Preface

Decision Neuroscience: an Integrative Perspective addresses fundamental questions about how the brain makes perceptual, value-based, and more complex decisions in nonsocial and social contexts. This book presents recent and compelling neuroimaging, electrophysiological, lesional, and neurocomputational studies, in combination with hormonal and genetic studies, that have led to a clearer understanding of the neural mechanisms behind how the brain makes decisions. The neural mechanisms underlying decision-making processes are of critical interest to scientists because of the fundamental role that reward plays in a number of cognitive processes (such as motivation, action selection, and learning) and because they have theoretical and clinical implications for understanding dysfunctions of major neurological and psychiatric disorders.

The idea for this book grew up from our edition of the *Handbook of Reward and Decision Making* (Academic Press, 2009). We originally thought to revise and reedit this book, addressing one fundamental question about the nature of behavior: how does the brain process reward and makes decisions when facing multiple options? However, given the developments in this active area of research, we decided to feature an entirely different book with new contents, covering results on the neural substrates of rewards and punishments; perceptual, value-based, and social decision-making; clinical aspects such as behavioral addictions; and the roles of genes and hormones in these various aspects. For example, an exciting topic from the field of social neuroscience is to know whether the neural structures engaged with various forms of social interactions are cause or consequence of these interactions (Fernald, Chapter 28).

A mechanistic understanding of the neural encoding underlying decision-making processes is of great interest to a broad readership because of their theoretical and clinical implications. Findings in this research field are also important to basic neuroscientists interested in how the brain reaches decisions, cognitive psychologists working on decision-making, as well as computational neuroscientists studying probabilistic models of brain functions. Decision-making covers a wide range of topics and levels of analysis, from molecular mechanisms to neural systems dynamics, neurocomputational models, and social system levels. The contributions to this book are forward-looking assessments of the current and future issues faced by researchers. We were fortunate to assemble an outstanding collection of experts who addressed various aspects of decision-making processes. The book is divided into five parts that address distinct but interrelated topics.

STRUCTURE OF THE BOOK

A decision neuroscience perspective requires multiple levels of analyses spanning neuroimaging, electrophysiological, behavioral, and pharmacological techniques, in combination with molecular and genetic tools. These approaches have begun to build a mechanistic understanding of individual and social decision-making. This book highlights some of these advancements that have led to the current understanding of the neuronal mechanisms underlying motivational and decision-making processes.

Part I is devoted to animal studies (anatomical, neurophysiological, pharmacological, and optogenetics) on rewards/punishments and decision-making. In their natural environment, animals face a multitude of stimuli, very few of which are likely to be useful as predictors of reward or punishment. It is thus crucial that the brain learns to predict rewards, providing a critical evolutionary advantage for survival. This first part of the book offers a comprehensive view of the specific contributions of various brain structures as the dopaminergic midbrain neurons, the amygdala, the ventral striatum, and the prefrontal cortex, including the lateral prefrontal cortex and the orbitofrontal cortex, to the component processes underlying reinforcement-guided decision-making, such as the representation of instructions, expectations, and outcomes; the updating of action values; and the evaluation process guiding choices between prospective rewards. Special emphasis is made on the neuroanatomy of the reward system and the fundamental roles of dopaminergic neurons and the basal ganglia in learning stimulus—reward associations.

Chapter 1 (Haber SN) describes the anatomy and connectivity of the reward circuit in nonhuman primates. It describes how cortical—basal ganglia loops are topographically organized and the key areas of convergence between functional regions.

Chapter 2 describes three novel electrophysiological properties of the classical dopamine reward-prediction error (RPE) signal (Schultz W). Studies have identified three novel properties of the dopamine RPE signal. In particular, concerning its roles in making choices, the dopamine RPE signal may not only reflect subjective reward value and formal economic utility but could also fit into formal competitive decision models. The RPE signal may code the chosen value suitable for updating or immediately influencing object and action values. Thus, the dopamine utility prediction error signal bridges the gap between animal learning theory and economic decision theory.

Chapter 3 focuses on the electrophysiological properties of another important component of the reward system in primates, namely the amygdala (Bernardi S and Salzman D). The amygdala contains distinct appetitive and aversive networks of neurons. Processing in these two amygdalar networks can both regulate and be regulated by diverse cognitive operations.

Chapter 4 extends the concept of appetitive and aversive motivational processes to the striatum (Saga Y and Tremblay L). This chapter describes how the ventral striatum and the ventral pallidum, two parts of the limbic circuit in the basal ganglia, are involved not only in appetitive rewarding behavior, as classically believed, but also in negative motivational behavior. These results can be linked with the control of approach/avoidance behavior in a normal context and with the expression of anxiety-related disorders. The disturbance of this pathway may induce not only psychiatric symptoms, but also abnormal value-based decision-making.

Chapter 5 (Tian J, Uchida N, and Eshel N) highlights new advances in the physiology, function, and circuit mechanism of decision-making, focusing especially on the involvement of dopamine and striatal neurons. Using optogenetics in rodents, molecular techniques, and genetic techniques, this chapter shows how these tools have been used to dissect the circuits underlying decision-making. It describes exciting new avenues to understand a circuit, by recording from neurons with knowledge of their cell type and patterns of connectivity. Furthermore, the ability to manipulate the activity of specific neural types provides an important means to test hypotheses of circuit function.

Chapter 6 (Bradfield L and Balleine B) describes the neural bases of the learning and motivational processes controlling goal-directed action. By definition, the performance of such action respects both the current value of its outcome and the extant contingency between that action and its outcome. This chapter identifies the neural circuits mediating distinct processes, including the acquisition of action-outcome contingencies, the encoding and retrieval or incentive value, the matching of that value to specific outcome representations, and finally the integration of this information for action selection. It also shows how each of these individual processes are integrated within the striatum for successful goal-directed action selection.

Chapter 7 (Robbins TW and Dalley JW) describes animal models (mostly in rodents) of impulsivity and risky choices. It reviews the neural and neurochemical basis of various forms of impulsive behavior by distinguishing three main forms of impulsivity: waiting impulsivity, risky choice impulsivity, and stopping impulsivity. It shows that dopamine- and serotonin-dependent functions of the nucleus accumbens are implicated in waiting impulsivity and risky choice impulsivity, as well as cortical structures projecting to the nucleus accumbens. For stopping impulsivity, dopamine-dependent functions of the dorsal striatum are implicated, as well as circuitry including the orbitofrontal cortex and dorsal prelimbic cortex. Differences and commonalities between the forms of impulsive responding are highlighted. Importantly, various applications to human neuropsychiatric disorders such as drug addiction and attention deficit hyperactivity disorder are also discussed.

Chapter 8 (Fuster JM) proposes that the neural mechanisms of decision-making are understandable only in the structural and dynamic context of the perception−action cycle, defined as the biocybernetic processing of information that adapts the organism to its environment. It presents a general view of the role of the prefrontal cortex in decision-making, in the general framework of the perception−action cycle, including prediction, preparation toward decision, execution, and feedback from decision.

Part II covers the topic of the neural representation of motivation, perceptual decision-making, and value-based decision-making in humans, mostly combining neurocomputational models and brain imaging studies.

Chapter 9 (Tobler P and Kahnt T) reviews several definitions of value and salience, and describes human neuroimaging studies that dissociate these variables. Value increases with the magnitude and probability of reward but decreases with the magnitude and probability of punishment, whereas salience increases with the magnitude and probability of both reward and punishment. At the neural level, value signals arise in striatum, orbitofrontal and ventromedial prefrontal cortex, and superior parietal areas, whereas magnitude-based salience signals arise in the anterior cingulate cortex and the inferior parietal cortex. By contrast, probability-based salience signals have been found in the ventromedial prefrontal cortex.

Chapter 10 (Louie K and Glimcher PW) reviews an approach centered on basic computations underlying neural value coding. It proposes that neural information processing in valuation and choice relies on computational principles such as contextual modulation and divisive normalization. Divisive normalization is a nonlinear gain control algorithm widely observed in multiple sensory modalities and brain regions. Identification of these computations sheds light on how the underlying neural circuits are organized, and neural activity dynamics provides a link between biological mechanism and computations.

Chapter 11 (Philiastides M, Diaz J, and Gherman S) introduces the general principles guiding perceptual decision-making. Perceptual decisions occur when perceptual inputs are integrated and converted to form a categorical choice. It reviews the influence of a number of factors that interact and contribute to the decision process, such as prestimulus state, reward and punishment, speed−accuracy trade-off, learning and training, confidence, and neuromodulation. It shows how these decision modulators can exert their influence at various stages of processing, in line with predictions derived from sequential-sampling models of decision-making.

Chapter 12 (Summerfield C) reviews the neural and computational mechanisms of perceptual decisions. It addresses current controversial questions, such as how we decide when to draw our decisions to a conclusion, and how perceptual decisions are biased by prior information.

Chapter 13 (Soltani A, Chaisangmongkon W, and Wang XJ) presents possible biophysical and circuit mechanisms of valuation and reward-dependent plasticity underlying adaptive choice behavior. It reviews mathematical models of reward-dependent adaptive choice behavior, and proposes a biologically plausible, reward-modulated Hebbian synaptic plasticity rule. It shows that a decision-making neural circuit endowed with this learning rule is capable of accounting for behavioral and neurophysiological observations in a variety of decision-making tasks.

Part III of the book focuses on the rapidly developing field of social neuroscience, integrating neuroscience data from both nonhuman primates and humans. Primates are fundamentally social animals, and they may share common neural mechanisms in diverse forms of social behavior. Examples of such behavior include tracking intentions and beliefs from others, being observed by others during prosocial decisions, or learning the social hierarchy in a group of individuals. It is also likely that at the macroscopic level, important differences exist concerning social brain structures and connectivity, and there is a need to directly compare between species to answer this fundamental question. Indeed, studies in both humans and monkeys report not only an increase in gray matter density of specific brain structures relative to the size of our social network, but also species differences in prefrontal−temporal brain connectivity. Furthermore, this part of the book presents neurocomputational approaches starting to provide a mechanistic understanding of social decisions. For example, reinforcement learning models and strategic reasoning models can be used when learning social hierarchies or during social interactions.

A social neuroscience understanding requires multiple approaches, such as electrophysiology and neuroimaging in both monkeys (Chapters 14, 15, 19) and humans (Chapters 16, 18, 20), as well as causal (Chapter 21), neurocomputational (Chapters 17−19), endocrinological, genetics, and clinical approaches (Part V).

Chapter 14 (Duhamel JR and colleagues) presents monkey electrophysiological data revealing that the orbitofrontal cortex is tuned to social information. For example, in one experiment, macaque monkeys worked to collect rewards for themselves and two monkey partners. Single neurons encoded the meaning of visual cues that predicted the magnitude of future rewards, the motivational value of rewards obtained in a social context, and the tracking of social preferences and partner's identity and social rank. The orbitofrontal cortex thus contains key neuronal mechanisms for the evaluation of social information. Moreover, macaque monkeys take into account the welfare of their peers when making behavioral choices bringing about pleasant or unpleasant outcomes to a monkey partner. Thus, this chapter reveals that prosocial decision-making is sustained by an intrinsic motivation for social affiliation and controlled through positive and negative vicarious reinforcements.

Chapter 15 (Sallet J and colleagues) reviews the similarities between monkeys and humans in the organization of the social brain. Using MRI-based connectivity methods, they compare human and macaque social areas, such as the organization of the medial prefrontal cortex. They revealed that the connectivity fingerprint of macaque area 10 best matched that of the human frontal pole, suggesting that even high-level areas share features between species. They also showed that animals housed in large social groups had more gray matter volume in bilateral mid-superior temporal sulcus and rostral prefrontal cortex. Beyond species similarities, there are also distinct differences between human and macaque prefrontal−temporal brain connectivity. For example, functional connections between the temporal cortex and the lateral prefrontal cortex are stronger in humans compared to connections with the medial prefrontal cortex in humans, but the opposite pattern is observed in macaques.

Chapter 16 (Izuma K) focuses on two forms of social influence, the audience effect, which is an increased prosocial tendency in front of other people, and social conformity, which consists in adjusting one's attitude or behavior to those of a group. This chapter discusses fMRI findings in healthy humans in these two types of social influence and also shows how reputation processing is impaired in individuals with autism. It also links social conformity and reward-based learning (reinforcement learning).

Chapter 17 (Ligneul R and Dreher JC) examines how the brain learns social dominance hierarchies. Social dominance refers to relationships wherein the goals of one individual prevail over the goals of another individual in a systematic manner. Dominance hierarchies have emerged as a major evolutionary force to drive dyadic asymmetries in a social group. This chapter proposes that the emergence of dominance relationships are learned incrementally, by accumulating positive and negative competitive feedbacks associated with specific individuals and other members of the social group. It considers such emergence of social dominance as a reinforcement learning problem inspired by neurocomputational approaches traditionally applied to nonsocial cognition. This chapter also reports how dominance hierarchies induce changes in specific brain systems, and it reviews the literature on interindividual differences in the appraisal of social hierarchies, as well as the underlying modulations of cortisol, testosterone, and serotonin/dopamine systems, which mediate these phenomena.

Chapter 18 (Seo H and Lee D) describes reinforcement learning models and strategic reasoning during social decision-making. It shows that dynamic changes in choices and decision-making strategies can be accounted for by reinforcement learning in a variety of contexts. This framework has also been successfully adopted in a large number of neurobiological studies to characterize the functions of multiple cortical areas and basal ganglia. For complex decision-making, including social interactions, this chapter shows that multiple learning algorithms may operate in parallel.

Chapter 19 (Ugazio G and Ruff C) reports brain stimulation studies on social decision-making, which test the causal relationship between neural activity and different types of processes underlying these decisions, including social emotions, social cognition, and social behavioral control.

Chapter 20 (Chierchia G and Singer T) shows that two important social emotions, empathy and compassion, engage distinct neurobiological mechanisms, as well as different affective and motivational states. Empathy for pain engages a network including the anterior insula and anterior midcingulate cortex, areas associated with negative affect; compassionate states engage the medial orbitofrontal cortex and ventral striatum and are associated with feelings of warmth, concern, and positive affect.

Part IV of the book focuses on clinical aspects involving disorders of decision-making and of the reward system that link together basic research areas, including systems, cognitive, and clinical neuroscience. Dysfunction of the reward system and decision-making is present in a number of neurological and psychiatric disorders, such as Parkinson's disease, schizophrenia, drug addiction, and focal brain lesions. The study of pathological gambling, for example, and other motivated states associated with, and leading to, compulsive behavior provides an opportunity to learn about the dysfunctions of reward system activity, independent of direct pharmacological activation of brain reward circuits. On the other hand, because drugs of abuse directly activate brain systems, they provide a unique challenge in understanding how pharmacological activation influences reward mechanisms leading to persistent compulsive behavior.

Chapter 21 (Murray GK, Tudor-Sfetea C, and Fletcher PC) shows that principles of reinforcement learning are useful to understand the neural mechanisms underlying impaired learning, reward, and motivational processes in schizophrenia. Two symptoms characteristic of this disease is considered in this framework, namely delusions and anhedonia.

Chapter 22 (Vaidya AR and Fellows LK) takes a neuropsychological approach to review focal frontal lobe damage effects on value-based decisions. It reveals the necessary contributions of specific subregions (ventromedial, lateral, and dorsomedial prefrontal cortex) to decision-making, and provides evidence as to the dissociability of component processes. It argues that the ventromedial frontal lobe is required for optimal learning from reward under dynamic conditions and contributes to specific aspects of value-based decision-making. It also shows a necessary contribution of the dorsomedial frontal lobe in representing action-value expectations.

Chapter 23 (Palminteri S and Pessiglione M) reviews reinforcement learning models applied to reward and punishment learning. These studies include fMRI and neural perturbation following drug administration and/or pathological conditions. They propose that distinct brain systems are engaged, one in reward learning (midbrain dopaminergic nuclei and ventral prefrontostriatal circuits) and another in punishment learning, revolving around the anterior insula.

Chapter 24 (Voon V) discusses decision-making impairments and impulse control disorders in Parkinson's disease. The author reports enhancement of the gain associated with levodopa, reinforcing properties of dopaminergic medications, and enhancement of delay discounting in these patients. Lower striatal dopamine transporter levels preceding medication exposure, and decreased midbrain D2 autoreceptor sensitivity, may underlie enhanced ventral striatal dopamine release and activity in response to salient reward cues, anticipated and unexpected rewards, and gambling tasks.

Impairments in decisional impulsivity (delay discounting, reflection impulsivity, and risk taking) implicate the ventral striatum, orbitofrontal cortex, anterior insula, and dorsal cingulate. These findings provide insight into the role of dopamine in decision-making processes in addiction and suggest potential therapeutic targets.

Chapter 25 (Witt K) reports that motor control is the result of a balance between activation and inhibition of movement patterns. It points to a central role of the subthalamic nucleus within the indirect basal ganglia pathway, acting as a brake on the motor system. This subthalamic nucleus function occurs when an automatic response must be suppressed to have more time to choose between alternative responses.

Chapter 26 (Grupe DW) discusses value-based decision-making as one of a key behavioral symptoms present in anxiety disorders. This chapter highlights alterations to specific processes: decision representation, valuation, action selection, outcome evaluation, and learning. Distinct anxious phenotypes may be characterized by differential alterations to these processes and their associated neurobiological mechanisms.

Chapter 27 (Clark L) presents a conceptualization of disordered gambling as a behavioral addiction driven by an exaggeration of multiple psychological distortions that are characteristic of human decision-making, and underpinned by neural circuitry subserving appetitive behavior, reinforcement learning, and choice selection. The chapter discusses the neurobiological basis of pathological gambling behavior in loss aversion, probability weighting, perceptions of randomness, and the illusion of control.

Part V focuses on the roles of hormones and genes involved in motivation and social decision-making processes. The combination of molecular genetic, endocrinology, and neuroimaging has provided a considerable amount of data that help in the understanding of the biological mechanisms influencing decision processes. These studies have demonstrated that genetic and hormonal variations have an impact on the physiological response of the decision-making system. These variations may account for some of the inter- and intra-individual behavioral differences observed in social cognition.

Chapter 28 (Fernald RD) presents an original approach for cognitive neuroscientists by focusing on the difficult question of how an animal's behavior or perception of its social and physical surroundings shapes its brain. Using a fish model system that depends on complex social interactions, this chapter reports how the social context influences the brain and, in turn, alters the behavior and neural circuitry of animals as they interact. Gathering of social information vicariously produces rapid changes in gene expression in key brain nuclei and these genomic responses prepare the individual to modify its behavior to move into a different social niche. Both social success and failure produce changes in neuronal cell size and connectivity in key brain nuclei. This approach bridges the gap between social information gathering from the environment and the levels of cellular and molecular responses.

Chapter 29 (Rabl U, Ortner N, and Pezawas L) examines the use of imaging genetics to explore the relationships between major depressive disorder and decision-making.

Chapters 30–32 report neuroendocrinological findings in social decision-making, likening variations in the levels of different types of hormones (cortisol, oxytocin, ghrelin/leptin) to brain systems engaged in social decisions and food choices. Chapter 30 (Hermans EJ and colleagues) integrates knowledge of the effects of stress at the neuroendocrine, cellular, brain systems, and behavioral levels to quantify how stress-related neuromodulators trigger time-dependent shifts in the balance between two brain systems: a "salience" network, which supports rapid but rigid decisions, and an "executive control" network, which supports flexible, elaborate decisions. This simple model elucidates paradoxical findings reported in human studies on stress and cognition.

Chapter 31 (Lefevre A and Sirigu A) reviews evidence for a role for oxytocin in individual and social decision-making. It discusses animal and human studies to link the behavioral effects of oxytocin to its underlying neurophysiological mechanisms.

Chapter 32 (Dagher A, Neseliler S, and Han JE) examines the neurobehavioral factors that determine food choices and food intake. It reviews findings on the interactions between brain systems that mediate feeding behavior and the gut and adipose peptides that signal the current state of energy balance.

Chapter 33 (Dreher, Tremblay, and Schultz) concludes this decision neuroscience book by integrating perspectives from all contributors.

We anticipate that while some readers may read the volume from the first to the last chapter, other readers may read only one or more chapters at a time, and not necessarily in the order presented in the book. This is why we encouraged an organization of this volume whereby each chapter can stand alone, while making references to others and minimizing redundancies across the volume. Given the consistent acceleration of advances in the various approaches described in this book on decision neuroscience, you are about to be dazzled by a first look at the new stages of an exciting era in brain research. Enjoy!

Jean-Claude Dreher
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