

BOOK REVIEW

Review of:

Understanding the Prefrontal Cortex

By Richard E. Passingham

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Navigating the recurrent perplexity of prefrontal function

By now, it is widely understood that the prefrontal cortex is hard to understand. Some of the greatest thinkers in neuroscience have introduced the problem of prefrontal function as a ‘paradox’, an ‘enigma’, or a ‘riddle’, whether they intended to offer us an answer or merely a paper-length shrug of the shoulders. Yet, as common as these descriptions are, I think they slightly miss the mark. Rather, my favourite description comes from Hans-Lukas Teuber’s famous essay on frontal lobe function; the same one that calls the frontal lobe a riddle in its title. But, it is not the title that I like. It is the first line. Teuber starts his essay referring to prefrontal function as a ‘recurrent perplexity’. I wish he’d used that turn of phrase in the title because it is a perfect description of the state of affairs then, as now.

The prefrontal cortex has been a challenge to scientific study not simply because we don’t understand it, but because we are repeatedly certain we do, only to be entirely overthrown by

new observations. And these coups are not merely subtle adjustments to theory. Our recurring perplexity results in wide-swinging oscillations that have seen scientists conclude on the one extreme that the prefrontal cortex is the seat of all higher mental function only to then resolve for a period that it is not essential for any function at all! Other parts of the cortex are surely mysterious, but can any others claim such a theoretical range?

If we have learned anything through our recurring perplexities, however, it has been that successfully navigating the wreckage of grand theories cluttering the shores of prefrontal neuroscience requires a broad approach. We must consider multiple sources of data, across multiple species and across multiple levels of analysis. While this broad approach is perhaps a recommendation for all of neuroscience, the study of the prefrontal cortex is the paradigmatic case for the value of multidisciplinary, cross-level neuroscience.

It is commonly noted that the prefrontal cortex is greatly expanded in the human brain relative to other species, and we often associate it with quintessentially human functions like planning, decision making, language, and cognitive control. Yet, considering data only from the study of the prefrontal cortex in humans is perilous. First, there is the practical issue that we mostly lack direct access to the organ of primary interest in humans, which limits the data we have available. By contrast, there is now a wealth of data available about prefrontal cortex, from anatomy to detailed physiology, in non-human primates. Ignoring these developments is almost sure to lead one astray. Further, a narrow view on the human brain also directs attention away from the commonalities in function humans share with other species that also have a prefrontal cortex.

That commonality is essential to keep in mind, as it constrains how we theorize, whether it is at a functional or computational level of analysis or at the level of neural operations in the brain.

For this reason, Richard Passingham's new book, *Understanding the Prefrontal Cortex*, lives up to its brazen title and is essential reading for any neuroscientist interested in this area. Drawing on his remarkable depth of knowledge, built over a long and distinguished career, Passingham brings the latest developments in prefrontal neuroscience to his readers across a staggering array of data sources, species, and theoretical levels. From this breadth of scientific observation, he paints a unique, coherent, and compelling picture of prefrontal cortex function.

In its opening, the book lays out a recipe for understanding prefrontal cortex that is built on three rubrics. First, we should understand the function of prefrontal areas in terms of their advantages for natural selection among our primate ancestors. Thus, rather than a primary focus on psychological or computational functions, Passingham's functional analysis focuses on foraging behaviours of primates and how these changed and adapted to their ecological niche over time, while that niche itself changed. This approach offers us principles by which to consider functional homology between human and other primate prefrontal cortex.

Second, different prefrontal areas are distinguished in terms of their anatomical connection with other areas of the brain. Connectivity determines the input to an area and its output. As such, the particular pattern of connections of a given region – what Passingham terms its connectional fingerprint – provides essential clues to its function.

Third, armed with an understanding of the selective advantage and connectivity of areas of the prefrontal cortex, the book seeks to characterize the neural operations that transform inputs to outputs. This last goal is perhaps where the book is most ambitious, but it is a crucial objective, nonetheless. Considering neural operations goes beyond a functional characterization of different areas. It promises insight into the interactions among the networks of prefrontal cortex in terms of the propagation and transformation of information needed for behaviour.

With this approach established, the book moves on in the next chapters to consider the evolution of granular cortex in the primate brain and then the functions of five major subdivisions of the prefrontal cortex. Throughout, the rubrics of selective advantage, connectivity, and neural operations serve as thematic touchstones for discussing these topics. Thus, for example, it is argued that medial prefrontal cortex is distinguished by its role in retrieval of actions that would be useful for foraging, transforming information about the context into memories of actions and their outcomes. In contrast, dorsal prefrontal cortex is crucial for supporting memory for order, and thus transforms inputs from other association cortices into sequences of action that influence premotor areas. And so forth. What emerges from these discussions is a picture of an interactive prefrontal network for planning, evaluating, and performing actions that have adaptive value for the animal. In these sections, Passingham is clearly in his element, integrating across studies of anatomy and physiology in the non-human primate with ease, while also considering the ecological niche in which this all evolved. His scholarship and depth on these topics come across clearly throughout these chapters.

The final chapters of the book move to more integrative questions of what characterizes prefrontal cortex function as a whole and then the particular expansions and functions of the human prefrontal cortex. Though the focus is broader here, and necessarily more speculative, the book still grounds its theory in data across species and with reference to its three rubrics. The comparative approach remains strong throughout, such as in considering the evolutionary changes in the human prefrontal cortex and their relationship to selection pressures. The task is also notably harder here, particularly in the final chapters that focus on topics like reasoning, language, and culture for which the connection to the non-human primate is not as clear cut as in earlier chapters. Nonetheless, the book manages to maintain its theme and focus, and we are treated to several unique insights about these higher functions offered from the perspective of primate evolution.

Throughout, the insights into prefrontal function that can be gleaned from careful comparative work, whether in anatomy or function, are the book's clearest strength. Its further emphasis on the brain as a computational network, gives it a welcome theoretical heft. And really, for anyone who wants to gain a strong background in what we have learned from the study of the macaque monkey, this book should be your first resource. Passingham is a foremost scholar in this domain, and his sophisticated understanding comes through in every chapter.

My one minor critique of the book is that its cross-level emphasis is mostly only one way. Specifically, insight and discovery are usually presented as coming from observations in the monkey, whereas data from humans are mostly confirmatory of those observations. This approach misses an opportunity to take full advantage of cross-species data because true

divergences can often be informative. Furthermore, human cognitive neuroscience of prefrontal function has grown in its sophistication considerably in the last decade or so; and it will continue to do so. Thus, in addition to data from a number of sources beyond fMRI, including a recent growth in data from intracranial recordings, computational cognitive neuroscience approaches to both analysis and theory have offered a number of core insights that have transformed thinking about how the prefrontal cortex carries out its functions. It would be informative to know how these insights from human neuroscience also affect how we look at data from the non-human primate.

But, really, this is a quibble. The book's strength is in its full embrace of its particular approach. Given its recipe, it pushes theory as far as it is able. As a result, Passingham gives us a fascinating and masterful look at what cross-species work, and particularly research with the macaque monkey, can teach us about prefrontal function. At this, he is brilliant. It is his prerogative to leave other perspectives and approaches to others.

Understanding the Prefrontal Cortex should be required reading for anyone interested in prefrontal cortex function. It offers a comprehensive and coherent view of prefrontal function informed by a large body of scientific work from one of the top scholars in the field. This book is an antidote to narrow thinking about prefrontal cortex. If we learn the lessons of this approach, perhaps we won't suffer our recurrent perplexity about the prefrontal cortex. Indeed, maybe we'll start to understand it.

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