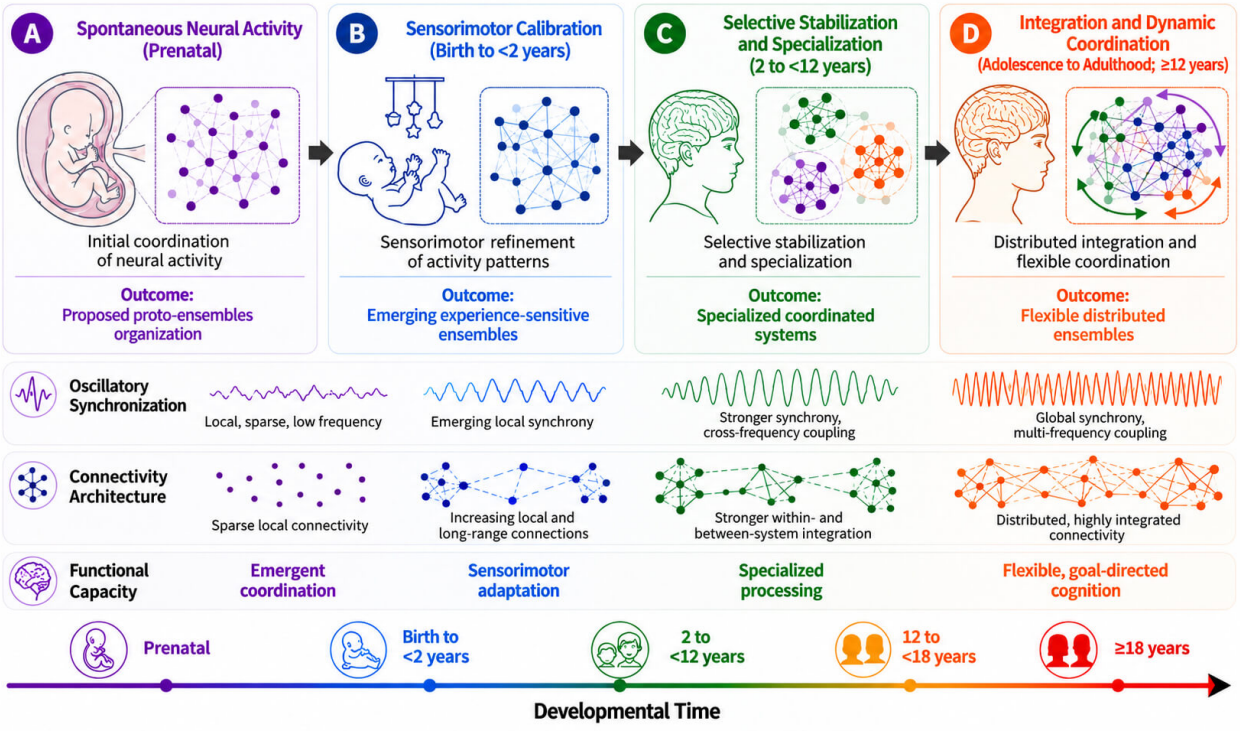


Fig. 5. Proposed developmental cascade from proto-ensemble organization to flexible distributed coordination of neural activity. This figure summarizes the developmental framework advanced in this review, illustrating how patterns of coordinated neural activity may emerge, stabilize, specialize, and become increasingly integrated across development. (A) Spontaneous neural activity (prenatal phase). Intrinsically generated neural activity establishes early patterns of coordination across neuronal populations before extensive sensory experience. Within the present framework, these coordinated activity patterns are hypothesized to provide the basis for proto-ensemble organization and the earliest substrate for functional neural architecture [3,4,5,7]. (B) Sensorimotor calibration (early postnatal phase; birth to <2 years). Following birth, self-generated movement and sensory feedback progressively refine early activity patterns. Through repeated interactions between action and sensation, neural dynamics become increasingly aligned with environmental contingencies, contributing to the emergence of more structured and experience-sensitive patterns of coordination [10,11,12,13,14,15,16,17]. (C) Selective stabilization and specialization (childhood; 2 to <12 years). Repeated activation, activity-dependent plasticity, synaptic refinement, and increasing network organization strengthen efficient co-activation patterns while less stable or redundant connections are reduced. Coordinated neural activity becomes increasingly specialized, supporting perceptual, motor, and cognitive functions [16,17,18,19,20,21,22,23,24,34,36,37]. (D) Integration and dynamic coordination (adolescence to adulthood; ≥12 years). Maturation of long-range connectivity, oscillatory synchronization, and top-down regulatory systems enables increasingly flexible coordination across distributed neural systems. Within the proposed framework, mature cognition is understood as arising from the dynamic recruitment, interaction, coordination, and suppression of neural activity patterns according to contextual and task demands [25,35,38,39,40,41,42,43,44,45,46,47,48,50,52,53,54,55]. The lower rows illustrate parallel developmental changes in oscillatory synchronization, connectivity architecture, and functional capacity. Across development, neural organization progresses from relatively local and weakly coordinated activity toward increasingly integrated, distributed, and flexible forms of coordination. The developmental timeline distinguishes the prenatal period, infancy (birth to <2 years), childhood (2 to <12 years), adolescence (12 to <18 years), and adulthood (≥18 years). These age ranges are operational approximations rather than discrete biological boundaries. Developmental trajectories are schematic and are intended to summarize broad patterns derived from developmental neuroscience rather than represent discrete or strictly sequential stages.

works, forming nested and interacting systems that support complex cognition.

These properties distinguish ensembles from both individual neurons and large-scale networks, positioning them as the intermediate level at which neural activity becomes functionally meaningful.

7.3 Ensembles as the Link Between Development and Cognition

A central implication of this framework is that functional neural ensembles are proposed to provide a link between early neural activity and higher-order cognition. Rather than assuming that cognition emerges from the mat-

uration of predefined modules or networks, this perspective emphasizes the role of developmental processes in constructing the units of cognition themselves.

Early spontaneous activity establishes the conditions for coordination but does not specify functional outcomes. Sensorimotor experience refines these patterns, embedding them within the structure of the environment. Subsequent processes of stabilization and integration transform these patterns into ensembles capable of supporting perception, action, and cognition. In this sense, cognition may be understood as emerging from the progressive organization of neural activity into coordinated ensembles.

This view is consistent with developmental evidence demonstrating that early competencies are not direct reflections of mature cognitive mechanisms but arise from processes of reorganization and refinement. The presence of non-linear developmental trajectories, including periods of regression and reorganization, further supports the idea that neural systems undergo qualitative transformations over time, rather than simple quantitative increases in capacity [12].

7.4 Movement, Timing, and the Regulation of Ensemble Dynamics

A critical extension of this framework concerns the role of movement and temporal regulation in shaping ensemble dynamics. Across development, sensorimotor activity provides a primary mechanism through which neural systems interact with the environment. Movement generates structured input that drives the calibration and refinement of neural activity while also contributing to the maintenance and adaptation of ensemble organization throughout the lifespan.

The relationship between activity and cognitive function is not linear but reflects a balance between variability and stability. Moderate and context-sensitive engagement appears to support optimal neural development, while extremes of under- or over-activation can lead to suboptimal outcomes. This principle underscores the importance of regulated activity and timing in maintaining effective ensemble dynamics, both during development and in mature systems [12].

Temporal coordination, mediated by oscillatory activity [8,9] and conduction dynamics, further constrains the formation and integration of ensembles. Precise timing of neural activation is essential for synchronization across populations, enabling the binding of information across spatially distributed regions. Disruptions in timing, whether due to developmental perturbations or pathological processes, can therefore have widespread effects on cognitive function by altering the coordination of ensemble activity.

7.5 A Unified Framework for Typical and Atypical Development

By conceptualizing cognition in terms of functional neural ensembles, it becomes possible to integrate findings across multiple domains of neuroscience and development [18,25]. Within this framework, typical development may be understood as the progressive refinement and integration of ensemble dynamics, while atypical development reflects deviations in the timing, coordination, or stability of these processes [12,56].

This framework provides a unified basis for interpreting diverse empirical findings, including changes in functional connectivity across development [18], the role of oscillatory dynamics in cognitive function [25], the impact of sensorimotor experience on neural organization [70], and patterns of disruption observed in developmental conditions [56]. Rather than viewing these observations as independent phenomena, the developmental ensemble framework proposes that they represent complementary manifestations of the progressive organization of coordinated neural activity across development. In doing so, the focus shifts from isolated structures to the dynamic organization of interacting neural populations, providing a more comprehensive account of brain-behavior relationships [12].

The developmental principles proposed here may also extend beyond human neurodevelopment. Across many species, spontaneous neural activity, sensorimotor exploration, and experience-dependent plasticity contribute to the progressive organization of coordinated neural circuits during early development. Although the cognitive capacities ultimately supported by these circuits differ substantially across species, the developmental processes through which coordinated neural activity becomes increasingly specialized, integrated, and functionally adaptive appear to reflect broadly conserved neurobiological principles. Comparative developmental studies may therefore help distinguish fundamental mechanisms of ensemble formation from evolutionary adaptations associated with uniquely human cognitive functions, providing an additional avenue for evaluating and refining the developmental ensemble framework proposed here.

7.6 Implications and Future Directions

The conceptualization of functional neural ensembles as developmental units of cognition has several important implications for future research. Understanding ensemble dynamics requires multiscale investigation integrating evidence across levels of biological organization, from cellular activity and local neural circuits to large-scale functional networks. Longitudinal developmental studies will be particularly important for determining how ensemble organization evolves across development and for evaluating the developmental hypotheses proposed in this review. Equally important will be the integration of movement, behavior, and neural activity within the same experimental

paradigms, allowing sensorimotor calibration and ensemble refinement to be examined as interacting developmental processes rather than isolated phenomena.

The present framework also has important implications for clinical translation. Interventions that modify activity patterns, developmental timing, and environmental structure may influence ensemble dynamics and contribute to more adaptive developmental trajectories. At a theoretical level, the framework aligns with emerging perspectives emphasizing prediction, interaction, developmental plasticity, and neuroconstructivist principles while proposing that functional neural ensembles constitute the intermediate developmental organization through which these processes become integrated over time.

Experimental Roadmap for Testing the Developmental Ensemble Framework

A central objective of the present framework is not only to provide a developmental account of functional neural ensemble formation but also to generate experimentally tractable hypotheses that can be evaluated across multiple levels of analysis. The framework therefore lends itself naturally to prospective longitudinal investigation in which neural, behavioral, and environmental measures are obtained repeatedly from early development through adolescence. Such studies would permit evaluation of whether ensemble organization emerges through the progressive stabilization, refinement, and integration of distributed neural activity, as proposed here, or whether alternative developmental models more adequately explain developmental change.

A particularly informative design would begin during late fetal life or early infancy and follow participants across successive developmental transitions. Early assessments could combine structural and functional neuroimaging, electroencephalography, and standardized behavioral measures to characterize the emergence of proto-ensembles, oscillatory synchronization, hemispheric specialization, and early sensorimotor organization. Repeated assessments throughout infancy, childhood, and adolescence would permit examination of how early ensemble dynamics relate to the subsequent development of perception, action, language, executive function, memory, and social cognition.

The framework predicts that developmental change will be reflected less by the appearance of entirely new neural representations than by progressive increases in the stability, flexibility, and coordination of functional neural ensembles across distributed cortical and subcortical networks. Accordingly, longitudinal investigations should emphasize developmental trajectories of ensemble organization rather than relying exclusively on cross-sectional group comparisons. Growth-curve modeling, latent trajectory analyses, network analyses, and computational modeling may provide complementary approaches for examining how ensemble dynamics evolve and how developmental pathways diverge among individuals.

Equally important will be experimental studies capable of directly manipulating developmental variables proposed to influence ensemble formation. Carefully designed interventions involving sensorimotor experience, environmental enrichment, language exposure, social interaction, movement training, sleep regulation, and cognitive learning paradigms could be used to determine whether altered developmental experience produces predictable changes in ensemble organization and behavioral adaptation. Such investigations would provide substantially stronger evidence concerning developmental mechanisms than observational correlations alone.

Rapid advances in developmental single-cell transcriptomics, high-resolution neuroimaging, electrophysiology, and developmental functional-connectivity mapping provide new opportunities to evaluate the developmental ensemble framework across multiple spatial and temporal scales. For example, single-cell transcriptomic studies of the developing human brain have identified temporally and regionally organized patterns of neuronal and glial differentiation, providing cellular-level evidence of progressive developmental specialization [73]. At the systems level, developmental functional-connectivity studies demonstrate progressive reorganization along the sensorimotor-association axis and increasing maturation of cortical hierarchical organization across childhood and adolescence [18,19]. Integrating these complementary approaches with measures of local circuit dynamics and oscillatory synchronization may clarify how molecular and cellular differentiation relates to the emergence of increasingly stable and integrated patterns of neural coordination. Such multiscale investigations provide direct opportunities to test the developmental ensemble framework.

Implementing such longitudinal investigations will nevertheless present substantial methodological challenges. Functional neural ensembles are dynamic developmental entities whose composition, temporal organization, and functional roles are expected to change continuously across maturation. Consequently, longitudinal analyses cannot assume that identical ensemble configurations remain stable throughout development. Future studies will therefore require analytical approaches capable of tracking evolving patterns of coordinated neural activity while accommodating developmental changes in brain structure, oscillatory organization, behavior, and environmental experience. Integrating electrophysiological, neuroimaging, computational, and behavioral measures within the same longitudinal cohorts will be essential for distinguishing stable developmental trajectories from transient developmental adaptations and for evaluating the developmental ensemble framework proposed here.

Importantly, the present framework generates explicit and potentially falsifiable predictions. Failure to ob-

serve developmental relationships among ensemble stability, neural synchronization, behavioral specialization, and adaptive cognitive performance would require revision or rejection of the proposed model. Conversely, convergent evidence demonstrating that ensemble organization progressively emerges through coordinated interactions among neural activity, experience-dependent plasticity, and behavior would provide empirical support for the developmental account advanced here. The scientific value of the present framework therefore lies not only in its integration of existing findings but also in its capacity to generate experimentally testable hypotheses capable of advancing developmental neuroscience.

Although the developmental framework advanced here is grounded in converging evidence from developmental neuroscience, many of its central propositions remain to be tested directly. The experimental strategies outlined above provide increasingly realistic opportunities to evaluate these hypotheses prospectively. Continued advances in longitudinal neuroimaging, electrophysiology, connectomics, computational modeling, and multiscale developmental neuroscience will determine whether ensemble-level organization provides the explanatory bridge between early neural activity and mature cognition proposed in the present framework.

7.7 Testable Predictions of the Developmental Ensemble Framework

The developmental ensemble framework advanced here generates a series of explicit, empirically testable predictions concerning the emergence, organization, and refinement of functional neural ensembles across development. These predictions distinguish the present framework from descriptive accounts of neural maturation by specifying developmental relationships that can be evaluated prospectively and, where appropriate, falsified.

First, the framework predicts that functional neural ensembles emerge progressively through the stabilization and refinement of initially dynamic proto-ensemble activity rather than appearing as fully differentiated functional units. Longitudinal neurophysiological studies should demonstrate increasing temporal stability, reproducibility, and functional specialization of ensemble activity from infancy through adolescence.

Second, developmental changes in ensemble organization should parallel improvements in behavioral performance. As neural ensembles become increasingly coordinated and efficient, corresponding developmental gains should be observed in perception, motor control, language, executive function, memory, and social cognition. Conversely, delayed or atypical ensemble maturation should be associated with greater variability in the acquisition of these cognitive functions.

Third, the framework predicts that experience-dependent plasticity will influence ensemble refinement throughout development. Variations in sensorimotor experience, language exposure, social interaction, environmental enrichment, and educational opportunity should produce measurable differences in the maturation, flexibility, and functional integration of neural ensembles while remaining constrained by underlying developmental neurobiology.

Fourth, atypical neurodevelopment should be characterized not by the absence of neural ensembles but by alterations in their developmental organization, temporal coordination, or adaptive flexibility. Different neurodevelopmental conditions may therefore exhibit distinct developmental trajectories of ensemble maturation despite overlapping behavioral characteristics.

Fifth, interventions that successfully modify developmental experience should also influence the organization and functional properties of neural ensembles. Longitudinal studies combining behavioral intervention with repeated neurophysiological measurement should therefore demonstrate parallel changes in ensemble dynamics and behavioral adaptation.

Finally, the framework predicts that ensemble development will reflect interactions among multiple biological and environmental influences operating across time rather than the effects of any single developmental mechanism. Consequently, prospective studies incorporating neural, behavioral, genetic, and environmental measures should explain developmental variability more effectively than investigations examining any single domain in isolation.

Collectively, these predictions provide a basis for evaluating the developmental ensemble framework through prospective empirical investigation. Confirmation would strengthen the proposed developmental account, whereas systematic failure to observe these predicted developmental relationships would require modification or rejection of the framework. The scientific value of the present proposal therefore rests on its capacity to generate specific, falsifiable hypotheses rather than simply accommodate existing observations.

8. Conclusion

The evidence reviewed here supports the proposal that cognition may be understood as the outcome of developmentally constructed and dynamically coordinated neural ensembles rather than solely as the product of fixed brain regions or static networks. Across fetal, postnatal, and later developmental stages, neural activity is progressively organized through processes of intrinsic coordination, sensorimotor calibration, selective stabilization, and large-scale integration. These processes give rise to ensembles that serve as the functional units through which perception, action, and higher-order cognition emerge.

This framework encourages a shift in the focus of neuroscience from static structures to the temporal dynamics of coordinated activity. It emphasizes that the fundamental properties of cognition, flexibility, context sensitivity,

and integration reflect the dynamic organization of neural ensembles shaped over developmental time. From this perspective, early neural activity is not preparatory but constitutive, establishing the conditions under which cognitive function can arise.

Understanding cognition in terms of ensemble dynamics also provides a unified account of variability across development. Within this framework, typical trajectories may reflect the progressive refinement and coordination of ensemble activity, whereas atypical development can be understood in terms of disruptions to timing, stability, or integration. This view offers a mechanistic basis for linking early neural processes to later cognitive outcomes and highlights the importance of developmental timing and experience in shaping brain function.

Finally, this framework underscores the role of movement, interaction, and temporal regulation in neural development. Sensorimotor activity appears to function not merely as an output of neural systems but as a central mechanism through which ensemble organization is calibrated and maintained. The mature brain is not defined by structural completion but by its capacity for flexible, context-dependent coordination of distributed neural activity.

In summary, the concept of functional neural ensembles provides a developmental framework linking early neural dynamics to the emergence of complex and adaptive behavior across the lifespan.

Author Contributions

GL contributed to the conception. The author contributed to critical revision of the manuscript for important intellectual content. The author read and approved the final manuscript. The author has participated sufficiently in the work and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

Not applicable.

Acknowledgment

Not applicable.

Funding

This research received no external funding.

Conflicts of Interest

Given his role as an Editorial Board member, Gerry Leisman had no involvement in the peer review of this article and has no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to Bettina Platt.

Declaration of AI and AI-Assisted Technologies in the Writing Process

The scientific concepts, theoretical framework, interpretations, and conclusions presented in this manuscript were developed by the author. OpenAI's ChatGPT was used during manuscript preparation and revision to assist with language editing, textual organization, reference checking, and the preparation of graphical materials. Specifically, Figures 1–5 were generated using AI-assisted graphical tools available through ChatGPT, based on scientific descriptions, conceptual relationships, and developmental models provided by the author. The figures were subsequently reviewed and revised under the author's direction to ensure consistency with the manuscript's theoretical framework. The graphical abstract was also prepared using AI-assisted graphical generation and revised under the author's supervision. Generative AI was not used to conduct experiments, generate empirical research data, or independently establish the scientific conclusions of the manuscript. The author reviewed and approved the final text and graphical materials and accepts full responsibility for their scientific accuracy, interpretation, and presentation.

References

[1] Yuste R, Cossart R, Yaksi E. Neuronal ensembles: Building blocks of neural circuits. Neuron. 2024; 112: 875–892. https://doi.org/10.1016/j.neuron.2023.12.008

[2] Hebb DO. The organization of behavior: A neuropsychological theory. Psychology Press: Hove, UK. 2005.

[3] Khazipov R, Luhmann HJ. Early patterns of electrical activity in the developing cerebral cortex of humans and rodents. Trends in Neurosciences. 2006; 29: 414–418. https://doi.org/10.1016/j.tins.2006.05.007

[4] Molnár Z, Luhmann HJ, Kanold PO. Transient cortical circuits match spontaneous and sensory-driven activity during development. Science (New York, N.Y.). 2020; 370: eabb2153. https://doi.org/10.1126/science.abb2153

[5] Kostović I, Judas M. The development of the subplate and thalamocortical connections in the human foetal brain. Acta Paediatrica. 2010; 99: 1119–1127. https://doi.org/10.1111/j.1651-2227.2010.01811.x

[6] Molnár Z, Higashi S, López-Bendito G. Choreography of early thalamocortical development. Cerebral Cortex. 2003; 13: 661–669. https://doi.org/10.1093/cercor/13.6.661

[7] Leisman G, Alfasi R, D'Angiulli A. From sensory motor and perceptual development to primary consciousness in the fetus: converging neural, behavioral, and imaging correlates of cognition-mediated emergent transitions. Current Opinion in Behavioral Sciences. 2024; 60: 101455. https://doi.org/10.1016/j.cobeha.2024.101455

[8] Buzsáki G. Rhythms of the Brain. Oxford University Press: New York. 2006.

[9] Uhlhaas PJ, Roux F, Rodriguez E, Rotarska-Jagiela A, Singer W. Neural synchrony and the development of cortical networks. Trends in Cognitive Sciences. 2010; 14: 72–80. https://doi.org/10.1016/j.tics.2009.12.002

[10] Craighero L. An embodied approach to fetal and newborn perceptual and sensorimotor development. Brain and Cognition. 2024; 179: 106184. https://doi.org/10.1016/j.bandc.2024.106184

[11] Leisman G, Moustafa AA, Shafir T. Thinking, Walking, Talking: Integratory Motor and Cognitive Brain Function. Frontiers in Public Health. 2016; 4: 94. https://doi.org/10.3389/fpubh.2016.00094
[12] Leisman G, Alfasi R, Meiron O, D'Angiulli A. The Inverted U: Exploring the Interconnectedness of Movement and Cognitive Function Across the Lifespan. Wiley Interdisciplinary Reviews. Cognitive Science. 2026; 17: e70020. https://doi.org/10.1002/wcs.70020
[13] Hinnekens E, Barbu-Roth M, Do MC, Berret B, Teulier C. Generating variability from motor primitives during infant locomotor development. Elife. 2023; 12: e87463. https://doi.org/10.7554/eLife.87463
[14] Hadders-Algra M. Early human motor development: From variation to the ability to vary and adapt. Neuroscience and Biobehavioral Reviews. 2018; 90: 411–427. https://doi.org/10.1016/j.neubiorev.2018.05.009
[15] Khazipov R, Milh M. Early patterns of activity in the developing cortex: Focus on the sensorimotor system. Seminars in Cell & Developmental Biology. 2018; 76: 120–129. https://doi.org/10.1016/j.semcdb.2017.09.014
[16] Larsen B, Sydnor VJ, Keller AS, Yeo BTT, Satterthwaite TD. A critical period plasticity framework for the sensorimotor-association axis of cortical neurodevelopment. Trends in Neurosciences. 2023; 46: 847–862. https://doi.org/10.1016/j.tins.2023.07.007
[17] Bianco V, Borgatti R, Berchicci M. Behavioral and Neural Mechanisms Underlying Sensory-Motor Integration. Brain Sciences. 2024; 14: 812. https://doi.org/10.3390/brainsci14080812
[18] Sydnor VJ, Larsen B, Seidlitz J, Adebimpe A, Alexander-Bloch AF, Bassett DS, et al. Intrinsic activity development unfolds along a sensorimotor-association cortical axis in youth. Nature Neuroscience. 2023; 26: 638–649. https://doi.org/10.1038/s41593-023-01282-y
[19] Luo AC, Sydnor VJ, Pines A, Larsen B, Alexander-Bloch AF, Cieslak M, et al. Functional connectivity development along the sensorimotor-association axis enhances the cortical hierarchy. Nature Communications. 2024; 15: 3511. https://doi.org/10.1038/s41467-024-47748-w
[20] Vinck M, Uran C, Spyropoulos G, Onorato I, Broggini AC, Schneider M, et al. Principles of large-scale neural interactions. Neuron. 2023; 111: 987–1002. https://doi.org/10.1016/j.neuron.2023.03.015
[21] Starkey J, Horstick EJ, Ackerman SD. Glial regulation of critical period plasticity. Frontiers in Cellular Neuroscience. 2023; 17: 1247335. https://doi.org/10.3389/fncel.2023.1247335
[22] Munn BR, Müller EJ, Favre-Bulle I, Scott E, Lizier JT, Breakspear M, et al. Multiscale organization of neuronal activity unifies scale-dependent theories of brain function. Cell. 2024; 187: 7303–7313.e15. https://doi.org/10.1016/j.cell.2024.10.004
[23] 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
[24] Wang XJ. Theory of the Multiregional Neocortex: Large-Scale Neural Dynamics and Distributed Cognition. Annual Review of Neuroscience. 2022; 45: 533–560. https://doi.org/10.1146/annurev-neuro-110920-035434
[25] Shine JM, Müller EJ, Munn B, Cabral J, Moran RJ, Breakspear M. Computational models link cellular mechanisms of neuromodulation to large-scale neural dynamics. Nature Neuroscience. 2021; 24: 765–776. https://doi.org/10.1038/s41593-021-00824-6
[26] Volzhenin K, Changeux JP, Dumas G. Multilevel development of cognitive abilities in an artificial neural network. Proceedings of the National Academy of Sciences of the United States of America. 2022; 119: e2201304119. https://doi.org/10.1073/pnas.2201304119
[27] Ciaunica A, Levin M, Rosas FE, Friston K. Nested Selves: Self-Organization and Shared Markov Blankets in Prenatal Development in Humans. Topics in Cognitive Science. 2023. https://doi.org/10.1111/tops.12717
[28] Borsani E, Della Vedova AM, Rezzani R, Rodella LF, Cristini C. Correlation between human nervous system development and acquisition of fetal skills: An overview. Brain & Development. 2019; 41: 225–233. https://doi.org/10.1016/j.braindev.2018.10.009
[29] Bourgeois JP, Goldman-Rakic PS, Rakic P. Synaptogenesis in the prefrontal cortex of rhesus monkeys. Cereb Cortex. 1994; 4: 78–96. https://doi.org/10.1093/cercor/4.1.78
[30] Huttenlocher PR, Dabholkar AS. Regional differences in synaptogenesis in human cerebral cortex. The Journal of Comparative Neurology. 1997; 387: 167–178. https://doi.org/10.1002/(sici)1096-9861(19971020)387:2%3C167::aid-cne1%3E3.0.co;2-z
[31] Zhang LI, Poo MM. Electrical activity and development of neural circuits. Nature Neuroscience. 2001; 4: 1207–1214. https://doi.org/10.1038/nn753
[32] Hua JY, Smith SJ. Neural activity and the dynamics of central nervous system development. Nature Neuroscience. 2004; 7: 327–332. https://doi.org/10.1038/nn1218
[33] Friston K, FitzGerald T, Rigoli F, Schwartenbeck P, Pezzulo G. Active Inference: A Process Theory. Neural Computation. 2017; 29: 1–49. https://doi.org/10.1162/NECO_a_00912
[34] West AE. Genetic Mechanisms of Experience-Dependent Neuronal Plasticity. Annual Review of Genetics. 2025; 59: 435–459. https://doi.org/10.1146/annurev-genet-020325-103824
[35] Cho RY, Walker CP, Polizzotto NR, Wozny TA, Fissell C, Chen CMA, et al. Development of sensory gamma oscillations and cross-frequency coupling from childhood to early adulthood. Cerebral Cortex (New York, N.Y. : 1991). 2015; 25: 1509–1518. https://doi.org/10.1093/cercor/bht341
[36] Derbie AY, Altaye M, Wang J, Allahverdy A, He L, Tamm L, et al. Early life brain network connectivity antecedents of executive function in children born preterm. Communications Biology. 2025; 8: 345. https://doi.org/10.1038/s42003-025-07745-1
[37] Bethlehem RAI, Seidlitz J, White SR, Vogel JW, Anderson KM, Adamson C, et al. Brain charts for the human lifespan. Nature. 2022; 604: 525–533. https://doi.org/10.1038/s41586-022-04554-y Erratum in: Nature. 2022; 610: E6. https://doi.org/10.1038/s41586-022-05300-0
[38] Shenhav A, Banich MT, Beste C, Buschman TJ, Friedman NP, Gratton C, et al. Integrative psychological, computational, and mechanistic approaches to frontal lobe function. In Banich MT, Haber SN, Robbins TW (eds.) The Frontal Cortex: Organization, Networks, and Function. MIT Press: Cambridge (MA). 2024.
[39] Gratton C, Sun H, Petersen SE. Control networks and hubs. Psychophysiology. 2018; 55: 10.1111/psyp.13032. https://doi.org/10.1111/psyp.13032
[40] Uddin LQ, Yeo BTT, Spreng RN. Towards a Universal Taxonomy of Macro-scale Functional Human Brain Networks. Brain Topography. 2019; 32: 926–942. https://doi.org/10.1007/s10548-019-00744-6
[41] Cocuzza CV, Ito T, Schultz D, Bassett DS, Cole MW. Flexible Coordinator and Switcher Hubs for Adaptive Task Control. The Journal of Neuroscience : the Official Journal of the Society for Neuroscience. 2020; 40: 6949–6968. https://doi.org/10.1523/JNEUROSCI.2559-19.2020
[42] Shine JM, Breakspear M, Bell PT, Ehgoetz Martens KA, Shine R, Koyejo O, et al. Human cognition involves the dynamic integration of neural activity and neuromodulatory systems. Nature Neuroscience. 2019; 22: 289–296. https://doi.org/10.1038/s41593-018-0312-0

[43] de Mooij-van Malsen JG, Röhrdanz N, Buschhoff AS, Schiffelholz T, Sigurdsson T, Wulff P. Task-specific oscillatory synchronization of prefrontal cortex, nucleus reuniens, and hippocampus during working memory. iScience. 2023; 26: 107532. https://doi.org/10.1016/j.isci.2023.107532
[44] 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
[45] Rubenstein JLR, Merzenich MM. Model of autism: increased ratio of excitation/inhibition in key neural systems. Genes, Brain, and Behavior. 2003; 2: 255–267. https://doi.org/10.1034/j.1601-183x.2003.00037.x
[46] Song Y, Li Z, Zhu X, Pei G, Hou J, Liu S, et al. A characterization study on electroencephalographic changes and lateralization of functional brain connectivity in boys with developmental coordination disorder. Frontiers in Neurology. 2025; 16: 1591236. https://doi.org/10.3389/fneur.2025.1591236
[47] Sütçübaşı B, Ballı T, Roeyers H, Wiersema JR, Çamkerten S, Öztürk OC, et al. Differentiating Functional Connectivity Patterns in ADHD and Autism Among the Young People: A Machine Learning Solution. Journal of Attention Disorders. 2025; 29: 486–499. https://doi.org/10.1177/10870547251315230
[48] Lum JAG, Hamilton K, Fuelscher I, Barhoun P, Deconinck FJA, De Raeve A, et al. Resting State Electroencephalography (EEG) Reveals Atypical Oscillatory Power in Children With Development Coordination Disorder (DCD). Psychophysiology. 2025; 62: e70084. https://doi.org/10.1111/psyp.70084
[49] Marzola P, Melzer T, Pavesi E, Gil-Mohapel J, Brocardo PS. Exploring the Role of Neuroplasticity in Development, Aging, and Neurodegeneration. Brain Sciences. 2023; 13: 1610. https://doi.org/10.3390/brainsci13121610
[50] Weiss H, Luciana M. Neurobehavioral maturation of motor response inhibition in adolescence - A narrative review. Neuroscience and Biobehavioral Reviews. 2022; 137: 104646. https://doi.org/10.1016/j.neubiorev.2022.104646
[51] Parker AJ, Walker JC, Jordan LS, Takarae Y, Wiggins JL, Dougherty LR. Neural mechanisms of inhibitory control in preadolescent irritability: Insights from the ABCD study. Biological Psychology. 2024; 192: 108856. https://doi.org/10.1016/j.biopsycho.2024.108856
[52] Meredith WJ, Silvers JA. Experience-dependent neurodevelopment of self-regulation in adolescence. Developmental Cognitive Neuroscience. 2024; 66: 101356. https://doi.org/10.1016/j.dcn.2024.101356
[53] Baker AE, Galván A, Fuligni AJ. The connecting brain in context: How adolescent plasticity supports learning and development. Developmental Cognitive Neuroscience. 2025; 71: 101486. https://doi.org/10.1016/j.dcn.2024.101486
[54] Green R, Meredith LR, Mewton L, Squeglia LM. Adolescent Neurodevelopment Within the Context of Impulsivity and Substance Use. Current Addiction Reports. 2023; 10: 166–177. https://doi.org/10.1007/s40429-023-00485-4
[55] Insel C, Cohen AO. More than just a phase: adolescence as a window into how the brain generates behavior. Current Directions in Psychological Science. 2025; 34: 149–156. https://doi.org/10.1177/09637214251313733
[56] Carriba P, Lorenzón N, Dierssen M. Neurodevelopmental disorders: 2023 update. Free Neuropathology. 2023; 4: 8. https://doi.org/10.17879/freeneuropathology-2023-4701
[57] Ampollini S, Ardizzi M, Ferroni F, Cigala A. Synchrony perception across senses: A systematic review of temporal binding window changes from infancy to adolescence in typical and atypical development. Neuroscience and Biobehavioral Reviews. 2024; 162: 105711. https://doi.org/10.1016/j.neubiorev.2024.105711
[58] Dickinson A, Jones M, Milne E. Measuring neural excitation and inhibition in autism: Different approaches, different findings and different interpretations. Brain Research. 2016; 1648: 277–289. https://doi.org/10.1016/j.brainres.2016.07.011
[59] Wang J, Barstein J, Ethridge LE, Mosconi MW, Takarae Y, Sweeney JA. Resting state EEG abnormalities in autism spectrum disorders. Journal of Neurodevelopmental Disorders. 2013; 5: 24. https://doi.org/10.1186/1866-1955-5-24
[60] Odriozola P, Uddin LQ, Lynch CJ, Kochalka J, Chen T, Menon V. Insula response and connectivity during social and non-social attention in children with autism. Social Cognitive and Affective Neuroscience. 2016; 11: 433–444. https://doi.org/10.1093/scan/nsv126
[61] Smyser CD, Wheelock MD, Limbrick DD, Jr, Neil JJ. Neonatal brain injury and aberrant connectivity. NeuroImage. 2019; 185: 609–623. https://doi.org/10.1016/j.neuroimage.2018.07.057
[62] Laureano B, Irzan H, O'Reilly H, Ourselin S, Marlow N, Melbourne A. Myelination of preterm brain networks at adolescence. Magnetic Resonance Imaging. 2024; 105: 114–124. https://doi.org/10.1016/j.mri.2023.11.001
[63] Lenartowicz A, Mazaheri A, Jensen O, Loo SK. Aberrant Modulation of Brain Oscillatory Activity and Attentional Impairment in Attention-Deficit/Hyperactivity Disorder. Biological Psychiatry. Cognitive Neuroscience and Neuroimaging. 2018; 3: 19–29. https://doi.org/10.1016/j.bpsc.2017.09.009
[64] Diamond A, Ling DS. Conclusions about interventions, programs, and approaches for improving executive functions that appear justified and those that, despite much hype, do not. Developmental Cognitive Neuroscience. 2016; 18: 34–48. https://doi.org/10.1016/j.dcn.2015.11.005
[65] Sale A, Berardi N, Maffei L. Environment and brain plasticity: towards an endogenous pharmacotherapy. Physiological Reviews. 2014; 94: 189–234. https://doi.org/10.1152/physrev.00036.2012
[66] Karbach J, Verhaeghen P. Making working memory work: a meta-analysis of executive-control and working memory training in older adults. Psychological Science. 2014; 25: 2027–2037. https://doi.org/10.1177/0956797614548725
[67] Nelson CA 3rd, Zeanah CH, Fox NA, Marshall PJ, Smyke AT, Guthrie D. Cognitive recovery in socially deprived young children: the Bucharest Early Intervention Project. Science. 2007; 318: 1937–1940. https://doi.org/10.1126/science.1143921
[68] Rasch B, Born J. About sleep's role in memory. Physiological Reviews. 2013; 93: 681–766. https://doi.org/10.1152/physrev.00032.2012
[69] Lupien SJ, McEwen BS, Gunnar MR, Heim C. Effects of stress throughout the lifespan on the brain, behaviour and cognition. Nature Reviews. 2009; 10: 434–445. https://doi.org/10.1038/nrn2639
[70] van Praag H. Exercise and Neural Plasticity. Brain Plasticity (Amsterdam, Netherlands). 2024; 9: 1–3. https://doi.org/10.3233/BPL-249000
[71] Thomason ME, Dassanayake MT, Shen S, Katkuri Y, Alexis M, Anderson AL, et al. Cross-hemispheric functional connectivity in the human fetal brain. Science Translational Medicine. 2013; 5: 173ra24. https://doi.org/10.1126/scitranslmed.3004978
[72] Schöpf V, Kasprian G, Brugger PC, Prayer D. Watching the fetal brain at 'rest'. International Journal of Developmental Neuroscience. 2012; 30: 11–17. https://doi.org/10.1016/j.ijdevneu.2011.10.006
[73] Kim S, Lee J, Koh IG, Ji J, Kim HJ, Kim E, et al. An integrative single-cell atlas for exploring the cellular and temporal specificity of genes related to neurological disorders during human brain development. Experimental & Molecular Medicine. 2024; 56: 2271–2282. https://doi.org/10.1038/s12276-024-01328-6