
This book – in part history of neuroscience primer, in part philosophy of science reflections, in part a description of path-breaking neuroscience experiments (including the author’s), and in part a proposal for a paradigm shift in neuroscience based on modern economic theory – is an amazing tour de force. Its author – Associate Professor of Neural Science and Psychology at the Center for Neural Science, New York University – is a young researcher who dared to write this book notwithstanding the fact that publishing books early in one’s career is rarely rewarded in economics, (cognitive) psychology, or neuroscience. Clearly, Glimcher was convinced he had an important story to tell. We are persuaded.

The book has two parts. The first part titled “Historical Approaches” leads us through a history of neuroscience: from Vaucanson’s Duck – an early robot resembling a duck that apparently could raise its head, look around, flap its wings, and even eat and process food --, via Descartes’ mechanistic, deterministic explanations, to Charles Scott Sherrington’s more complicated reflex models attempting to explain mechanistically how behaviors are generated in response to sensory stimuli, and, finally, to David Marr’s vision research representing a paradigm change of sorts because he insisted that in order to understand the relationship between stimuli, brain, and behavior, one had to understand what exactly it was that the neurobiological architecture was trying to accomplish.

Marr’s argument was evolutionary, drawing on the notions of fitness and ability to survive as the main driving forces, and incorporating these forces into the top-down computational theories of neurobiological architectures. While Marr’s vision of how to understand the brain-behavior link represented a radical departure from the Cartesian-Sherringtonian reflexology tradition of trying to trace back well-defined bits of behavior in the neurobiological architecture, and while the vision reoriented neuroscience – in Glimcher’s view in the right direction --, the vision was marred by its lack of acceptance of probabilistic methods which at that point were already widely used in other sciences, including behavioral ecology and economics.

This first part of the book is an acquired taste. Some reviewers have lauded it and even considered it the major contribution of the book. And indeed it often makes for rather absorbing reading: Glimcher knows how to tell a good story, and has no qualms about throwing in biographical details: for example, young David Marr’s way from Cambridge, England, to Cambridge, MA, USA, his there being diagnosed with a fatal form of leukemia in December 1977, and his decision to spend the remaining year of his life writing a book which, with the help of his colleagues and students, was finally published in 1982, in the same year as Maynard Smith’s Evolution and the Theory of Games.\footnote{Both books, of course, have deservedly become classics in their respective fields, with Maynard Smith’s book having also done its fair share to refocus the spotlight on classic game theory, which after a rush of glowing reviews and predictions of success in the wake of Von Neumann & Morgenstern’s Theory of Games and Economic Behavior had fallen out of the limelight for reasons that are in dispute (see Giocola, 2003; Ortmann, forthcoming).}

The problems of the research strategies of Sherrington and Marr notwithstanding, the two are clearly
Glimcher’s heroes, as the dedication of the book also suggests. Glimcher’s other heroes are those economists that created game theory, specifically the deductive game theory encapsulated in Kreps (1990), the leading microeconomics textbook of the first half of the nineties, and one of two economics books that Glimcher recommends for further reading. For it is that brand of game theory that Glimcher proposes in the second part of his book as the modeling tool that might enable us to better understand the brain-behavior link. Especially, Glimcher argues, that brand of game theory makes it possible for us to overcome the deterministic strictures of the Cartesian-Sherringtonian approach.2

Chapters 10 through 12, which draw heavily on Glimcher’s work with Michael Platt and Michael Dorris, explain why. Chapter 12 offers amazing fare. Here Glimcher describes a series of experiments with humans and monkeys whose aim was to show that economic theory describes reasonably well not only human behavior but also the “behavior” of neurological circuits that produce the behavior.

The vehicle used in this series of experiments were various parameterizations of a principal-agent game (here called the “work or shirk” game) that matches an employer and an employee (see Ortmann and Colander, 1997; Kreps, 1990). The employee has the option of shirking or working, the employer has the option of monitoring or not monitoring. For the parameterizations used by Glimcher and his collaborators, and for finitely repeated games under complete information, game theory identifies a Nash equilibrium in mixed strategies allowing the employee to shirk as much as he can get away with (so as not to get fired), and requiring the employer to monitor as much as she must (so as to maximize profits given monitoring costs).

Glimcher and Dorris implemented the first set of experiments by having student subjects play against each other repeatedly for blocks of 150 rounds. Interestingly, these subjects were not given payoff tables – they had to infer the payoffs from the feedback to the actions they chose. Glimcher and Dorris’ subjects managed to play the predicted mixed strategies reasonably well within a few rounds.3 Similar results were reported for a second set of experiments where, as the only alteration, Glimcher and Dorris substituted the human employer with a computer program that was instructed to play optimally (as prescribed by game theory for finitely repeated games under complete information). The computer was also programmed to react optimally to patterns of action choices of employees that deviated from the mixed strategy equilibrium.

Glimcher and Dorris next substituted their human participants with monkey participants that were made to play the same game, with two eccentric light stimuli representing the choices available to them and choices being indicated by looking at one of the stimuli. After each round the monkey participants were

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2 Not really surprisingly, as game theory indeed aspires to model the optimal behavior under all kinds of conditions, including interactive situations where the other player attempts to be unpredictable.

3 It’s difficult to say more because the design, implementation, and results are reported in ways that are not always up to the standards required in economics journals. For example, the employer’s expected payoffs in one of the work-shirk games shown in Table 12.2. are negative for equilibrium play; this fact is hard to reconcile with the reported earnings, unless some fee was paid upfront. It is also surprising to see that the players did not manage to coordinate on the Pareto-efficient outcome, and it would therefore be interesting to know more details.
rewarded, depending on their (and the computer program’s) choice, by Berry Berry Fruit Juice, a delicacy that monkeys value highly. Like their human counterparts, the animal subjects managed to play the predicted mixed strategies reasonably well within a few rounds.

While this result makes the experiment already into a remarkable accomplishment from the design, implementation, and result perspective, the real kicker was the ability of Glimcher and his colleagues to track the excitement patterns of neurons connected to the work or shirk task. In earlier work, Glimcher and Dorris had demonstrated that area LIP neurons reflected the expected utility of the actions that they encoded. In fact, they had shown that the degree of excitement that those neurons showed was closely, if somewhat noisily, linked to the rewards associated with the actions. For mixed strategies, therefore, the excitement triggered in neurons should be the same for the available action choices as long as these choices had the same expected value. Indeed, this is exactly what Glimcher and Dorris found. Even further, area LIP neurons seemed to “understand” profitable deviations from the optimal game strategy potentially triggered in the computer program as a response to temporary deviations from the optimal strategy by the animal participant. Neurons behaved as if they were Bayesian optimizers. This notion has recently been captured mathematically by Gold and Shadlen (2001).

Clearly, Glimcher’s book describes to some extent a reductionist program and is likely on these grounds not to sit well with those who like to conceptualize humans as more than stimulus-reaction machines, if rather noisy ones. It will also be attacked by those who view the book as an unfortunate manifestation of a tools-to-theories heuristic. There is something to that objection. Humans are, after all, not just the kind of sophisticated animal whose major goal in life is to maximize the intake of the equivalent of Berry Berry Fruit Juice.

We are, however, only at the very early stages of the explorations for which Glimcher has given us an impressive blueprint. As he makes clear in several places (e.g., p. 322), what we know so far are appetizers that make us hungry for the main menu (sketched on pp. 321-334). He will be delighted to know that some of the mathematical tools that he looks for have been successfully developed by game theorists working on dynamic models of the evolutionary kind (e.g., Weibull, 1995; Samuelson, 1997; Vega-Redondo, 1996 and 2003), a fact that Glimcher seems unaware of, given what some of his remarks concerning the state of the art of game theoretic modeling suggest (e.g., p. 288, p. 297). But this is a minor flaw in light of the tremendous research program and accomplishments he has reported here. All in all, the results of Glimcher and his colleagues are indeed a very beautiful and fascinating demonstration that using game theory as a tool for analyzing the brain-behavior link is a viable and promising research strategy. The encyclopedic knowledge displayed, and the intriguing research agenda proposed, by the author, make this book a must-read for everyone interested in the brain-behavior link.

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4 LIP neurons, located in the lateral intraparietal (LIP) area of the posterior parietal cortex, have long been known as a key interface between sensation and action.

5 Clearly, some of the proposed experiments and their predicted results could be modeled by simple reinforcement models (see e.g. Camerer, 2003, chapter 6).
References


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