Uncertainty rules

Neuroeconomics seeks to move brain studies beyond the fixed reflex.

Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics
by Paul W. Glimcher
MIT Press: 2003. 375 pp. $37.95, £25.50

P. Read Montague

> *"Doubt is not a pleasant condition, but certainty is an absurd one."*
> **Voltaire**

Uncertainty. The mere sound of the word elicits a shaky feeling, and in Voltaire's case, an unpleasant one. Uncertainty makes investments risky and decisions difficult, and, for better or worse, it spices most experiences. Engineers try to control it, financiers try to reduce it, and it haunts most of our everyday decisions. According to Paul Glimcher, we should embrace uncertainty, model it and use it to connect our growing knowledge of brain function to cognition. And from where will the new neural models of uncertainty arise? Economics. This premise is enticing, but the scientific issues in this book require a lot of unpacking. Who is Paul Glimcher and what is he saying?

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Crash course: what can the 1929 New York stock-market collapse teach us about the brain?

A talented neuroscientist at New York University, Glimcher has produced the first full-length book in the fledgling field of neuroeconomics. This nascent area, which has already attracted several economists and neuroscientists, assumes that the brain generates economic behaviour; consequently, economics can benefit from neuroscience. The benefits can also flow in the reverse direction: economic theory can be used to frame, model and understand neuroscience experiments. Glimcher is not just enthusiastic about this latter direction, he's downright evangelistic. To fully understand the nature of his fervour, one has to tackle the entire book.

Glimcher's enthusiasm derives from a conceptual problem that he thinks has plagued most neuroscience research since the time of René Descartes. Glimcher argues (across four chapters) that Descartes' legacy is an implicit model, shared by most neuroscientists, in which the reflex is the underlying mechanism from which more complicated functions such as decision-making are constructed.

We all know about reflexes. If you knock the knee with a rubber mallet, signals return to the spinal cord, relay to output neurons there, and cause an extension of the lower limb. Hold a candle to an outstretched hand and the hand withdraws, again a simple reflex. Glimcher's claim is that this idea of the reflex ossified into a neural prescription for the way in which all complex behaviours are constructed. According to Glimcher, the idea of the reflex provides "a simple set of basic operations that could be combined in different ways to yield a working model for any determinate behavior". He calls this idea 'reflexology'. Most readers will probably assume that Descartes and maybe some of the more strident behaviourists are the only reflexologists. Wrong, says Glimcher — the vast majority of neuroscientists are basically reflexologists in this sense. And so too are all the neural-network people. Yikes! And what's worse, we really aren't aware of our problem. The case that Glimcher builds has many parallel streams and can be difficult to follow. Let's continue to unpack his ideas.

Glimcher thinks that neuroscience is in this state because we wrongly view 'reflex thinking' merely as a way of collecting data about simple nervous systems or small isolated parts of complex nervous systems. Instead, says Glimcher, reflexology is really a theory, or a philosophical stance on how to break neural function into its component pieces, and it is woefully inadequate. But there is a solution: computational goals and economic analysis.

According to Glimcher, the computer scientist and neural theorist David Marr was the first to propose a way out of the murky waters of reflexology. Glimcher praises Marr's focus on the types of computational problem that the nervous system is trying to solve. He quotes Marr: "An algorithm is likely to be understood more readily by understanding the nature of the problem being solved than by examining the mechanism (and the hardware) in which it is embodied."

With that development in hand, Glimcher defines the objective of all behaviour: "The goal of the nervous system, ultimately, must be to produce motor responses that yield the highest possible inclusive fitness for an organism." The idea is that the invisible hand of fitness has long sculpted the way that neural systems deal with an uncertain world, and that we should expect to find neural modules dedicated to dealing with uncertainty. As Glimcher explains over five chapters, these modules are best examined using economically framed theories.

The next section of the book is the most engaging as the author has personalized the descriptions. These chapters cover a series of experiments in which behaviour and neural activity were measured concurrently to discover how neural activity relates to the optimal and suboptimal behaviour expressed by the experimental animals. Glimcher also delivers a short primer on game theory and its applications to behavioural ecology and neuroscience.

The most interesting discussion point is Glimcher's assertion that there are two types

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of uncertainty: reducible and irreducible. The former is uncertainty about the external world, and can be reduced through exploration and learning. Only limited resources prevent this type of uncertainty from being completely eliminated.

Irreducible uncertainty, on the other hand, is more interesting, especially for its effect on behaviour. As Glimcher points out, Werner Heisenberg's uncertainty principle makes clear that the physical world has a quantifiable level of irreducible uncertainty that no amount of measurement or knowledge can eliminate. Glimcher extends this claim to the behavioural realm using game theory. The basic idea is that organisms will express irreducible uncertainty in their behaviour. The driving constraint that selected for such irreducible uncertainty is the need for interacting organisms to outperform others with whom they compete or on whom they prey. If organisms had only very complicated strategies for behaviour, it is conceivable that over millions of years a competitor could adapt to those strategies. Irreducible uncertainty, as a component of a behavioural strategy, cannot be learned and exploited by an opponent. Glimcher offers several concrete examples of these ideas. One take-home message is that most complex creatures should have internal processes that are roughly equivalent to a random-number generator.

Glimcher's central programme outlined in the book is laudable: determine exactly what a particular behaviour is 'for', quantify it in formal economic terms, and design experiments around the formal model. As he freely admits, this formula, although beguiling, is easy to state but hard to carry out. It reminds me of the maxim of novelist W. Somerset Maugham: "There are three rules for writing the novel. Unfortunately, no one knows what they are." Although it's not quite that bad in neuroscience, some features such as conscious awareness are difficult to understand from a computational perspective.

On balance, the book is provocative, encouraging a serious reconsideration of the utility of most neurophysiological work in alert animals. Is it really true that all such efforts are hamstrung by the implicit bogeyman of reflex theory? In what sense do present-day neurophysiologists make implicit assumptions consistent with such a limited view? Glimcher's claim in this area will certainly raise the hackles of more than a few, but what good is a book if it does not provoke? This book will surely ignite discussion and soul searching among serious neuroscientists, and Glimcher has bravely offered us a clear model to talk about. ■

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Beauty and the bees

Form and Function in the Honey Bee

by Lesley Goodman
International Bee Research Association (www.ibra.org.uk): 2003. 220 pp. £25 (pbk), £55 (hbk)

Thomas D. Seeley

The best-studied of all the millions of insect species in the world is the honeybee, *Apis mellifera*, particularly with regard to its sensory physiology and functional morphology. Since the pioneering studies of Karl von Frisch and Robert E. Snodgrass in the early part of the twentieth century, several generations of biologists have carefully measured the powers of discrimination of worker bees in every known sensory modality, analysed the mechanisms underlying these abilities with behavioural and electrophysiological techniques, and used light and electron microscopy to explain the anatomical bases of the bee's behaviour. As a result, the honeybee provides a solid baseline for comparative studies of most aspects of insect behaviour, physiology and morphology.

The composite picture assembled from all this work is one of highly developed sensory capacities and motor performances. Honeybees see the world in colour, perceive shapes and patterns, and can resolve rapid movement. Their olfactory sense is almost identical to ours, and their sense of taste is similar but generally less sensitive. Mechanosensory perception — including touch and sensitivity to airborne and substrate-borne vibrations — is also extremely rich as the bees have thousands of sensory hairs all over the body (even on the compound eyes) and stretch receptors inside the body, giving information on position, movement and orientation relative to gravity. Honeybees even have at least a limited responsiveness to Earth's magnetic field.

These impressive sensory abilities are used for sophisticated manipulatory behaviours such as building beeswax combs and negotiating complicated flowers, flying over distances of several kilometres to reach flower patches rich with nectar and pollen, and communicating with hivemates by means of diverse shakings, tappings and buzzings, and puffings of chemicals.

Form and Function in Honeybees by the late Lesley Goodman is a modern synthesis of honeybee sensory physiology and functional morphology. The last attempt at a comprehensive treatment of the sensory basis of this insect's behaviour was von Frisch's classic *The Dance Language and Orientation of Bees*, published in 1967. Not only has the literature on the subject increased enormously since then, but there is now a greater sophistication in understanding the ecological significance of each sensory ability. For example, it is now known how the bee's colour vision system, which renders bees maximally sensitive to differences in light at wavelengths of about 400 nm (violet) and 500 nm (blue), has fostered the evolution of flowers with pigment combinations that have sharp rises and falls in reflectance in these two regions; such combinations are most easily discriminated and recognized by the bees. There can be no doubt that this book addresses an important need — and meets it beautifully.

Touchy-feely: the antennae and hairs of honeybees are equivalent to human fingertips.

Goodman started planning this book in 1996 with the ambitious goal of producing a volume on how bees function that would be both scientifically rigorous and yet readable (and also affordable) to a broad audience of beekeepers, undergraduate biologists and research scientists. She was unable to finish this project before her death from lung cancer in 1998, but did set up the L. J. Goodman Insect Physiology Research Trust to ensure that the book was completed posthumously. Thanks to the dedicated work of Richard J. Cooter, one of her first PhD students, and Pamela Munn, deputy director of the International Bee Research Association, this final wish was fulfilled magnificently.

The book is utterly gorgeous: each page is lavishly illustrated with beautiful coloured diagrams, specially commissioned paintings

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