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Not peer-reviewed version

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[Kyrylo Somkin](#) *

Posted Date: 11 February 2026

doi: 10.20944/preprints202602.0837.v1

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Concept Paper

Cognitive Functions of the NCL and PFC: A Comparative Perspective

Kyrylo Somkin

Independent Researcher, Czech Republic; somkinkirilo@gmail.com

Abstract

The prefrontal cortex (PFC) in primates has undergone significant evolutionary expansion, supporting advanced cognitive abilities that underlie complex decision-making, working memory, and planning, ultimately enabling the emergence of human intelligence. In birds, the nidopallium caudolaterale (NCL) functions as a structural and functional analog to the mammalian PFC, exhibiting convergent cognitive capacities despite distinct neuroanatomical organization. This conceptual article presents a comparative analysis of the PFC in primates (e.g., chimpanzees) and the NCL in birds (e.g., crows and African grey parrots), drawing upon current scientific literature to examine their respective roles in higher-order cognition. The study discusses similarities and differences in neural architecture, connectivity, and functional specialization, highlighting both convergent evolution and species-specific adaptations. By integrating findings from neurophysiology, behavioral studies, and evolutionary biology, this article provides insights into how diverse neural structures can give rise to analogous cognitive abilities across taxa, contributing to our understanding of the evolutionary mechanisms that support complex cognition.

Keywords: PFC; neuroscience; animal science; evolutionary psychology; NCL; brain

1. Introduction

1.The brains of birds and primates exhibit profound evolutionary differences, providing a unique opportunity to study alternative neural architectures and the ways in which cognition and behavior can emerge under different evolutionary constraints. While the primate prefrontal cortex (PFC) has become highly developed, supporting advanced executive functions and abstract reasoning, the nidopallium caudolaterale (NCL) in birds has evolved along a distinct pathway, optimizing neural processing in ways that differ from the primate lineage. These divergent evolutionary strategies have resulted in unique cognitive profiles, distinct responses to environmental cues, and varied mechanisms for integrating instinctual drives, hormonal influences, and learned behaviors. By examining these differences, we can gain insight into the evolutionary flexibility of the brain and the interplay between neuroanatomy, genetics, and environment in shaping behavior.

2.The NCL in birds and the PFC in primates represent two solutions to similar cognitive challenges, yet they are structured differently and operate under different physiological constraints. In primates, the PFC supports high-level integration of sensory input, planning, and abstraction, while in birds, the NCL facilitates comparable cognitive capacities despite a radically different organization of neural circuits. Genetic factors have played a key role in these developments. For example, genes involved in neurogenesis, cortical expansion, and synaptic plasticity influenced the development of the PFC in primates, whereas similar but distinct genetic pathways contributed to the elaboration of the NCL in birds. Differences in gene expression and neural development not only shaped structural properties but also affected behavioral tendencies, responses to hormonal stimuli, reliance on instinct, and motivational drives. These differences provide a framework for understanding how cognition can emerge from distinct neuroanatomical substrates.

3.Environmental pressures further shaped these neural adaptations. Birds such as crows and African grey parrots experience ecological and social conditions that select for high cognitive flexibility, problem-solving skills, and sophisticated social learning, while primates, including chimpanzees, evolved under pressures favoring complex social interactions, tool use, and cooperative behaviors. These ecological factors interact with underlying genetic and neurophysiological mechanisms to produce species-specific cognitive profiles. In this context, the large PFC in primates and the NCL in birds have created the potential for the conceptual propagation of cultural units, often referred to as memes. Although the precise mechanisms of meme transmission remain incompletely understood, it is plausible that differences in neural architecture influence how such units are encoded, interpreted, and propagated within social groups. In birds, NCL-mediated processing may favor highly adaptive, context-specific behaviors, whereas in primates, PFC-mediated integration allows for abstract representation and complex social transmission.

4.The interplay between genes, neuroanatomy, and environment also extends to the interaction between instinctual and learned behaviors. Neural structures such as the limbic system interact with higher cortical areas to regulate emotional responses, decision-making, and social cognition. Variations in the prefrontal and NCL circuitry affect how these interactions manifest in behavior, influencing both individual and group-level dynamics. For example, heightened abstraction in the PFC may allow primates to represent symbolic ideas, social hierarchies, or moral concepts, while the NCL's processing may enhance the efficiency of associative learning and adaptive behavioral routines in birds. These divergent pathways offer a lens through which to understand the evolution of cognition and culture across species, as well as the emergence of conceptual behaviors that can be described using the framework of memes.

5.Importantly, memes in this context are not limited to human culture but can be viewed as neurocultural agents that interact with genetic and neural substrates. The propagation of these units is influenced by cognitive constraints, social interactions, and environmental pressures, creating a dynamic system in which memes compete, adapt, and sometimes conflict with instinctual drives or genetic predispositions. In both birds and primates, the combination of advanced neural structures and complex social environments allows for rich interactions between memes, instincts, and genes. These interactions likely contributed to species-specific adaptations in learning, communication, and problem-solving, and in primates, they may have supported the emergence of symbolic thought and culturally transmitted belief systems.

6.This article therefore aims to examine how genes, neural architecture, and environmental conditions contributed to the development of the PFC in primates and the NCL in birds, how these differences manifest in behavior, cognition, and abstraction, and how they facilitated the propagation and interaction of cultural units or memes. By synthesizing evidence from neuroanatomy, genetics, and behavioral studies, we propose a conceptual framework for understanding the evolutionary underpinnings of cognition and the ways in which abstract cultural and social constructs emerge from neural substrates. In doing so, we highlight not only the distinct evolutionary strategies of birds and primates but also the broader implications for understanding the co-evolution of genes, brain, and culture.

2. Main

2.1. Conditions of Brain Development, Evolutionary Trajectories, and Biological Differences

7.The evolutionary divergence between avian and primate brains represents not merely a difference in size or organization, but a fundamentally different solution to similar cognitive and environmental challenges. Birds and primates evolved under distinct ecological pressures, which shaped the development of their higher cognitive centers: the nidopallium caudolaterale (NCL) in birds and the prefrontal cortex (PFC) in primates. These structures are not homologous in a strict anatomical sense, yet they perform partially analogous functions, offering an opportunity to examine alternative evolutionary pathways toward advanced cognition.

8. In primates, the expansion of the neocortex—particularly the PFC—occurred alongside increasing social complexity, tool use, and environmental variability. The PFC integrates sensory input, memory, emotional signals, and social information, enabling long-term planning, behavioral inhibition, abstract reasoning, and flexible decision-making. Its layered cortical structure and extensive connectivity with limbic and sensory regions provide a biological foundation for complex personality traits, social awareness, and the capacity to construct internal models of the external world. These features contribute to the emergence of individuality, self-regulation, and psychologically stable behavioral patterns in primates.

9. In contrast, birds followed a distinct evolutionary trajectory. Their brains are more compact, with a high neuronal density and a nuclear rather than laminar organization. The NCL emerged as a central hub for executive-like functions, integrating sensory information, reward signals, and learned associations. Despite lacking a layered neocortex, the avian brain compensates through dense neural packing and efficient circuitry. This optimization allows for rapid information processing, strong associative learning, and impressive problem-solving abilities, as observed in corvids and African grey parrots. The NCL supports behavioral flexibility and adaptive decision-making, even under conditions requiring innovation and delayed gratification.

10. These biological differences shape the potential development of character, psyche, and personality in each group. Primates, supported by a large PFC, tend toward reflective cognition, extended evaluation of consequences, and complex emotional regulation. This enables nuanced social behavior but may also introduce cognitive constraints, such as increased susceptibility to overanalysis or slower immediate responses. Birds, by contrast, often display swift behavioral adaptation, curiosity, and exploratory tendencies, driven by efficient NCL-mediated processing. Their personalities may appear more situational and context-dependent, yet remain highly consistent within ecological and social frameworks.

12. However, both neural architectures impose limitations. The primate PFC, while enabling abstraction and symbolic thought, is energetically costly and developmentally prolonged, making it sensitive to environmental disruption during critical periods. Additionally, its reliance on higher-order integration may reduce efficiency in rapidly changing or time-critical situations. The avian NCL, although highly efficient, may face constraints in sustaining deeply hierarchical or symbolic representations over extended timescales, potentially limiting the complexity of abstract internal narratives.

13. From an evolutionary perspective, these differences suggest that intelligence, personality, and psychological complexity are not the product of a single optimal brain design, but rather multiple viable solutions shaped by ecological demands. The presence of sophisticated cognition in both birds and primates demonstrates that executive control, behavioral flexibility, and adaptive learning can arise from distinct neural substrates. This challenges anthropocentric assumptions that the primate PFC represents the only or highest pathway to complex mental life.

14. Based on these biological foundations alone, we can already identify meaningful distinctions in cognitive style, emotional regulation, and behavioral tendencies between birds and primates. These distinctions provide a framework for understanding how later layers—such as epigenetic modulation, hormonal influences, and higher-order cognition—build upon different neural starting points. The evolutionary conditions that shaped the NCL and PFC thus establish the biological boundaries and potentials within which more complex psychological, cultural, and abstract phenomena emerge.

2.2. *Epigenetics, Instincts, Hormonal Differences, and Divergent Responses to Identical Stimuli*

15. While evolutionary neuroanatomy defines the structural potential of cognition, the functional realization of this potential is shaped by epigenetic regulation, gene expression dynamics, instinctual mechanisms, and hormonal modulation. In both birds and primates, these interacting factors influence how neural circuits develop during early life and how they later respond to identical environmental stimuli. Differences in these regulatory layers contribute to distinct behavioral strategies, motivational systems, and modes of reward processing.

16. Several genes play a central role in shaping cognitive development and neural plasticity across species. Brain-derived neurotrophic factor (BDNF) is critical for synaptic growth, neuronal survival, and activity-dependent plasticity. In primates, BDNF expression is strongly associated with prolonged cortical development, particularly within prefrontal regions, supporting extended periods of learning, emotional regulation, and executive control. Epigenetic modulation of BDNF during childhood and adolescence can significantly influence stress sensitivity, motivation, and long-term behavioral stability. In birds, BDNF also contributes to neural plasticity but is often linked to rapid learning phases and critical developmental windows, such as song acquisition or spatial learning, reflecting a more temporally concentrated pattern of neural refinement.

17. Early growth response protein 1 (EGR1) is another key gene involved in learning, memory consolidation, and experience-dependent neural adaptation. In primates, EGR1 activity is closely tied to prefrontal and hippocampal circuits, facilitating complex associative learning and behavioral flexibility over extended timescales. In birds, EGR1 expression is strongly activated during tasks involving problem-solving, social interaction, and environmental novelty, particularly within the NCL. This suggests that while the gene serves a conserved function across species, its integration into distinct neural architectures results in different cognitive strategies and learning dynamics.

18. Cell adhesion molecules, including cadherins (CDH), play a fundamental role in neural wiring, synaptic specificity, and the stabilization of neural networks during development. In primates, cadherin-mediated connectivity supports the layered organization of the neocortex and the formation of long-range prefrontal networks essential for abstraction and social cognition. In birds, cadherins contribute to the efficient clustering of neurons within nuclear structures, enabling dense connectivity and rapid signal integration. These differences influence how early experiences shape personality traits, learning styles, and emotional responsiveness.

19. GLUD2, a gene involved in glutamate metabolism and synaptic efficiency, further differentiates cognitive processing between primates and birds. In primates, GLUD2 supports high-energy synaptic transmission in cortical regions, facilitating sustained cognitive effort and complex information integration. In birds, glutamatergic signaling is optimized for speed and efficiency, aligning with the NCL's role in rapid decision-making and associative learning. These metabolic distinctions contribute to species-specific balances between cognitive endurance and responsiveness.

20. Epigenetic regulation interacts closely with these genetic factors, allowing environmental conditions to fine-tune neural development without altering the genetic code itself. Stress, social structure, learning intensity, and hormonal exposure during early life can modify gene expression patterns, influencing long-term behavior. In primates, prolonged developmental plasticity enables sustained epigenetic shaping of prefrontal circuits, often resulting in nuanced emotional control and socially mediated behavior. Birds, while exhibiting shorter developmental periods, display highly sensitive epigenetic responses during critical learning phases, leading to rapid but robust behavioral specialization.

21. Instinctual mechanisms further differentiate how these genetic and epigenetic systems manifest behaviorally. In primates, instinct-driven responses are frequently moderated by PFC-mediated evaluation, allowing impulses to be delayed or recontextualized. In birds, instinctual behavior is more tightly integrated with learning and environmental feedback, producing swift adaptive responses. Consequently, identical stimuli—such as threat, novelty, or reward—can evoke markedly different behavioral patterns across species.

22. Hormonal systems add another layer of divergence. Stress hormones, reward-related neurotransmitters, and reproductive hormones interact differently with the PFC and NCL due to variations in receptor distribution and neural connectivity. In primates, extensive top-down regulation enables hormonal signals to be reinterpreted through social context and long-term planning. Birds, although capable of hormonal modulation, often exhibit a more direct translation of physiological states into behavior, resulting in faster motivational shifts.

23. These distinctions are especially evident in reward processing and the experience of pleasure. Primates often contextualize reward within future outcomes, social expectations, and symbolic

meaning, reflecting the integrative role of the PFC. Birds tend to associate reward more closely with immediate task success, exploration, and environmental interaction, although advanced species demonstrate delayed gratification and strategic choice.

24. Together, genetic regulation, epigenetic modulation, instincts, and hormonal systems gradually shift behavior beyond purely biological imperatives. As responses become partially decoupled from immediate physiological states, cognitive space emerges for behaviors not strictly governed by survival or reproduction. This transition establishes the necessary conditions for abstraction, cultural transmission, and the emergence of higher-order cognitive phenomena, which become central in the next section.

2.3. *Abstract Thinking, Culture, and the Emergence of Memes*

25. The gradual decoupling of behavior from immediate instinctual and hormonal control creates the conditions necessary for abstract cognition and culturally mediated behavior. In both birds and primates, this transition enables actions that are not strictly tied to survival imperatives, such as play, exploratory social interaction, ritualized behavior, and rudimentary forms of humor. These behaviors represent a critical cognitive threshold, where neural processing supports internal representations, symbolic associations, and the transmission of non-genetic information across individuals and generations.

26. Abstract thinking does not emerge uniformly across species, but its foundational elements can be observed in both avian and primate cognition. In primates, the prefrontal cortex supports the manipulation of abstract concepts, hypothetical reasoning, and symbolic representation. This capacity allows individuals to operate on mental models rather than immediate sensory input alone. Birds, particularly corvids and parrots, demonstrate a different but functionally comparable form of abstraction mediated by the NCL. Through associative learning, categorical perception, and flexible problem-solving, birds can generalize rules, recognize patterns, and apply learned strategies to novel contexts.

27. Play behavior provides one of the clearest indicators of abstraction beyond instinct. In primates, play often involves role reversal, symbolic substitution, and socially negotiated rules, suggesting an ability to temporarily suspend instinct-driven hierarchies. Birds similarly engage in play-like behaviors, including object manipulation, aerial acrobatics, and social teasing, which appear to serve cognitive exploration rather than immediate functional goals. These activities are neither directly hormonally driven nor strictly adaptive in the short term, indicating the presence of internally motivated cognitive processes.

28. Humor and playfulness further illustrate this phenomenon. While humor is difficult to define cross-species, behaviors resembling teasing, deliberate violation of expectations, or playful deception have been documented in both primates and birds. Such actions require an understanding of social context, anticipation of another individual's reaction, and the ability to recognize incongruity—key components of abstract cognition. These behaviors suggest that both neural systems can support proto-symbolic interactions that transcend basic instinctual responses.

29. Within this cognitive space, cultural units—commonly referred to as memes—can emerge and propagate. In this framework, memes are not restricted to human language or explicit symbols but include patterns of behavior, social strategies, vocalizations, traditions, and learned norms. In birds, examples include song dialects, tool-use techniques, foraging strategies, and socially transmitted preferences. In primates, memes encompass grooming customs, social rituals, tool traditions, and group-specific behavioral norms. These cultural units persist beyond individual lifespans, indicating transmission mechanisms independent of genetics.

30. Memes interact dynamically with genetic, epigenetic, and instinctual systems. Rather than replacing biological influences, they operate alongside them, sometimes reinforcing and sometimes competing with innate tendencies. For instance, a genetically predisposed behavior may be suppressed or reshaped by culturally learned norms, while epigenetic modulation can enhance receptivity to certain cultural patterns during critical developmental periods. This interaction creates a multilayered system in which behavior is shaped by overlapping biological and cultural constraints.

31. Importantly, memes are subject to variation, selection, and competition. Cultural units that enhance social cohesion, problem-solving efficiency, or environmental adaptation are more likely to persist and spread. Others may fade or be actively suppressed. In this sense, memetic evolution mirrors certain principles of biological evolution, though it operates on different timescales and through different mechanisms. Birds and primates exhibit distinct memetic landscapes shaped by their neural architectures: primates tend toward hierarchical, socially embedded cultural systems, while birds often display distributed, context-dependent cultural transmission.

32. Socialization plays a crucial role in stabilizing and propagating memes. In both groups, juveniles learn through observation, imitation, and interaction rather than direct genetic instruction. Social learning accelerates the spread of cultural units and allows rapid adaptation to changing environments. The presence of play, tradition, and social norms indicates that cognition has moved beyond immediate biological imperatives into a domain where abstract representations influence behavior.

33. These developments also mark the emergence of cognitive phenomena that approach proto-symbolic or proto-cultural systems. While not equivalent to human language or formal religion, such systems demonstrate how abstraction, cultural transmission, and shared meaning can arise from distinct neural substrates. The PFC and NCL thus enable parallel pathways toward cultural complexity, each shaped by its own biological constraints and ecological pressures.

34. The increasing influence of memes represents a fundamental shift in behavioral regulation. As cultural units gain prominence, they begin to guide behavior in ways that are not directly predictable from genetics, epigenetics, or hormonal state alone. This shift sets the stage for higher-order social structures, symbolic traditions, and belief-like systems, which are explored in the following section.

2.4. Social Hierarchies, Ritualization, Fear, and the Emergence of Proto-Religious Structures

35. As abstract cognition and culturally transmitted memes gain stability, they begin to reorganize social behavior at the group level. One of the most visible outcomes of this process is the emergence of structured hierarchies, ritualized interactions, and shared behavioral norms. These phenomena are observed in both birds and primates, yet their underlying neural implementation differs in ways that reflect the distinct properties of the prefrontal cortex (PFC) and the nidopallium caudolaterale (NCL).

36. In primates, social hierarchy is strongly mediated by PFC-dependent integration of memory, emotional evaluation, and predictive modeling. Individuals do not merely respond to dominance cues but actively track social relationships over time, including alliances, reputation, and indirect consequences. This allows primates to navigate complex, multilayered hierarchies in which power is not solely determined by physical strength but by social positioning, manipulation, and strategic behavior. Memes in such systems often take the form of socially reinforced norms, taboos, and ritualized behaviors that stabilize group structure and reduce uncertainty.

37. Birds, particularly corvids and parrots, also demonstrate hierarchical organization, but it is implemented through a different cognitive strategy. The NCL supports rapid assessment of social context, associative learning, and flexible role adjustment rather than long-term social modeling. Hierarchies in birds are often more dynamic and context-dependent, with rank shifting based on immediate interactions, environmental conditions, or coalition formation. Memetic units in avian societies tend to be more behavioral than symbolic, expressed through learned displays, vocal patterns, or interaction strategies rather than explicit social rules.

38. Ritualization emerges as a stabilizing mechanism in both systems. In primates, rituals—such as grooming sequences, synchronized behaviors, or repeated social interactions—serve to reinforce bonds, reduce aggression, and encode social expectations. These rituals are sustained through memetic transmission, often acquiring meaning beyond their immediate function. In birds, ritualized behaviors appear in courtship displays, coordinated group movements, and socially learned routines. Although less symbolically layered, these rituals perform a similar function by structuring social interaction and reinforcing group coherence.

39. Fear, particularly fear of death or existential threat, plays a critical role in shaping these systems. In primates, the PFC enables anticipatory fear by integrating memory, imagination, and abstract representation. This allows individuals to respond not only to immediate danger but to potential or symbolic threats. As a result, fear can become detached from direct stimuli and embedded within cultural narratives, taboos, and proto-belief systems. Memes associated with danger, punishment, or social exclusion gain strength through repetition and collective reinforcement.

40. Birds experience fear primarily through more immediate sensory and associative mechanisms, mediated by rapid NCL-limbic interactions. While anticipatory behavior exists, it is typically grounded in learned environmental cues rather than abstract future scenarios. Consequently, fear-related memes in birds tend to be situational and context-bound, such as learned avoidance patterns or alarm call systems, rather than generalized symbolic constructs.

41. These differences influence the emergence of proto-religious behavior. In primates, especially in early human ancestors, the capacity to abstract fear, death, and agency enables the formation of belief-like structures that attribute intention or meaning to natural phenomena. Such structures are memetically transmitted and reinforced through ritual, storytelling, and social sanction. In birds, while no direct equivalent to religion exists, proto-analogous behaviors can be observed in ritualized responses to environmental forces, persistent traditions, and collective behavioral patterns that transcend individual experience.

42. Altruism further differentiates these systems. In primates, altruistic behavior is often conditional and strategically deployed, influenced by long-term social memory and reputation. The PFC allows individuals to weigh costs and benefits across extended timescales, making altruism a tool for social cohesion or influence. In birds, altruism frequently arises from kin selection, reciprocal interaction, or learned group behavior, mediated by rapid associative processes rather than explicit long-term calculation.

43. Finally, the capacity for social manipulation and proto-political behavior diverges sharply. Primates exploit PFC-mediated abstraction to deceive, form alliances, and reshape social structures through indirect influence. Birds also demonstrate manipulation—such as tactical deception or social learning—but these behaviors are typically immediate and context-specific rather than embedded within complex symbolic frameworks.

44. In summary, both the PFC and NCL support sophisticated social systems shaped by memetic transmission, but they do so through distinct cognitive strategies. The primate pathway emphasizes abstraction, symbolic stabilization, and long-term social modeling, while the avian pathway prioritizes efficiency, flexibility, and rapid behavioral adaptation. These differences illuminate how similar social outcomes can arise from fundamentally different neural architectures, setting the stage for higher-order cognition and structured planning discussed in the next section.

45. Like humans, animals have processes of gradual behavioral normalization. Similar to the Overton window, this can be viewed as the result of the spread of stable group patterns reinforced through social learning and conformity. Experimental data show that in birds, new behavioral patterns spread and become reinforced through observation and imitation, mediated by NCL functions. This mechanism ensures high flexibility and rapid acquisition of new strategies, but limits the ability to abstractly assess acceptable behavioral boundaries.

46. In primates, analogous processes operate differently, in the PFC, where the integration of social cues and executive functions enables the formation of more complex, context-dependent norms. Here, behavioral adaptation takes into account risk assessment, potential consequences, and long-term social consequences, enabling more precise regulation of the acceptable range of behavior at the group level. Thus, in birds, the social reinforcement of behavioral patterns occurs primarily through imitation and conformity, whereas in primates, it is additionally mediated by cognitive control and contextual regulation.

2.5. Logical Reasoning, Problem-Solving, and Experimental Comparisons of Cognitive Efficiency

47. A direct comparison between the prefrontal cortex (PFC) in primates and the nidopallium caudolaterale (NCL) in birds reveals not a simple hierarchy of intelligence, but a competition between distinct cognitive strategies. Experimental data demonstrate that each system excels in different domains of logic, problem-solving, and error correction, highlighting contrasting forms of cognitive complexity.

48. In primates, the PFC enables multi-step reasoning, hierarchical planning, and the manipulation of abstract variables. Experimental tasks involving delayed gratification, sequential decision-making, and rule switching consistently show strong PFC involvement. For example, in tasks where individuals must suppress an immediate reward in favor of a larger delayed outcome, primates rely heavily on PFC-mediated inhibitory control. This capacity allows for long-term planning, hypothesis testing, and the construction of internal models—features essential for scientific reasoning and systematic problem-solving.

49. However, this complexity comes at a cost. PFC-dependent reasoning is slower, energetically demanding, and vulnerable to overload. Experiments involving rapid environmental changes or time-limited decision-making often show that primates hesitate, reevaluate, or commit errors due to excessive integration of variables. In this sense, the PFC introduces cognitive friction: greater logical depth, but reduced immediacy.

50. Birds, by contrast, demonstrate remarkable efficiency in tasks requiring rapid rule acquisition, pattern recognition, and flexible problem-solving. Studies involving corvids and parrots show performance comparable to or exceeding that of primates in certain logical tasks, such as tool use, causal inference, and problem recombination. The NCL supports fast associative learning and parallel processing, allowing birds to adapt quickly to novel challenges with fewer trials.

51. In tasks designed to test causal reasoning—such as string-pulling experiments or multi-step puzzle boxes—birds often reach solutions through rapid hypothesis elimination rather than explicit stepwise planning. This suggests a form of logic that is less hierarchical but highly optimized for environmental interaction. The NCL appears to favor operational simplicity paired with execution speed, rather than deep symbolic manipulation.

52. Error correction provides another critical contrast. Primates typically engage in reflective error analysis, using the PFC to reassess strategies and adjust future behavior. This allows for cumulative improvement over time and the refinement of complex skills. Birds, while also capable of learning from mistakes, tend to rely on immediate feedback loops. Errors are corrected through rapid behavioral adjustment rather than explicit internal reevaluation. This makes avian cognition highly resilient in dynamic environments but less suited to constructing long-term abstract frameworks.

53. Scientific-style reasoning—defined here as systematic testing, hypothesis revision, and rule abstraction—emerges more naturally from PFC-based cognition. Primates can generalize principles across domains and apply learned rules to novel contexts with minimal sensory overlap. Birds can achieve similar outcomes, but often through domain-specific strategies rather than generalized abstraction. This distinction reflects the difference between symbolic reasoning and procedural intelligence.

54. Importantly, experiments comparing working memory capacity reveal that birds achieve high performance despite smaller brain volumes. The dense neuronal packing and efficient connectivity of the avian brain allow the NCL to perform complex computations with fewer resources. In this sense, avian cognition represents an optimization strategy, prioritizing efficiency and speed over representational depth. Primate cognition, by contrast, emphasizes representational richness, enabling layered reasoning but requiring greater biological investment.

55. This contrast can be framed as a competition between two forms of intelligence: depth versus efficiency. The primate PFC enables the construction of theoretical models, long-term plans, and abstract systems such as mathematics, science, and formal logic. The avian NCL excels at real-time problem-solving, adaptive innovation, and rapid learning under constraint. Neither system is universally superior; each reflects a different evolutionary solution to cognitive challenges.

56. Ultimately, the struggle for “intelligence” is not a linear ascent but a branching path. The PFC and NCL represent competing cognitive architectures, each optimizing different aspects of logic and

reasoning. Understanding these differences clarifies how intelligence can manifest through multiple forms of neural organization, setting the stage for an integrated conceptual synthesis in the concluding section.

2.6. Aging

57. Early postnatal development represents the period of maximal neuroplasticity in all vertebrates; however, the temporal allocation, intensity, and functional targets of this plasticity differ markedly between birds and primates. In avian species, pallial structures such as the nidopallium undergo rapid post-hatching maturation. Neurogenesis, synaptogenesis, and activity-dependent refinement occur within a compressed developmental window, often spanning weeks rather than years. Elevated expression of neurotrophic factors, including BDNF and its receptor TrkB, supports rapid stabilization of sensorimotor and associative circuits. This front-loaded plasticity enables young birds to achieve behavioral autonomy early, which is evolutionarily advantageous given high juvenile mortality and ecological demands.

58. In primates, by contrast, early-life plasticity is more prolonged and heterogeneous across brain regions. While primary sensory cortices mature relatively early, associative and executive regions, particularly the prefrontal cortex (PFC), remain highly plastic well into adolescence. BDNF-mediated synaptic remodeling in primates supports not only rapid learning but also the gradual construction of hierarchical and context-dependent representations. As a result, learning speed in early childhood is high in both clades, but in birds it is biased toward fast, task-specific optimization, whereas in primates it supports broader generalization and abstraction.

59. Adolescence represents a critical divergence point between avian and primate neurodevelopment. In birds, most pallial circuits, including those in the nidopallium caudolaterale (NCL), reach functional maturity relatively early. Although experience-dependent plasticity persists, large-scale circuit reorganization is limited. Neurogenesis continues in specific regions, but its role is primarily homeostatic or related to seasonal behaviors rather than structural expansion.

60. In primates, adolescence is characterized by extensive synaptic pruning, myelination, and refinement of long-range connectivity, particularly within the PFC. BDNF signaling during this period supports the stabilization of recurrent networks underlying executive control, working memory, and behavioral inhibition. The prolonged adolescent phase allows primates to adapt neural architecture to complex and variable social environments, but it also introduces an extended window of vulnerability to stress, metabolic disruption, and neurodevelopmental disorders.

61. The faster apparent neurogenesis in birds is not merely a matter of cell proliferation rate, but reflects differences in developmental strategy. High neuronal density, short axonal projections, and reduced reliance on long-range integrative circuits allow birds to achieve functional completeness with fewer developmental iterations. In primates, slower neurodevelopment reflects the need to coordinate multi-layered cortical circuits across large spatial scales.

62. The transition from developmental plasticity to adult stability occurs earlier in birds than in primates. In avian species, the end of growth coincides with the consolidation of behavioral repertoires, after which learning remains efficient but largely incremental. Adult birds exhibit high performance in tasks requiring working memory, problem-solving, and rule learning, supported by the NCL, which functionally parallels the primate PFC despite distinct cytoarchitecture.

63. In primates, full maturation of the PFC may extend into early adulthood. Adult learning speed in primates is generally slower than in juveniles but remains flexible due to persistent synaptic turnover and neuromodulatory plasticity. This allows for lifelong learning but increases energetic costs and susceptibility to age-related decline. Aging reveals some of the most striking differences between birds and primates. Empirical observations suggest that aged birds, including corvids, often maintain cognitive performance across lifespan. For example, an old crow (approximately 20 years) may perform working memory tasks at levels comparable to younger individuals. In contrast, aged primates frequently exhibit marked decline in executive functions; an old monkey (25–30 years) typically shows reduced cognitive control, increased impulsivity, and impaired working memory.

64. One contributing factor is differential vulnerability of executive regions. The primate PFC relies heavily on long-range recurrent connectivity, high metabolic activity, and sustained excitatory-inhibitory balance, making it particularly sensitive to oxidative stress and mitochondrial dysfunction. By contrast, the avian NCL operates with shorter-range circuits, higher neuronal packing density, and lower cumulative metabolic strain.

65. Birds exhibit a lower incidence of neurodegenerative-like phenotypes despite high metabolic rates. This paradox is partly explained by enhanced protection against oxidative damage. Avian genomes show upregulation of antioxidant pathways, efficient DNA repair mechanisms, and proteins that stabilize cellular structures under thermal and metabolic stress. Mitochondria in birds display reduced reactive oxygen species leakage and more resilient membrane compositions, forming a so-called "mitochondrial shield." Additionally, birds express thermally stable and chaperone-like proteins that preserve proteostasis under fluctuating physiological conditions. In primates, although protective mechanisms exist, prolonged lifespan and extended developmental plasticity increase cumulative exposure to oxidative and inflammatory insults. The PFC, with its late maturation and high reliance on BDNF-mediated plasticity, is especially prone to age-related dysregulation, increasing the risk of neurodegeneration.

66. Aging is accompanied by shifts in behavior, instinct expression, and gene transcription in both clades, but the patterns differ. In birds, aging often results in mild reductions in exploratory behavior or flexibility, while core cognitive and instinctual behaviors remain stable. Transcriptional changes tend to preserve neuronal identity and synaptic integrity.

67. In primates, aging is more frequently associated with alterations reminiscent of cognitive decline, including impaired decision-making and reduced inhibitory control. At the molecular level, age-related changes in gene expression affect synaptic plasticity genes, mitochondrial function, and inflammatory pathways, sometimes resembling early-stage neurodegenerative processes. These transcriptional shifts contribute to behavioral phenotypes analogous to senescent cognitive decline.

68. Taken together, these comparisons suggest that birds and primates allocate neuroplasticity differently across the lifespan. Birds concentrate plasticity early, achieving durable and resilient adult cognition, whereas primates distribute plasticity over extended development, enabling complex abstraction at the cost of increased vulnerability during aging.

2.7. Integrative Synthesis and Conceptual Framework

69. The comparative analysis of the prefrontal cortex (PFC) in primates and the nidopallium caudolaterale (NCL) in birds reveals that advanced cognition does not emerge from a single neural blueprint, but from multiple evolutionary solutions shaped by ecological, developmental, and social pressures. Across the preceding sections, a consistent pattern emerges: intelligence is not defined by the presence of specific structures, but by how neural systems organize, prioritize, and integrate information over time.

70. From an evolutionary and developmental perspective, the PFC and NCL represent divergent strategies of cognitive specialization. The primate PFC expands gradually during development, remaining highly plastic well into adolescence. This extended maturation enables the integration of executive control, abstraction, and long-term planning, but also introduces prolonged vulnerability to environmental and social influences. In contrast, the avian NCL develops within a more compact and energetically efficient brain, favoring early functional optimization, dense neuronal connectivity, and rapid acquisition of behavioral competence. These differences set foundational constraints on the potential trajectories of personality, cognition, and behavioral flexibility.

71. Epigenetic modulation, hormonal signaling, and instinctual frameworks further differentiate how these systems respond to identical stimuli. Rather than producing uniform reactions, the PFC and NCL filter sensory and motivational inputs through distinct regulatory architectures. In primates, internal states are often mediated through layered inhibitory control and delayed evaluation, whereas in birds, motivational signals are translated into action through faster feedback

loops. This divergence creates different experiential landscapes, shaping how reward, stress, and novelty are perceived and acted upon.

72. At higher cognitive levels, abstraction, culture, and the emergence of memes highlight the most striking contrast between the two systems. Both birds and primates demonstrate the ability to generate, transmit, and modify cultural units, yet the mechanisms of propagation differ. PFC-driven cognition supports symbolic abstraction, narrative construction, and cross-domain generalization, allowing memes to evolve into complex cultural systems. NCL-driven cognition, while less reliant on symbolic scaffolding, enables efficient imitation, innovation, and playful recombination of behaviors. In both cases, memes interact dynamically with genetic predispositions, epigenetic regulation, and instinctual drives—sometimes reinforcing them, sometimes competing with them.

73. Logical reasoning and problem-solving experiments reinforce the notion that cognitive complexity can manifest through different forms of optimization. The PFC emphasizes depth, hierarchical structuring, and theoretical coherence, while the NCL emphasizes speed, robustness, and adaptability. These are not merely quantitative differences in intelligence, but qualitative differences in how cognition is organized and deployed. Each system excels under specific constraints, revealing that “higher” cognition may be context-dependent rather than universally ranked.

74. Taken together, these findings suggest a conceptual model in which intelligence emerges from the interaction between neural architecture, developmental timing, cultural transmission, and environmental demands. The PFC and NCL can be viewed as alternative computational frameworks—each capable of supporting abstract thought, social complexity, and cultural evolution, but through distinct internal logics. This framework does not dissolve differences between species, nor does it impose a strict hierarchy. Instead, it emphasizes plurality in cognitive evolution.

75. This synthesis naturally leads to broader questions addressed in the Discussion section: how these divergent architectures constrain or enable future cultural complexity, whether similar principles apply to artificial cognitive systems, and how studying non-mammalian intelligence can refine our definitions of abstraction, reasoning, and consciousness itself.

3. Discussion

76. Rather than treating intelligence, culture, or proto-religion as outcomes of a single evolutionary pathway, the model emphasizes functional equivalence between the prefrontal cortex (PFC) in primates and the nidopallium caudolaterale (NCL) in birds, embedded within different biological and developmental constraints.

77. At the core of the model lies the interaction between three layers: (1) neurobiological substrates (PFC or NCL), (2) regulatory systems (genes, hormones, epigenetic modulation), and (3) culturally transmitted units—here conceptualized as memes. These layers do not operate independently; instead, they form a dynamic feedback system in which neural architecture constrains the form of abstraction, while memetic propagation reshapes behavioral norms beyond immediate instinctual or hormonal control.

78. In primates, the PFC supports hierarchical integration of social signals, enabling context-sensitive regulation of behavior, delayed gratification, and abstract evaluation of norms. This allows memes to take symbolic, narrative, and ritualized forms, supporting long-term cultural stability and the emergence of structured belief systems. In contrast, avian cognition, mediated by the NCL, prioritizes speed, flexibility, and associative learning. Here, memes manifest primarily as learned behaviors, vocalizations, and social routines, spreading rapidly through imitation and conformity rather than explicit abstraction.

79. The proposed model frames these differences not as disparities in “intelligence,” but as alternative evolutionary solutions to social coordination and uncertainty management. 80. Proto-religious behaviors, ritualization, fear regulation, and altruism emerge in both systems as byproducts of social normalization processes—analogue to an Overton window—where acceptable behaviors are gradually shaped by group-level reinforcement.

81. Thus, the model suggests that culture and proto-belief systems arise from the interaction of neural constraints and memetic dynamics, rather than from specific brain structures alone. This perspective allows for a unified explanation of convergent social complexity across taxa, while preserving biologically grounded differences in cognition, abstraction, and behavioral regulation.

3.1. Contradictions in the Literature and Novelty of the Model

82. The comparison between the avian nidopallium caudolaterale (NCL) and the mammalian prefrontal cortex (PFC) remains a central debate in comparative neuroscience, primarily framed around homology versus analogy. While there is broad agreement that these structures are not homologous, their functional similarities have fueled ongoing disagreement regarding the legitimacy of direct cognitive comparison.

83. A major source of contradiction lies in neuroanatomical organization. The mammalian PFC is characterized by a six-layered cortical structure, whereas the avian pallium exhibits a nuclear, cluster-based architecture. Historically, this structural divergence led some authors to argue that similar behavioral outputs must rely on fundamentally different computational principles, potentially limiting cross-species functional equivalence. Differences in connectivity patterns, including thalamic inputs, were often cited as evidence against deep comparability. In contrast, a growing body of experimental work supports functional convergence between the NCL and PFC. Both regions exhibit sustained neuronal activity during working memory tasks and show comparable dopaminergic modulation of executive functions. Researchers such as Güntürkün and colleagues have argued that evolutionary constraints significantly limit the number of viable neural solutions for core cognitive problems, leading to convergent functional outcomes despite anatomical divergence.

84. The novelty of the present model lies in moving beyond this binary debate. Rather than opposing structure and function, it reframes intelligence as an emergent property of interactions between neural architecture, regulatory systems (genes, hormones, epigenetics), and culturally transmitted units (“memes”). This approach introduces a non-hierarchical perspective, interpreting the PFC and NCL as distinct evolutionary strategies—favoring depth and symbolic abstraction in primates versus efficiency and rapid adaptation in birds—while explaining how both support complex social norms, rituals, and hierarchical organization.

3.2. Limitations and Self-Critique

85. Several limitations of the present work should be explicitly acknowledged. First, this article is conceptual in nature and does not introduce new empirical data. The proposed framework—particularly the interaction between neural substrates and culturally transmitted units (“memes”)—remains a theoretical construct that requires targeted experimental validation.

86. Second, comparative analysis between avian NCL and primate PFC is constrained by the heterogeneity of available datasets. Differences in experimental paradigms, developmental stages, and measured cognitive domains limit direct quantitative comparison and necessitate reliance on functional analogies. This introduces an inherent risk of oversimplification when mapping complex behaviors across distinct neural architectures and species.

87. Finally, the use of “memes” as a cross-species explanatory unit represents a deliberate abstraction. While useful for integrative modeling, it does not capture the full mechanistic diversity of cultural encoding and transmission, which likely differs substantially between symbolic primate systems and context-dependent avian learning. These limitations define the conceptual boundaries of the model and motivate further refinement.

4. Future Directions and Implications of the Model

88. The conceptual framework proposed in this work opens several important directions for future research across comparative neuroscience, cognitive ethology, and evolutionary psychology.

By treating the avian NCL and primate PFC as alternative evolutionary solutions to similar cognitive demands, the model encourages a shift away from hierarchical interpretations of intelligence toward strategy-based comparisons. This perspective has direct implications for experimental design, theory development, and cross-species interpretation of complex behavior.

89. One immediate research direction involves the development of parallel experimental paradigms capable of probing abstraction, norm formation, and behavioral flexibility in both birds and primates under comparable conditions. Tasks focused on delayed gratification, rule switching, social conformity, and symbolic substitution could help empirically test the predicted differences between depth-oriented (PFC) and efficiency-oriented (NCL) cognitive strategies. Neurophysiological recording and neuroimaging methods adapted for each taxon would allow examination of how similar behavioral outputs emerge from distinct neural architectures.

90. At the molecular and developmental level, future studies could investigate how differences in gene expression, epigenetic regulation, and neuroplasticity timing shape long-term cognitive trajectories. Longitudinal studies examining sensitive developmental periods in birds versus extended maturation in primates may clarify how early efficiency and prolonged flexibility influence learning strategies, aging, and vulnerability to cognitive decline.

91. The integration of “memes” as a conceptual layer offers additional opportunities for formalization. While currently abstract, this framework could be refined by linking specific culturally transmitted behaviors to measurable neural, hormonal, or social correlates. Such an approach may allow cultural dynamics—traditionally treated as qualitative phenomena—to be incorporated into quantitative comparative models without reducing them to purely genetic or instinctive explanations.

92. More broadly, the model has implications beyond comparative cognition. By framing proto-religious behaviors, ritualization, and norm stabilization as emergent properties of social regulation systems rather than species-specific traits, it provides a biologically grounded perspective on the origins of belief, cooperation, and moral behavior. This may contribute to interdisciplinary dialogue between neuroscience, anthropology, and philosophy, particularly in discussions surrounding the evolutionary roots of meaning-making and social cohesion.

93. In summary, the proposed framework is not intended as a final explanatory model, but as a structured lens through which future empirical and theoretical work can be integrated. Its value lies in connecting neural architecture, biological regulation, and cultural dynamics into a unified, testable perspective on cognitive evolution.

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