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# What Can Developmental and Comparative Cognitive Neuroscience Tell Us About the Adult Human Brain?

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## Introduction

An oft-repeated dictum in biology holds that ontogeny recapitulates phylogeny. Despite failures of Haeckl's principle to predict in strict form the morphological, behavioral, or cognitive stages an organism passes through during development, the underlying sentiment continues to inform contemporary approaches to mind and brain. For example, studies of behavior and cognition in developing humans provide an anchor for understanding both intellectual primitives and the nature of representation in animal minds. Conversely, comparative studies of cognition in animals serve to address seemingly intractable questions concerning the roles of innate capacities, culture and language in the development of mature human cognition. And both comparative and developmental studies shed light on the neural mechanisms that subserve the most complex and distinctive cognitive abilities of adult humans, such as the capacity for abstract thought.

Both developmental and comparative approaches to cognition provide uniquely powerful data that can inform the search for homologies in brain and mind. Homologous features of cognition are defined as those psychological and neurobiological traits that evolved in the common ancestor of related phyletic groups that emerge from shared developmental pathways and serve closely related behavioral functions. Nothing in this definition requires that such traits emerge early in development: the developmental pathways that produce homologous patterns of sexual or parental behavior, for example, may be long. Nevertheless, a central discovery of developmental and comparative research on cognitive neuroscience, over the last decades, is that the cognitive traits that humans share with other animals tend to emerge early in human development. This conclusion stems from research probing the behavioral and neurobiological signatures of specific cognitive abilities in human children and nonhuman animals.

Consider, for example, the sense of number. Even in adults, sensitivity to numerosity—a fuzzy sense of number—follows psychophysical principles that characterize the number sense in preverbal infants and animals. Most importantly, the number sense follows Weber's Law in that sensitivity improves with numerical distance and declines with numerical magnitude, as if the underlying representation of numerosity (at least for collections of objects or events greater than 2 or 3) were encoded on a ratio scale (i.e., logarithmically). Moreover, non-human animals, human infants, and human adults represent number abstractly, detecting the common cardinal values of visuo-spatial arrays of objects and temporal sequences of sounds or actions (Meck & Church, 1983; Izard, Sann, Spelke & Streri, in press; Jordan & Brannon, 2006; Jordan, MacLean, & Brannon, 2008; Barth et al., 2005). And finally, numerical representations enter into arithmetic operations of ordering, addition, and subtraction for animals, infants, and adults (Cantlon & Brannon, 2006, 2007; Brannon, 2002; McCrink & Wynn, 2004; Barth et al., 2005).

These three behavioral signatures of number sense are joined by evidence of common brain mechanisms for representing number in non-human animals, human children, and adults. Brain imaging studies show activation of parietal cortex in both adult humans and children when they make numerical discriminations (Piazza et al 2004; Cantlon, Brannon, Carter, and Pelphrey, 2006), and neurons in the fundus of the intraparietal sulcus in macaque monkeys show approximately logarithmic tuning functions for numerosity (Nieder and Miller 2003). In both types of experiments, responses to number are independent of sensory modality and stimulus format, providing evidence for abstract numerical representations (Diester and Nieder 2007). And these quantity representations are transformed by the operations of numerical comparison and arithmetic.

The above studies also begin to shed light on the neural mechanisms by which abstract concepts of number are formed and used. Studies of humans and monkeys implicate the intraparietal sulcus as an important locus of numerical processing. Yet this cannot be the whole story, since a wide array of animals, including birds, fish, and insects, without a cerebral cortex—let alone a parietal lobe—can discriminate number and do so in a way that obeys Weber’s Law (e.g., Gross et al 2009; Rugani, Regolin, and Vallortigara, 2008; Agrillo et al 2009). Number is such a fundamental aspect of the world that its core representation may depend on mechanisms that evolved early in the history of animal life: mechanisms whose operation was amplified by the higher brain systems that emerged later in evolution. Further studies of the underlying neurobiological mechanisms of numerical representation will be instrumental in reconstructing this evolutionary history and enriching understanding of how the human brain represents number abstractly.

The goal of this issue is to evaluate critically the case for cognitive homology in five domains considered fundamental to adult human cognition. Specifically, we have invited reviews of the literature on cognitive development, comparative cognition, and where these studies are sufficiently advanced, neural mechanism, by leading experts in their respective fields. We focus on the principles governing spatial cognition, tool use and physical cognition, social cognition, economic decision making, and numerical thinking as a precursor for symbolic representation. On balance, these reviews favor the hypothesis that both animals and preverbal children are endowed with biological primitives of adult human cognition in all these domains. Yet, uncertainties remain regarding the specific mechanisms that mediate these processes. Further, some of these reviews begin to shed light on unique features of cognition in humans and in other species that have confronted distinct selective pressures that propelled their development along diverging evolutionary paths. Together, these reviews point the way forward to both new approaches to understanding the development and comparative expression of cognition, as well as the kinds of neurobiological data that will be necessary to adjudicate current hypotheses regarding cognitive homologies and differences in these domains.

## The Evidence

Our reviews begin with a paper by Passingham who evaluates the evidence for and against the macaque monkey as a model for human brain function. The author notes that although macaques are often used in neurobiological studies to understand the way the human brain works, there are important differences in both cognition and brain structure between the two species. Although these differences might appear to limit the strong comparisons that can be drawn, Passingham argues that a parallel approach using brain imaging in humans and single neuron recordings in monkeys performing similar, if not identical, tasks provides an important means for assessing functional homology in brain and cognition.

Our focus next turns to the cognitive and neural mechanisms underlying spatial cognition in adult humans, children, and animals. Landau and Lakusta review evidence that reorienting behavior in humans and animals relies on geometric representations of spatial layout, and, moreover, that this information is encapsulated in a way consistent with a cognitive module (cf. Fodor 1983). The authors show that although infants as young as 18 months use geometry to reorient, this capacity changes dramatically over development by incorporating non-geometric information. The authors argue that the uniquely human faculty of language provides a tool that strengthens the integration of geometric and nongeometric information, thus enabling the uniquely human construction of maps of the environment. Complementing this review, Vallortigara reviews recent work on controlled rearing studies in animals to study the role of experience in the use of geometric information for navigation. He finds that, at least in domestic chicks, experience with specific geometries contributes little to the ability to learn and remember geometric information in other environments. He concludes that basic features of natural geometry are largely innate, but in agreement with Landau and Lakutsa allows that language and other types of nongeometric experience influence the development of uniquely human forms of spatial knowledge.

These reviews exemplify how understanding of spatial cognition has advanced through synergistic comparative and developmental studies. Studies of reorientation in human adults and children were based directly on pioneering studies of reorientation in rodents (Cheng, 1986; Gallistel, 1990). The system of representation found in rodents operates in a manner that is highly contrary to human spatial intuitions, and so it is unlikely that students of human development ever would have tested for it, had they not been spurred by comparative research. Moreover, questions concerning the role of experience in the development of the geometric reorientation system are intractable with humans, who do not begin to locomote independently until late in the first year of life. Once research established that the mechanisms of geometry-based reorientation were homologous in humans and other animals, however, the path was open to exploring the role of experience in their development, through the research that Vallortigara describes.

The case of spatial cognition also illustrates that the synergy of comparative and developmental research is symmetric. One vexed question in the study of animal cognition concerns the proper interpretation of animal behavior. What is it like to be a bat, and when is it right to attribute human concepts and computational processes to animals? In the case of spatial cognition, several investigators recently have proposed that animals' reorientation by the geometry of their surrounding layout depends on computational processes that are wholly non-geometric, such as pixel-based image-matching (Cheng, 2008; Wystrach & Beugnon, 2009). Because any given pattern of animal behavior is open to multiple computational accounts, central questions in animal cognition tend to be debated for decades. Studies of human development, however, can help to resolve these debates. Humans have representational capacities that are indisputably geometric: We make maps, measure objects, and prove theorems of formal geometry in high school. If human infants and non-human animals have common mechanisms for representing the geometry of the surrounding layout, and if those mechanisms depend on computational processes that are geometric in the strongest sense, then we should see linkages between children's and adults' use of geometry in navigation tasks and in symbolic, school-based tasks. The studies reviewed by Landau and Lakusta begin to reveal such linkages.

Our review moves from spatial cognition to the related question of knowledge of the physical environment, and specifically how this information is used to guide tool use. Emery reviews current understanding of physical cognition and tool use in both birds and mammals. Surprisingly, he finds that tool use proficiency does not closely predict knowledge of the physical environment in animals. In particular, some species of birds show striking abilities to reason about causality and plan for the future, but these abilities are not restricted to tool-using birds. Building on this review, Csibra argues that even very young children reason functionally about novel objects and their suitability as tools. The author argues that although animals can make and use tools, they do not form enduring representations of goal-oriented actions afforded by tools as children do.

The case of tool use illustrates a second kind of insight that comes from combining comparative and developmental approaches to cognition: These approaches can shed light not only on the cognitive capacities that humans share with other animals, but on those capacities that are unique to our species. Understanding the unique features of human cognition will require further studies of two kinds. First, because tool use emerges only at the end of human infancy, developmental psychologists must probe more deeply the events that lead to its emergence. Second, developmental and comparative neuroscientists must gain detailed knowledge of the neural mechanisms underlying tool use in humans and other animals.

We next consider the development and comparative biology of social cognition. First, Sugita describes his seminal work using controlled-rearing in macaques to study face processing. He finds that monkeys without any experience with faces nonetheless show a strong preference for faces and face-like objects, suggesting the ability to detect, discriminate, and orient to faces is innate. Yet, specific discrimination capacities and preferences are influenced by later experience, indicating a role for experience in the ultimate expression of social behavior. Building on this review, Hare and Rosati examine the diversity of social attention behaviors displayed by nonhuman primates. They argue that how primates attend to other individuals and the objects of their attention, particularly in natural environments, reveals a wide range of cognitive skills that can be applied to social interaction. Ultimately, these mechanisms serve to adapt each species to its particular ecological and social niche, thereby calling into question the very notion of a model species for social attention. Kingstone echoes this sentiment in his review of the cognitive neuroscience of social attention. He argues that laboratory studies often conclude that social attention is a highly specialized, recently evolved, and domain-specific faculty but that such conclusions are called into question by studies conducted in richer, more naturalistic environments. Kingstone advocates a cognitive ethology approach in which more descriptive, observational studies in natural situations inform laboratory studies of specific social cognitive functions. The final paper by Wellman in this section reviews understanding of intentions in developing infants and children. He finds that very young children show impressive understanding of the intentions of others; indeed adult nonhuman primates at best show intentional understanding comparable to a four year old child. Nonetheless, current neurobiological evidence points to a network of brain areas important for social reasoning and understanding intentions, thus endorsing the view that higher-order mentalizing abilities in humans build on ancestral mechanisms that evolved to solve social problems in our nonhuman primate ancestors.

These four reviews provide further examples of how comparative and developmental studies can be mutually illuminating. In particular, Sugita's controlled rearing experiments with monkeys address questions concerning the roles of nature and nurture in social development that are intractable if one restricts one's attention to development in humans. And Wellman's experiments, relating social behaviors that humans share with other animals to higher order cognitive competences that are indisputably social in humans, shed light on the proper interpretation of these same social behaviors in animals.

We next turn to the question of economic decision making in animals and children, and the brain mechanisms supporting such decisions. Santos and Hughes review the evidence for core mechanisms of economic cognition in humans and animals. They find that fundamental aspects of human decision making, which are often considered irrational, result from domain-specific learning mechanisms constrained by limited processing capacity that emerge early in ontogeny and are shared with closely-related nonhuman primates. Complementing this conclusion, Terrace and Son describe the capacity of young children and nonhuman animals to be aware of their own state of knowledge. They find surprising commonalities in these abilities, thus suggesting common underlying mechanisms. Building on these reviews, Rushworth, Mars, and Summerfield ask whether there is a general mechanism underlying both economic decision making and other types of learning. They focus on the hypothesis that experiences are compared with expectations to derive a prediction error that can be used to modify future behavior. Neural circuits involving frontal cortex and striatum contribute to these processes in humans, monkeys, and rats, thus suggesting a common underlying mechanism that may generalize to other types of behavior such as learning about visual and social environments. Finally, Kepecs and Mainen focus on one key component of the reward learning and decision system, the orbitofrontal cortex (OFC). They argue that OFC neurons represent outcome values, concrete outcome attributes, and internal state variables that can be used to evaluate behavior using reinforcement learning. In addition, the authors suggest that OFC also encodes information about confidence, which can also be used to generate predictions as well as inform metacognitive processes as described by Terrace and Son. Together these papers highlight key areas of convergence in the idea that core computational principles embodied in homologous neural circuits mediate learning and decision making in humans and nonhuman animals.

The final section of the volume focuses on the question of symbolic representations—a sine qua non of human cognition. Both papers in this section use numerical cognition as a means for exploring these issues. First Matsuzawa reviews the evidence that chimpanzees can be taught to represent both the cardinal and ordinal aspects of number using Arabic numerals. Although chimpanzees can outperform human adults in memorizing briefly presented numerals, they are far less proficient at matching numbers across modalities as well as other more abstract tasks, suggesting some unique features of human symbolic capacity. Finally, Nieder explores the role of prefrontal cortex in constructing symbolic reference systems. He builds this hypothesis on observations of the responses of neurons in macaque prefrontal cortex to numerosities as well as symbols monkeys have been trained to associate with these values. Nieder argues that granular prefrontal cortex, a novel brain structure in primates, uniquely enables higher-order associations between arbitrary signs and referents such as numerosities. Together, these papers suggest that although the number sense is ubiquitous amongst animals, the primate brain may contain the building blocks for more complex symbolic representation that lies at the core of human cognition.

## Conclusions

Together, the reviews collected in this volume suggest that the field of cognitive neuroscience stands at a pivotal point in its development. Over the last half of the 20$^{th}$ century, psychologists and neuroscientists together made striking progress in unraveling the neural and computational mechanisms that subserve our species' capacities to perceive and act on the world. No comparable progress occurred, however, in understanding our species' central cognitive capacities. What neural events underlie our abstract concepts of number and geometry? What neural processes allow for uniquely human capacities for tool use, language and symbolic mathematics?

Although the final answers to these questions remain to be discovered, the path toward answering them is now becoming clear. Uniquely human capacities build on evolutionarily more ancient capacities that humans share with other animals. Moreover, these capacities tend to emerge over the course of human development, as children harness phylogenetically older cognitive systems and apply them to newer, culturally modulated tasks. Comparative and developmental cognitive neuroscientists, working together, thus can resolve questions about the origins and nature of human knowledge that have mystified human thinkers for millennia.

## Biographies

Michael Platt is Associate Professor of Neurobiology and Evolutionary Anthropology at Duke University, and Director of the Center for Cognitive Neuroscience. His research focuses on the neuroethology and neuroeconomics of human and nonhuman primate behavior and cognition. Michael received his B.A from Yale and his Ph.D. from the University of Pennsylvania, both in biological anthropology, and was a post-doctoral fellow in neuroscience at New York University.

**Elizabeth Spelke** is The Marshall L. Berkman Professor of Psychology at Harvard University. Her laboratory focuses on the sources of uniquely human cognitive capacities, including the capacity for formal mathematics, the capacity for constructing and using symbolic representations such as maps, the capacity for developing comprehensive taxonomies of objects, and the capacity for reasoning about other humans and their social groups.

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