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From behavioural economics to neuroeconomics to decision neuroscience: the ascent of biology in research on human decision making☆

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Here, we briefly review the evolution of research on human decision-making over the past few decades. We discern a trend whereby biology moves from subserving economics (neuroeconomics), to providing the data that advance our knowledge of the nature of human decision-making (decision neuroscience). Examples illustrate that the integration of behavioural and biological models is fruitful especially for understanding heterogeneity of choice in humans.

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Economic theories of human choice

For a large part of the 20th century, research on human choice was dominated by economic theories, particularly *rational choice* and *revealed preferences* theory. This approach starts from a limited set of properties that are imposed on choices (rationality axioms). It then determines to what extent choices can be summarised (represented) by maximisation of some latent mathematical function, typically referred to as *utility* or *value function*. The form of the value function depends on the nature of the axioms [1]. The value function and its maximisation merely constitute a compact way to summarise choices. In binary (pairwise) choice, for instance, the economist does not need a look-up table: to determine whether one option would be chosen over the alternative, the economist merely picks the option with the maximum value.

In economic theory, the value function does not necessarily reflect subjective preferences, or the agent's 'needs' or 'wants.' Preferences are formulated in a way that is independent of the type of agent (human, market, firm) whose choices the preferences describe. Thus, the economist's definition of the term 'preferences' is fundamentally different from the psychologist's. To economists, preferences are merely a description of choices, and preferences and choices are observationally equivalent.

Soon after the emergence of the first instances of axiomatic choice theories, it became apparent that they could not capture many key regularities of human choice. The two most famous examples are the Allais [2] and Ellsberg [3] paradoxes. In subsequent years, new value functions were proposed that improved the fit with the empirical data [4,5]. This development culminated in Prospect Theory [6], which summarised salient characteristics of actual human choice under uncertainty in terms of maximisation of a utility index that featured a reference point, a kink, probability weighting, and differential curvature in the gain and loss domains. Some of these features accommodated cognitive biases. Loss aversion, for instance, is not merely a tendency to avoid risk (which rational agents are allowed to do). Instead, it is a cognitive bias that makes an agent choose differently depending on whether a prospect is presented as losses or as gains [7].

Prospect Theory models capture human cognitive biases within a framework of utility maximisation. Thus, its approach is consistent with the approaches of earlier economic theories. The success of Prospect Theory was sealed when an axiomatic version of the theory emerged [8]. At the time, alternative (complementary or substitutable) theories were proposed such as Herbert Simon's 'satisficing' [9] or Gerd Gigerenzer's 'heuristics toolbox' [10]. However, those theories cannot readily be

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translated into the language of traditional economic choice theory. Some have argued that Simon's theory could be translated into a value maximisation framework, by adding constraints to cognition [11]. Unfortunately, constrained optimisation often presupposes cognitive capabilities that contradict the bounded rationality that underlies satisficing behaviour. Indeed, constrained optimisation problems may be very 'hard' [12]. Still, this is not a concern for traditional economics, where the agent would choose merely 'as if' implementing constrained optimisation.

The strength of the axiomatic approach cannot be overestimated. It provides a disciplined way of modelling choice as utility maximisation. It avoids the pitfalls of other approaches that merely fit value functions to data. Indeed, a value function may fit data well but may be such that it violates rationality constraints that may be far less controversial than the observed cognitive biases that the value function was meant to capture in the first place. Such was the case with the original version of Prospect Theory [6], where the probability weighting function was at odds with the sure-thing principle — outcomes that would occur under any alternative prospect ended up influencing choice. (The subsequent, axiomatic version of Prospect Theory corrected this [13].)

The axiomatic approach and behavioural economics alike start and finish with choice data. The value or utility function that is maximised is just another way to describe choices. The maximisation process (which, as already mentioned, could be rather complex) is not to be taken literally: the agent chooses 'as if' maximising utility. Importantly, the axiomatic approach does not provide a mechanistic account of how choice is implemented but only describes the properties of choices. Equally importantly, both approaches assume that preferences are exogenous, which unfortunately precludes an important type of intervention. 'Bad' choices (compulsive gambling, insufficient retirement savings, eating disorders, drug addiction, etc.) cannot be changed through a change of preferences, but only through a change of the available options or re-framing of the options [14], or through education [15].

From understanding choice to understanding neural circuitry: the advent of neuroeconomics

With the emergence of non-invasive human brain imaging techniques such as functional magnetic resonance imaging (fMRI), it was only a matter of time before economists and neuroscientists set out to determine if there was any biological foundation of economic theories of choice. Key aims were to determine how choices were implemented biologically, which neural circuitry was involved, and what algorithms were employed. A new field emerged, referred to as *neuroeconomics*, focusing on the description of algorithms underlying observed choice and their biophysical implementation. Human decision-making would thereby become understandable at a lower level of description than the traditional, abstract, axiomatic approach had done. It corrected a situation which actually was the opposite of that in vision research, where the biophysical took precedence over the abstract [16].

Very quickly, this research program led to some fascinating results, including the discovery of, and subsequently, ability to manipulate, the very value (utility) signals that constitute the core of the axiomatic theory [17–21][17–19,20•,21]. More recently, it has provided more detail into how value maximisation is implemented at a neural level, borrowing ideas from drift-diffusion models in psychophysics [22] and detailed neural networks with mutual inhibition [23], among others. This line of research also led to the discovery that some basic axioms of choice theory such as Irrelevance of Independent Alternatives (IIA) are violated due to fundamental properties of the central nervous system, namely, divisive normalisation [24]. Violations occur when the availability of a third, clearly inferior option, makes people choose the lower-valued option in a pair more frequently than in the absence of this third option. Under divisive normalisation, inputs (e.g., sources of light, auditory signals, values of available options) are re-scaled to fit a preset range. Biophysically, divisive normalisation happens because neuronal firing is affected by activation of nearby neurons. The discovery was particularly exciting, because divisive normalisation may predict behavioural features that economists had not detected yet. One small step in that direction is the prediction that independent alternatives may actually have the reverse effect on choice when the values of options are relatively close. The example is also important because it shows how biological data, hitherto outside the field of view of economists, can help to make sense of choice anomalies.

To date, neuroeconomic data have mainly been used to better distinguish between competing valuation models when choice data alone were not sufficient (given typical sample sizes). Neuroeconomics has shown, for example, that valuation based on Bayesian principles better explains neural activation and choices in a reversal learning task [25]. Similarly, neurobiology demonstrated that in certain settings, choice under uncertainty seems to be based on mean-variance analysis rather than more traditional expected utility theory [26]. Mean-variance analysis is popular in financial economics, yet unlike expected utility theory, can cause violations of simple rationality principles [27].

Despite all the successes of the neuroeconomic research program, economists may argue that it is of little relevance to economic theory, because of the perception that