The neural basis of choice and decision-making.

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Decision-making refers to the ability of humans and other animals to choose between competing courses of action based on the relative value of their consequences. This capacity is, therefore, fundamentally integrative, melding the complex cognitive processes through which causal relations between actions and consequences are encoded, retrieved, and maintained in working memory with the motivational processes through which the value, or utility, of alternative actions or sequences of actions is established. As readers of this journal will be well aware, research in decision-making has expanded in a variety of directions in recent years, but most notably into neuroscience. There are many reasons for this development, some merely technical – such as the increased use of functional magnetic resonance imaging (fMRI) in humans – but there are others that are more obviously innovative and that appear to mark a change in the dominant approach to investigating the neural bases of the complex capacities of animals. There appears to be a developing consensus that the long tradition of studying these capacities by examining analogous processes in simple model systems has become an old tradition; that, rather than using a simple neural or behavioral preparation, methodologies better suited to examining functional, as opposed to structural, problems will provide a more secure basis for rapid progress. Indeed, much of the success of recent research in decision-making has come from recognizing that the interaction of the cognitive, motivational and behavioral processes engaged during the course of specific decisions cannot be reified to a single specialized circuit, cell type or intracellular process and is best understood at a systems level.

As a consequence, the neuroscience of decision-making is a very broad enterprise and crosses many traditional boundaries between research disciplines, species, and brain regions. This breadth is immediately apparent from a cursory survey of the range of interests of the authors of the following minireviews. There are, however, clear areas of overlap and these have been exploited to explore what we see as emerging themes in decision-making research. In this series these include descriptions of studies integrating computational and neuroeconomic approaches to investigate subjective decision variables, financial decisions, the executive and evaluative functions of prefrontal cortex - particularly the role of orbitofrontal cortex in establishing a common

currency of value - together with reviews of recent research examining the functions of discrete cortico-striatal networks and their integrated dopaminergic afferents in the acquisition and control of goal-directed and habitual instrumental actions.

Although the individual papers review themes that are, themselves, complex areas of issue around which substantial research efforts are currently organizing, each paper describes these specific issues and trends within a larger context and, together, they can be seen to provide a general overview of this developing area. For example, in their description of the application of computational approaches to decision making, Doya and Corrado review both the development of computational models capable of capturing the dynamics of individual choice as well as specific cases in which the internal variables of these models have provided the basis for extracting the correlates of subjective choice variables from the electrophysiological data of primates. In this case it is the dynamic integration of the computational, neural and behavioral data that has provided insight into the hidden subjective variables controlling choice. Similarly, Knutson and Bossaerts describe the emerging neurofinance approach to decision making but also examine the specific application of models of decision-making under risk and the behavioral tasks that have been developed to examine financial decisions processes in human subjects together with their neural correlates derived from fMRI.

Lee, Rushworth, Walton, Watanabe and Sakagami review research on decision making in primates and the involvement of prefrontal cortex generally but, in the light of the connectivity of subdivisions of this region and of formal theories of decision making, describe evidence suggesting, more specifically, that the lateral, medial and ventral sub-regions may have the more specialized task of deriving predictions regarding the future value of reward on the basis of states, actions and local predictive cues, respectively. Interestingly, Murray, O'Doherty and Schoenbaum come to similar conclusions with regard to the role of orbitofrontal cortex (OFC) based on a comparative review of research investigating its role in decision-making. They point particularly to its role in deriving reward value from predictive cues as well as to evidence suggesting that the OFC may play a specialized role in decision-making by allowing animals to compare the values of events that fall into quite distinct categories.

Finally, it is interesting to note convergence in the proposed functions of corticostriatal circuits and their midbrain dopaminergic afferents in decision-making emerging in recent research. Although the involvement of the basal ganglia in motor learning, particularly in sensorimotor association, has long been recognized, recent evidence, reviewed by Balleine, Delgado and Hikosaka, suggests that they also play a critical role in the acquisition of actions instrumental to gaining access to reward; i.e. in goal-directed instrumental actions. Importantly, studies using rodent, non-human primate and human subjects have converged in this regard finding evidence of a heterogeneity of neural function, particularly in the striatum, not previously anticipated. Furthermore, there is evidence of a corresponding heterogeneity both in the neurodegenerative disorders and neuronal plasticity characteristic of different regions of stratum and apparently also involving distinct dopaminergic processes. The suggestion that the burst-firing pattern of midbrain dopamine neurons serves as an error signal for the prediction of reward has generated close collaboration between researchers in computational and neurophysiological studies of dopamine function. More recently, alternations in dopamine signaling have been reported to lead to regional changes in plasticity in the corticostriatal pathway together with changes in the excitability of the striatal output neurons. Indeed, as reviewed by Wickens, Costa, Horwitz & Killcross, rapid alterations in dopamine transmission can cause substantial changes in the coordinated activity of neuronal ensembles in discrete corticostriatal circuits that can lead to the emergence of distinct patterns of behavioral abnormality. Clearly, the involvement of dopamine in striatal function and in decision making generally is rich and varied and is something that we are only beginning to understand.

There are, of course, still many open questions, a number of which are signaled in the following minireviews and the interested reader will undoubtedly think of many more worthy of investigation that we have not mentioned. Of course, when coupled with the rich opportunities for collaboration and integration across research areas that this area of investigation provides, these open issues and questions serve mostly to emphasize how even more generative the neuroscience of decision-making is likely to be in the future.

Number: JN-MR-1561-07
Title: Functional Specialization of the Primate Frontal Cortex during Decision Making
Authors: Lee, Daeyeol; Rushworth, Matthew; Walton, Mark; Watanabe, Masataka; Sakagami, Masamichi

Economic theories of decision making are based on the principle of utility maximization, and reinforcement learning theory provides computational algorithms that can be used to estimate the overall reward expected from alternative choices. These formal models not only account for a large range of behavioral observations in human and animal decision makers, but also provide useful tools for investigating the neural basis of decision making. Nevertheless, in reality, decision makers must combine different types of information about the costs and benefits associated with each available option, such as the quality and quantity of expected reward and required work. In this article, we put forward a hypothesis that different subdivisions of the primate frontal cortex may be specialized to focus on different aspects of dynamic decision-making processes. In this hypothesis, the lateral prefrontal cortex is primarily involved in maintaining the state representation necessary to identify optimal actions in a given environment. By contrast, the orbitofrontal cortex and the anterior cingulate cortex might be largely involved in encoding and updating the utilities associated with different sensory stimuli and alternative actions, respectively. These cortical areas are also likely to contribute to decision making in a social context.

Number: JN-MR-1556-07
Title: Lions and tigers and bears, oh my! What we know (and don't know) after 20 years of investigating orbitofrontal function across species
Authors: Murray, Elisabeth; O'Doherty, John; Schoenbaum, Geoffrey

When Pat Goldman-Rakic described the circuitry and function of primate prefrontal cortex in her influential 1987 monograph (Goldman-Rakic, 1987), she included only a few short paragraphs on the orbitofrontal cortex (OFC). That year, there were only 9 papers published containing the term 'orbitofrontal', an average of less than 1 paper per month. Twenty years later, this rate has increased to 32 papers per month. This explosive growth is partly due to the remarkable similarities that exist in structure and function across species. These similarities suggest that OFC function can be usefully modeled in nonhuman and even nonprimate species. Here we review some of these similarities.

Number: JN-MR-1554-07
Title: The role of dorsal striatum in reward and decision-making.
Authors: Balleine, Bernard; Delgado, Mauricio; Hikosaka, Okihide
Although the involvement in the striatum in the refinement and control of motor movement has long been recognized, recent description of discrete frontal cortical-basal ganglia networks in a range of species has focused attention on the role particularly of

the dorsal striatum in executive functions. Current evidence suggests that the dorsal striatum contributes directly to decision-making, especially to action selection and initiation, through the integration of sensorimotor, cognitive, and motivational/emotional information within specific corticostriatal circuits involving discrete regions of striatum. We review key evidence from recent studies in rodent, non-human primate and human subjects.

Number: JN-MR-1564-07
Title: Neural antecedents of financial decisions
Authors: Knutson, Brian; Bossaerts, Peter

To explain investing decisions, financial theorists invoke two opposing metrics -- expected reward and risk. Recent advances in the spatial and temporal resolution of brain imaging techniques enable investigators to visualize changes in neural activation prior to financial decisions. Research using these methods indicates that while the ventral striatum plays a role in representation of expected reward, the insula may play a more prominent role in the representation of expected risk. Accumulating evidence also suggests that antecedent neural activation in these regions can be used to predict upcoming financial decisions. These findings have implications for predicting choices and for building a physiologically constrained theory of decision-making.

Number: JN-MR-1590-07
Title: Understanding neural coding through the model-based analysis of decision
Authors: Corrado, Gregory; Doya, Kenji

The study of decision making poses new methodological challenges for systems neuroscience. Whereas our traditional approach linked neural activity to external variables that the experimenter directly observed and manipulated, many of the key elements that contribute to decisions are internal to the decider. Variables such as subjective value or subjective probability may be influenced by experimental conditions and manipulations, but can neither be directly measured nor precisely controlled. Pioneering work on the neural basis of decision circumvented this difficulty by studying behavior at steady state, where knowledge of the average state of these quantities was sufficient. More recently, a new wave of studies has confronted the conundrum of internal decision variables more directly by leveraging quantitative behavioral models. When these behavioral models are successful in predicting a subject’s choice based on the history of choice and reward experiences, the model’s internal variables can then be used as proxies for the unobservable decision variables that actually drive the decider's behavior. This new methodology has allowed researchers to localize neural subsystems that encode hidden decision variables related to free choice, and to study these variables under dynamic conditions

Number: JN-MR-1671-07
Title: Dopaminergic mechanisms in actions and habits
Authors: Wickens, Jeffery; Horvitz, Jon; Costa, Rui; Killcross, Simon

No abstract – this is first paragraph

Dissociable associative processes in actions and habits may correspond to different dopaminergic actions

Goal-directed choices among alternative actions initially reflect the intent to obtain preferred outcomes, but with repetition behaviour may come to be more habitual. Recent studies suggest a different action of dopamine in goal-directed performance compared to habitual responding. In the early stages of learning dopamine plays an essential role. With extended training dopamine appears to play a decreasing role in response expression. The actions of dopamine on synaptic plasticity in the corticostriatal pathway suggest possible mechanisms for this changing role in behaviour.