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Chapter 1 : Decision Making in Frontal Cortex: From Single Units to fMRI - MIT Press Scholarship

This chapter presents recent findings from single neuron electrophysiology and functional neuroimaging with respect to the role of the anterior cingulate cortex (ACC), the lateral prefrontal cortex (LPFC), the orbitofrontal cortex (OFC), and the ventromedial prefrontal cortex (VMPFC) in decision making.

Nature Human Behavior in press. Soc Cogn Affect Neurosci. Epub ahead of print. Hormones and Behavior
Potential explanation for weight gain in schizophrenia? Neuroscience and Biobehavioral Reviews. The Journal
of Neuroscience 37 6: A new phenomenon affecting medical decision-making in multiple sclerosis care?
Patient Preference and Adherence Frontiers in Neurology 8: Stimulating frontopolar cortex enhances
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Human Neuroscience 4: Trends in Neurosciences The European Journal of Neuroscience Philosophical
Transactions of the Royal Society of London. Series B, Biological Sciences Dissociating decision- from
motor- and sensory-related brain activation during perceptual choices. Behavioral and Brain Functions 1: JC
Dreher, L Tremblay eds. An integrative approach pp. Progress in Brain Research The basics of dopamine and
reinforcement learning. Decision making and the brain 2nd ed , Amsterdam: From single-units to fMRI.

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Chapter 2 : Decision neuroscience: neuroeconomics - WIREs Cognitive Science

Decision making in frontal cortex: from single units to fMRI. By Steven W Kennerley and Philippe N Tobler. Topics: Department of Economics.

Hunt and Timothy E. Mars Contributors Index Preface This volume deals with a simple question: How does the brain choose efficiently and adaptively among available options to ensure coherent, goal-directed behavior? Hidden behind this question are many problems that necessitate a multidisciplinary approach. Indeed, to understand how humans and other animals solve this problem, we need answers from researchers versed in anatomy, traditional psychology, learning theory, neuroimaging, and mathematical modeling. The goal of this book is to provide the reader with an overview of key approaches that researchers are currently pursuing in this quest. The meeting was the fourth in a series that started around the turn of the century with a meeting in Jena, Germany, organized by Michael Coles and Wolfgang Miltner. That first meeting was motivated by an upsurge of research interest in the error-related negativity ERN, a component of the human event-related brain potential that is elicited in the anterior cingulate cortex following errors in simple choice reaction-time tasks. The discovery of the ERN by Michael Falkenstein and colleagues in the early s provided a clearly observable neural correlate of a key aspect of cognitive control: Meanwhile, the ERN was being investigated in an increasing number of research fields, extending from traditional cognitive neuroscience to developmental psychology and psychopathology. This meeting resulted in a book edited by the organizers and published by the Max Planck Institute for Human Cognitive and Brain Sciences. Reflecting the growing scope of research on cognitive control and performance monitoring, this meeting also included researchers working on nonhuman primate and rodent models of control. Ridderinkhof, Nieuwenhuis, and Todd Braver edited a special issue of the journal *Cognitive, Affective, and Behavioral Neuroscience*, 7: The fourth meeting, held in Oxford in , followed these trends of increasing the scope of the research presented while maintaining an emphasis on conceptual and methodological convergence in studies of the motivational and cognitive control of behavior. In addition to psychologists and cognitive neuroscientists, the speaker list included a zoologist, a behavioral economist, an anatomist, and a number of researchers with a background in engineering and machine learning. From a meeting focused on developments around a small number of event-related potentials, the meeting has expanded into a medley of approaches, each addressing the same underlying question: We have invited contributions to this volume from researchers working in a wide range of fields, reflecting the spectrum of approaches present at the meeting. Organization of the Book This book is aimed at a graduate audience in all fields of research that deal with motivational and cognitive control. We hope that, besides providing an overview of cutting-edge research in the area, the volume will serve as a handbook that can be used by psychologists, biologists, economists, and neuroscientists alike. The contributors have been asked to situate their own findings and theories in the context of authoritative overviews of the relevant fields. For ease of further study, each chapter includes boxes with suggestions for further reading and questions that are outstanding in the field. In addition, interim summaries between the parts aim to integrate their contents into the wider literature. Preface xi The book begins with a consideration of the anatomical basis of control. The three chapters in part I each deal separately with one core component of the control system: In the first chapter, Sallet and colleagues focus on anatomical aspects of the interaction between lateral and medial prefrontal cortex, a prominent feature of many models of cognitive control. The chapter by Haber focuses on the connectivity of basal ganglia circuits, which are increasingly recognized as providing a crucial point of convergence between cognitive and motivational influences on behavior. Haber describes the various pathways of communication within reward circuits of the brain and between reward and association circuits, and the interactions among these networks. In the third chapter, Ullsperger describes the role of modulatory neurotransmitters in control, focusing primarily on dopamine, serotonin, and norepinephrine. Part II addresses the contributions of the cerebral cortex to control. Building on the anatomical perspective taken in the first

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section, these chapters focus on the functional architecture of cortical control. The chapters by Boorman and Noonan and by Kennerley and Tobler provide complementary perspectives on the contributions of subregions within prefrontal cortex to action selection and choice based on reinforcement value. Laubach focuses on the frontal cortex in rats, providing a basis for the expanded cortex in human and nonhuman primates discussed in the following chapters. Mars and colleagues look at how the prefrontal cortex exerts control via modulation of activity in posterior brain areas. Pearson and colleagues extend the field of focus from the frontal lobes to the posterior cingulate cortex, a region of the brain often seen in imaging experiments of control but thus far largely neglected in the literature. Part III considers the many ways in which subcortical brain regions underpin the control functions of the cortex. Two of the contributions focus on the role of the basal ganglia: In the other chapters in the section, the focus is on the role of monoamine neurotransmitter systems: Walton and colleagues provide an in-depth look at the most widely studied neurotransmitter in the field of motivational control, dopamine. In the final chapter, Nieuwenhuis reviews work on the locus coeruleus norepinephrine system, which influences cortical functioning through its widespread network of cortical connections. Whereas most chapters in this volume focus on group-averaged data, assuming that the neural systems in question operate in a similar manner across individuals, xii Preface the contributions in part IV focus on three types of individual differences in control. First, Van den Bos and Crone look at changes in neural control of social decisions during the development from adolescence into adulthood, showing how neural functioning and behavior undergo substantial changes during this period. Ridderinkhof and colleagues then review evidence regarding individual differences in control in the adult population. Finally, De Bruijn and Ullsperger discuss performance monitoring in patient populations, showing how various neurological and psychiatric conditions are associated with specific and identifiable disturbances in cognitive control. Research on cognitive and motivational control has historically benefitted greatly from the use of explicit computational models of neural functioning. Part V takes a closer look at recent developments in computational approaches that have been particularly influential in this regard. Ribas-Fernandes and colleagues provide an overview of formal models of learning, proposing a hierarchical reinforcement model of behavior. This focus on reinforcement learning is followed in chapters by Cockburn and Frank and by Holroyd and Yeung. Both chapters consider the relationship between the basal ganglia and prefrontal cortex in motivational and cognitive control, while presenting somewhat contrasting accounts of the respective roles of the basal ganglia and anterior cingulate cortex. Once again, the focus is on lateral and medial prefrontal regions. Finally, Shenoy and Yu adopt a Bayesian approach that considers paradigmatic response inhibition tasks within a rational decision-making framework. The concluding part VI comprises three chapters that highlight recent overarching trends in the literature. Chierchia and Coricelli discuss the influence of concepts and methodologies from economic decision theory on theorizing and experiments in the study of control. Hunt and Behrens discuss how the approaches apparent in this volume are now starting to be used to solve problems in more complex and applied domains, focusing in particular on the neuroscience of social decision making. Finally, Bestmann and Mars look at how computational models such as those proposed in part V can be formally linked to the experimental data obtained in neuroimaging and electrophysiology experiments.

Acknowledgments As Jared Diamond and James Robinson state in their recent edited volume *Natural Experiments of History*, Harvard University Press, , completing an edited book Preface xiii costs each editor on average two friends, because of the various levels of stress involved in the process. We are grateful that this has not proven true in our case. We thank all of our contributors, as well as the speakers and attendees of the Oxford meeting, for making both the meeting and this book a success. We are delighted to be able to publish this book with MIT Press, and would like to thank specifically Susan Buckley and Robert Prior, who have provided unwavering support to a group of first-time editors. Finally, we would like to thank our colleagues, friends, and families for their support during periods of stress and strain as we worked on this volume deep into the night. In the first two chapters, the focus is principally on two prefrontal regions—the anterior cingulate cortex ACC and the dorsolateral prefrontal cortex dlPFC—and a basal ganglia region, the ventral

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striatum. The last chapter of this section takes a complementary approach to the classic neuroanatomical one by addressing the role of the different neurotransmitter systems in monitoring performance. One cannot understand the neural basis of control process without carefully considering the architecture of the brain. As Richard Passingham stated: With the appearance of modern computational and databasing techniques, it is now possible to compare individual differences and create large databases and probabilistic maps of not only cytoarchitecture, but also chemoarchitecture and connectivity. Chapters in this section emphasize the complexity of the connectivity patterns: Those results show that a lot remains to be done to achieve a level of understanding of control networks comparable to that of the visual system. Thus, work on animal models remains essential,⁷ especially in order to understand brain mechanisms at infra-voxel resolution—that is, at cortical layers, cell, and synaptic levels. Furthermore, understanding the microarchitecture of a network also implies one has to determine the neurochemical nature of the connections. For instance, dopamine DA is a key molecule in many models of motivational and cognitive control. In the reinforcement learning theory of performance monitoring,³ it is suggested that DA acts on ACC pyramidal cells via D1 receptor. In the prefrontal cortex, D1 and D5 receptors can be found on medium spiny neurons, with D5 receptors also found on aspiny neurons typical of cholinergic interneurons. Because DA effects within the prefrontal cortex are complex and vary depending on the family of DA receptors,¹⁰ it is important to determine how DA is acting in the considered network. In this section, but also in the wider literature, the focus is primarily on the prefrontal cortex and the basal ganglia. However, other areas are thought to play important roles in cognitive or motivational control. The pre-supplementary motor area pre-SMA, inferior frontal junction IFJ, intraparietal cortex, and insula have all been suggested to play an important role in control mechanisms. However, apart from pre-SMA, none of the aforementioned structures correspond to a specific cytoarchitectural territory. The IFJ refers to the region at the junction of the inferior frontal sulcus and the inferior branch of the precentral sulcus. In humans, caudal to this precentral sulcus lies the rostral premotor cortex, in front of it and ventral to the inferior frontal sulcus is area 44, and dorsal to this last sulcus is area 8. In monkeys, these sulci do not exist, making identification of between-species homologs difficult, although an equivalent area exists around the inferior branch of the arcuate sulcus. Furthermore, the term intraparietal cortex refers to a number of cytoarchitectonic areas lying within the intraparietal sulcus. Although multiple areas are also found within the human intraparietal sulcus, the precise homologs in humans and monkeys remain a topic of debate. Finally, the term insula does not refer to only one cortical territory. On the basis of their degree of lamination, three areas can be distinguished: It is suggested that the insula, in interaction with the ACC, plays a role in motivational control. As with the anterior cingulate and dorsolateral prefrontal cortex and basal ganglia, which are the topic of this section, the terms insula, intraparietal cortex, and IFJ should be used very carefully, as the ambiguity in the application of anatomical labels complicates our understanding of the neuroanatomical basis of control. Regional, cellular, and subcellular variations in the distribution of D1 and D5 dopamine receptors in primate brain. *Anatomical Basis of Control* 3 2. Neuronal circuits of the neocortex. *Annu Rev Neurosci* The neural basis of human error processing: Using diffusion imaging to study human connectional anatomy. A probabilistic atlas and reference system for the human brain: Parallel processing strategies of the primate visual system. *Nat Rev Neurosci* How good is the macaque monkey model of the human brain? *Curr Opin Neurobiol* Commentary on Devlin and Poldrack. The anatomical basis of functional localization in the cortex. *Nat Rev Neurosci* 3:

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Chapter 3 : UZH - Department of Economics - Complete List of Publications

The contributors, from fields as varied as anatomy, psychology, learning theory, neuroimaging, neurophysiology, behavioral economics, and computational modeling, present an overview of key approaches in the study of cognitive control and decision making.

Among them, Sina Weibo is one of the largest social networking channels in China. Millions of users repost information from Sina Weibo and share embedded emotion at the same time. Participants preferred to repost negative messages relative to positive and neutral messages. Reposting rate of negative messages was positively correlated to the functional connectivity of temporoparietal junction TPJ with insula, and TPJ with dorsolateral prefrontal cortex. Introduction Microblogging is a popular social medium for people to seek or share information. Imagine that a user writes a microblog message no more than characters and posts it to a number of friends on the web; at the same time, he or she may surf across hundreds of messages posted by friends or broadcasters e. The user can select some interesting activities, opinions, and viewpoints to comment on or further repost them through the Internet. That is the way that we seek and share information via social media today. In China, microblogs are increasingly popular in interpersonal communication and have brought a dramatic change to patterns of information diffusion data from China Internet Network Information Center [CINI], a, b. As of December, , over Million Chinese people had accounts on the largest microblog system in China, Sina Weibo weibo 1. Reposting is the step in which a microblog message is propagated. It is the key activity that characterizes microblogging as a new type of social medium of information dissemination. From among a massive amount of information obtained via friends and followed publishers, an active user can select pieces of microblog messages and further repost them in a short time. Through this activity, each user serves as an information recipient, producer and propagator at the same time Java et al. In contrast to conventional means of communication, which require plenty of time for diffusion, microblog messages spread information effectively and efficiently via divergent reposts China Internet Network Information Center [CINI], b. Several studies have investigated reposting behavior on the web or in a lab environment. One study used self-report questionnaires and daily diaries to statistics the frequency of sharing emotion information in all types of social media Choi and Toma, Besides, reward system is activated because information sharing is a prosocial activity, which gives us the same positive experience as what we feel when given rewards Falk et al. The self-relevance processing system is involved in tasks that evoke self-relatedness Tacikowski et al. The volume of the brain regions within this system is correlated to the online social networking services SNS size Kanai et al. Increased activity at these regions is observed when participants are engaged in mentalizing or theory of mind TOM task Hyatt et al. One recent study showed the decreased functional connectivity between TPJ and supramarginal gyrus in autism patients was paralleled with their deficiency in mentalizing Hoffmann et al. Therefore, we may further speculate the rs-functional connectivity between mentalizing system, e. Accompanied with reposting microblog messages, the embedded emotion in microblog is spontaneously shared. Empirical evidence shows that emotional information is more likely to be propagated than the neutral information obtained through conventional media Poels and Dewitte, and online networks Berger and Milkman, ; Hidalgo et al. Sharing an emotional event e. That means displaying and sharing emotion plays an important role in social communication. For example, sharing negative information attracts more attention from the public and benefits our survival Pratto and John, ; Baumeister et al. These results indicate that sharing information with different emotional valence might be associated with neural activity at distinct brain regions. In real-life SNS, microblog messages are displayed in different formats. Some of them are highlighted with conspicuous title, others were accompany with remarkable pictures. These confounding factors would make the microblog messages hyperarousal or blurry. In this study, we would exclude the confounding titles and pictures, and balance the arousal and familiarity of each type of experimental materials. Thus, these experiment materials would be revised into a standardized format and read by participants in lab. Here, we

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used standardized microblog messages as experimental materials. The rs-functional connectivity between brain regions can serve as indexes of corresponding ability and cognitive process. Based on pilot data, we hypothesized that the microblog messages with emotional valence would be discriminatively reposted. Negative messages would be more likely to repost. Moreover, the reposting rate of negative messages would be correlated with the functional connectivity between the mentalizing regions of interest, *i.* The results would be helpful in uncovering preferences for information propagation and emotion contagion through social media, as well as the neural activity associated with the corresponding psychological processes.

Materials and Methods

Participants We recruited 28 right-handed Chinese University students 14 males and 14 females. All participants had finished at least high school *i.* They each had their own microblog Weibo account and had experience reading and reposting information through social media. All of them had normal or corrected-to-normal vision. None had a history of traumatic brain injury, medical conditions, or any psychiatric disorder that could affect neural activity and brain functioning. All participants signed on a consent form which exhibited the study purpose, the experimental procedure and the amount of payment in the beginning of the study. They were allowed to quit at any stage of the experiment without any punishment.

Materials and Experimental Task Across three categories, pieces of microblog messages were extracted from Sina Weibo microblog system Weibo 2. The microblog messages in the positive category reported positive events in social life *e.* The microblog messages with no emotional significance were categorized as neutral and were included to provide a more realistic simulation of microblog messages. Each piece of microblog message was revised or modified to be a standard length 90 Chinese characters, and was written in the third person as is commonly used in the newspaper. In order to control for possible bias from the original poster, the microblog messages used in this study were posted by four different publishers: Thirty participants were recruited to rate the microblog messages on 1 the emotional valence shown by each piece of microblog message, 2 the emotional arousal elicited by each piece, and 3 their familiarity with the microblog message provided in each piece all on 7-point scales. Using these ratings, 90 out of the initial pieces of microblog messages were selected 30 in each category. In order to exclude a familiarity effect, pieces of microblog messages rated higher than 4. Average ratings toward three categories of microblog messages and average length. Participants read all microblog messages after resting state fmri scanning in the scanner. Each trial began with a fixation cross in the center of the screen for 1 s. A piece of microblog message was then presented on the screen for 15 s. This duration was based on the average reaction time from participants in the pilot study. The screen layout mimicked the interface of the Sina Weibo microblog. The inter-stimulus interval was jittered between 3 and 6 s. In total, each participant read 90 pieces of microblog messages all microblog messages were listed in Supplementary Materials. All microblog messages were pseudorandomized within each participant such that no more than three pieces of microblog messages with the same valence were presented successively. The total duration of the task was 36 min. The scanner was equipped with a standard eight-channel head coil. The first 10 volumes of rs-fMRI data were discarded and the preserved functional images were corrected to the middle slice in each volume in order to adjust the differences in acquisition times of multiple slices. They were realigned to the first volume in the resting state scanning session for head motion correction and resliced to form a mean image. They were then co-registered to high-resolution T1 images at an individual level. After that, six rigid body head motions parameters, white matter, CSF and global signal of the whole brain were regressed out Yan et al. The smoothed signals were detrended and band-pass filtered 0. The z-fc maps for all participants were entered into second-level, voxel-wise, multiple regression models for identifying the regions where we could observe significant correlations between z-fc and reposting rate of each type. The mean functional connectivity of all voxels within each activated cluster was further extracted to calculate the magnitude of correlation between rs-fMRI and reposting rate of corresponding type of microblog messages. The correlations between average functional connectivity with reposting rate of each type of microblog messages were compared with zero, respectively. All significantly correlated regions are shown in Table 2 and Figure 1. A Significant positive correlation between functional connectivity with right

temporoparietal junction TPJ and reposting rate of positive microblogs in right STS. B Significant positive correlations between functional connectivity with left TPJ and reposting rate of negative microblogs in right insula and left DLPFC middle frontal lobe , and significant positive correlation between functional connectivity with left dorsomedial prefrontal cortex DMPFC and reposting rate of negative microblogs in bilateral MOFC. The same case has been observed in microblogs. In the present study, we investigated the behavioral patterns of opinion propagation through microblog messages and rs-functional connectivity of related brain regions. In line with our hypothesis, negative messages were propagated more frequently compared with positive messages and neutral messages. The brain regions involved in mentalizing were associated with individual differentiated preference of emotional valence. These evidence reveal an important behavioral pattern in which negative information prevailed in the transmission through the social media, and helped to identify the neural correlates of this process. This result extends our knowledge of the reposting behavior in microblogs and the corresponding intrinsic neural connectivity. The Prevalence of Negative Microblog Messages Sharing information is a productive activity in the social network. However, our behavioral findings indicate that positive and neutral news tend to be ignored by microblog users, while negative microblog messages are more frequently reposted. In previous research, hearing negative gossip about others induce higher emotion ratings, as well as greater neural activity in the reward system Takahashi et al. Moreover, our findings further extend the boundary of existing knowledge of emotion contagion through SNS. People are not only attracted by negative messages but also were eager to distribute them, making the bad news travel fast. Our result further extends these results and demonstrates that TPJ also engaged in mentalizing, an essential process of information propagation through on-line SNS. The increased reposting rate of negative messages is parallel with increased rs-functional connectivity of TPJ with insula and with middle frontal lobe. It is worth noticing that increased rs-functional connectivity between TPJ with middle frontal lobe was also observed. Thus, the cognitive control network is engaged in reposting negative messages due to its significant effect on the survival of human beings. This regulation conflicts with an intuitive process that represents self-interest and motivation Feng et al. Our findings indicate participants are involved in a similar regulating process when participants are sharing on the web rather than face-to-face. The microblog messages that make us to undergo a feeling of pain disgust or pain might be those with significant social effects need to be reposted to the public. Participants with higher sensitivity to negative stimuli would have a higher tendency to intuitively avoid them but with have higher consciousness to its significance, so the simultaneous hyperactivity at these two regions leads to the increased rs-functional connectivity between TPJ with middle frontal lobe which compensates the increased rs-functional connectivity between TPJ with insula, as well as the increased reposting rate. This shows the reason why negative messages are given priority in the information sharing on the microblog. Limitation Firstly, the relationships between neural activity and emotional valence have eluded consensus Lamm et al. In this study, we only measured rs-fMRI and reposting rate of each emotional type in lab, exploring the association between rs-functional connectivity and reposting rate.

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Chapter 4 : Neural Basis of Motivational and Cognitive Control - PDF Free Download

Decision making in frontal cortex: From single units to fMRI Steven W. Kennerley & Philippe N. Tobler In: Neural Basis of Motivational and Cognitive Control The authors discuss the role of three frontal brain regions, the orbitofrontal, the anterior cingulate and the lateral prefrontal.

Tobler Laboratory for Social and Neural Systems Research, Department of Economics, University of Zurich, Zurich, Switzerland Probability and risk are important factors for value-based decision making and optimal foraging. In order to survive in an unpredictable world, organisms must be able to assess the probability and risk attached to future events and use this information to generate adaptive behavior. Recent studies in non-human primates and rats have shown that both probability and risk are processed in a distributed fashion throughout the brain at the level of single neurons. Reward probability has mainly been shown to be coded by phasic increases and decreases in firing rates in neurons in the basal ganglia, midbrain, parietal, and frontal cortex. Reward variance is represented in orbitofrontal and posterior cingulate cortex and through a sustained response of dopaminergic midbrain neurons. Animals in the wild must interact with the environment and harvest primary rewards such as food and reproductive opportunities to maximize the likelihood that their genetic information survives in future generations. Outside the controlled conditions of the laboratory the time and place that these positive events occur can often not be predicted with total accuracy. In order to survive in such an unpredictable and risky world, organisms must be able to assess not only the probabilities attached to future rewards but also the precision of these estimates and use this information to behave appropriately. Behavioral ecologists have studied the effects of uncertainty on foraging in animals for many decades, but only in recent years have we begun to understand how it is coded in the brain and how this information relates to choice. Before describing their neuronal correlates, we consider briefly the definition of unpredictability and risk and the methodological issues arising from studying them in humans and animals. In the lay concept, risk increases with the perceived chance that a bad outcome i . In the context of animals living in the wild, this typically translates as the probability of death, either through predation or starvation. However, because these long term hazards carry such extreme negative values it is difficult to examine them quantitatively in the laboratory on a trial-by-trial basis Real and Caraco, As a result, the majority of studies at both the behavioral and neural levels have defined uncertainty according to economic and mathematic principles, allowing researchers to define uncertainty at discrete points in time and to study the effects of these parameters on individual decisions. In contrast to the traditional and lay usage of uncertainty, these principles have provided a more precise and quantitative approach. However, other forms and conceptualizations of unpredictability are conceivable and the question whether humans outside the lab sharply distinguish between risk and ambiguity could be investigated further. In human terms, a risky decision might be to gamble on the outcome of a fair roulette wheel, whereas an ambiguous decision might be to gamble on the outcome of a football game. Formally, risk can be defined according to the statistical properties of outcome distributions, such as dispersion i . These objective statistical properties are not precisely known for an ambiguous option, thereby again providing, at least conceptually, a sharp distinction between risk and ambiguity. Different forms of reward-related uncertainty. Ambiguity arises when the probabilities associated with a reward distribution are not fully known. When probabilities are known, then the situation is risky. The definition of risk used in the described studies is distinct from that used in everyday language for example, risky prospect is one where the probability of a loss is non-zero. Instead, risk is defined by a number of parameters that describe the properties of the underlying reward distribution. Careful task design can allow researchers to disentangle neuronal responses to different forms of uncertainty through the independent manipulation of these parameters. Risk and ambiguity can also be separated through stimulus design Hayden et al. Note that entropy, SD, variance, and coefficient of variation correlate with each other but not monotonically with probability. Their separation is therefore more difficult to achieve through task design and might be particularly sensitive to noise in the

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data. Real and Caraco identify two problems that all organisms must overcome in a stochastic environment in order to generate adaptive behavior. Firstly, an organism must learn and keep in mind the outcome probability distributions attached to certain actions and then select a strategy for exploiting these distributions to maximize fitness. The goal of neuroscientific research on decision making under uncertainty has been to discover how the brain solves these two problems by coding the parameters and translating this information into actions. The vast majority of such research has been performed using human subjects, primarily in conjunction with functional magnetic resonance imaging fMRI. This has increased our understanding of the anatomical substrates of reward uncertainty processing to a large degree and has also revealed interesting parallels between sensorimotor and economic decision processes Braun et al. Yet, the low spatial and temporal resolution of fMRI data does not allow researchers to see the fast signaling of reward information by individual neurons. In order to elucidate the temporal propagation of reward uncertainty signals in subcortical and cortical regions, single cell recordings must be made in animals, typically in behaving rats and monkeys. However, using animals in research on the neural mechanisms of decision making under risk poses a different set of challenges from those in human studies. One such issue is whether the economic definitions of risk, envisaged to provide normative or descriptive explanations of human behavior, apply to animal behavior at all. Indeed, the ability of humans to process uncertainty and exploit the information to succeed in the environment may represent a recent evolutionary addition to our cognitive skills that may not be possessed by animals at all. For example, for foraging animals in the wild, the sharp distinction between risk and ambiguity may not be so clear. Animals have to infer the properties of outcome distributions through repeated sampling and learning, thereby gradually turning ambiguity into risk a similar process may also occur in more controlled lab conditions; Rosati and Hare, Moreover, mathematical abilities and the use of numerical representations are more limited in animals compared to humans. For these reasons, the cognitive tasks used to probe behavioral and neural responses to uncertainty in animals differ from those used in human experiments and are typically based on paradigms previously used in animal learning theory. In the present paper we separately review the forms of uncertainty that have been tested experimentally in animals and describe the neurophysiological data relating to each type. The experiments discussed in this review all use single or multiple microelectrodes to record the extracellular potential changes from cell bodies in the immediate vicinity of the electrode tip. In a similar manner to the normative delineations between different types of uncertainty, the descriptive neurophysiological results can be crudely separated into two groups. The majority of animal experiments on reward uncertainty signals have manipulated reward probability in an effort to elucidate the neural mechanisms of learning or value processing. By contrast, only a small number of studies have been conducted with a specific emphasis on economic risk or reward variance and these have focused primarily on cortical areas. Probability in Parietal and Frontal Cortex A simple way to manipulate reward uncertainty is to change the probability with which reward occurs following a cue or an action. Behaviorists have long known that animal decisions are based on reward probability in addition to reward magnitude Herrnstein and Vaughn, , with the assumed goal of maximizing the reward rate Stephens and Krebs, Although a number of studies had previously investigated neural responses to reward expectation Watanabe, ; Schultz et al. Motivated by previous research implicating the lateral intraparietal LIP area as an interface between sensory- and action-related neural information in the brain Goldberg et al. Indeed, LIP neurons were sensitive to expected reward magnitudes, but also modulated their firing rates in response to the probability that a specific rewarded action would be instructed Platt and Glimcher, This work laid the foundations for Sugrue et al. In this task the optimal behavior is to distribute choices for each option according to the relative probabilities that each option would be rewarded. The monkeys were able to perform this task exceptionally well, with similar behavior to computer simulations using an optimal strategy. The activity of LIP neurons correlated with the relative values of targets in the response field of the cells, and this value was related to the probability that a saccade to each target would result in a reward. These recordings robustly support the idea that the brain computes reward probability, although it remains unclear if LIP neurons code probabilities in a

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pure fashion, separately from other reward-related, sensory, or behavioral information. Other parts of parietal cortex, such as the parietal reach region PRR code reward probability between the sensory and motor phases of a memory-guided reaching task. More specifically, the activity of PRR neurons correlated with differential reward probability information during a memory period 1. Due to the suspected role of parietal cortex in integrating sensory and action information it is possible that these signals represent late and multiplexed information relevant to the decision process, with afferent or further upstream cells coding more basic reward information, such as probability. Many neurons in the orbitofrontal cortex OFC appear to code reward probability independent of other task-relevant information such as future action, sensory information, or other reward-related parameters. The OFC is innervated by dopaminergic neurons originating in the ventral tegmental area via the mesocortical pathway, and has strong reciprocal connections with other subcortical reward-related regions such as the amygdala and striatum Barbas and De Olmos, ; Cavada et al. During the course of one trial, rats were trained to sample an odor for 1. A number of neurons coded the probability of the reward during the waiting phase before food was delivered with increasing or decreasing firing rates. A small number of neurons were found to respond to reward probability in this manner during the movement from odor sampling to reward delivery ports and also after the reward was delivered. The result that small numbers of OFC neurons code reward probability in a pure manner is also supported by the work of Kennerley et al. In their task, monkeys were trained to choose between abstract stimuli that predicted rewards with different magnitudes, probabilities, or cost number of lever presses required to obtain the reward. The majority of cells in these areas coded two or more reward parameters, but a number of neurons in all three areas coded reward probability exclusively with increasing or decreasing firing rates. In addition, there were proportionally more neurons in the OFC that were tuned to a single reward parameter such as probability. This result is supported by previous work by Amiez et al. Interestingly, Kennerley et al. Probability in Basal Ganglia and Midbrain Neurons Electrophysiological studies of dopaminergic neurons in the substantia nigra pars compacta and ventral tegmental area have provided strong evidence that the brain codes reward probability. The monkeys showed increased anticipatory licking during cues predicting rewards with higher probabilities. Based on previous work on the phasic response of dopaminergic neurons to reward-predicting stimuli Schultz, the researchers predicted that the phasic response to the cue should increase with increasing probability, and the response to reward should decrease with probability. This hypothesis was supported by the data Figure 2 A , with the phasic response fulfilling the necessary requirements of a reward prediction error reflecting probability as predicted by animal learning theory Rescorla and Wagner, Neuronal responses to reward probability, as demonstrated in four separate experiments. The descending rows represent trials with decreasing reward probability. Each column contains data from a separate experiment. A Population responses of dopaminergic neurons of the substantia nigra pars compacta and ventral tegmental area during a Pavlovian conditioning task, as described in Fiorillo et al. In addition a sustained response that increases until the time of reward encodes reward risk. B An example of the responses of a single cell in the lateral habenula during a similar task as described in [A from Matsumoto and Hikosaka,]. Lateral habenula neurons typically show increased firing rates during the presentation of cues that predict reward with decreasing probability. The task did not include trials with 0. C Population responses of tonically active neurons in the putamen, as recorded by Apicella et al. Stimulus-related reward probability information is encoded in the pause and initial peak of a fraction of tonically active neurons. In addition reward probability exerts strong modulation of suppression and subsequent rebound activity at the time of the outcome. D Oyama et al. Shown here is a single cell demonstrating analogous reward probability coding to dopamine neurons of the VTA and SN, with the absence of a sustained uncertainty response. All figures reprinted with permission. It has recently been proposed that a potential input to these cells is the globus pallidus Hong and Hikosaka, , with neurons of the interior segment of the globus pallidus GPi responding to reward expectancy at a similar latency to that of dopamine neurons. Very few neurons of the GPe were found to respond exclusively to reward probability, with the majority responding to a combination of response direction and reward probability. The longer

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latency of these responses suggested that they may not be the source of reward probability signals observed at stimulus onset in dopamine neurons. A follow-up study using a probabilistic classical conditioning task with recordings from GPe, GPi, and substantia nigra pars reticulata SNr further characterized responses in these regions to reward-predicting cues Joshua et al. This study confirmed that GPi neurons encoded reward probability with latencies of around ms after cue onset, too slow to be the source of the dopaminergic signals demonstrated by Fiorillo et al. By contrast, SNr cells responded to increasing reward probability with increasing and decreasing firing rates in roughly equal proportions, with latencies in the range of ms, more similar to the latencies of dopamine neurons. Another potential source for the dopaminergic reward probability signal is the lateral habenula primarily glutamatergic , for example via projection through the rostromedial tegmental nucleus primarily GABAergic; Jhou et al. Neurons in this region code reward probability in an inverse manner to dopaminergic neurons, showing increased suppression of firing rates to stimuli predicting reward with increasing probability Figure 2 B; Matsumoto and Hikosaka, These neurons also increase their firing rates to stimuli that predict aversive events, suppressing dopaminergic activity in the substantia nigra pars compacta Bromberg-Martin et al. The latency of response suppressions reflecting reward probability information in lateral habenula neurons is roughly comparable to that of excitatory responses in SNc and VTA cells.

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Chapter 5 : Frontiers | Coding of Reward Probability and Risk by Single Neurons in Animals | Neuroscience

5 *Decision Making in Frontal Cortex: From Single Units to fMRI* 75 Steven W. Kennerley and Philippe N. Tobler 6 *A Comparative Perspective on Executive and Motivational Control* by.

Decision making in frontal cortex Decision making in frontal cortex: Although not mentioned as such, the work is interesting in relation to the involvement of subjective conscious experience in determining the decision making discussed here, and its apparent relationship to variations in the firing rate of single neurons. Decisions by humans and other animals require the consideration of multiple influences and possibilities. The decision of which of a choice of foods to eat, or how to reach a required destination is often influenced by a number of potentially conflicting factors. In the simple case of decision to eat, the outcome is at least influenced by the internal state how hungry , longer-term goals such as future health, and cost factors such as the effort etc. The brain then has to decide which of a number of options best meet the various needs and goals. A particular problem is to assign values for, or have a common neural currency for, experiences that do not appear to have a common currency, such as the taste of a food and the energy required to obtain it. The currency also needs to be able to compare the very different outcomes of the various possible courses of action. Evidence from the research of recent years combines to suggest that the frontal cortex has a role in decision making. The authors emphasise the role of the anterior cingulate , the lateral prefrontal, the orbitofrontal and also the ventromedial prefrontal. These are suggested to be involved in representing internal states, representing external variables, assigning values to actions and selection of options based on these action values. Internal reward representation also changes in response to experience. A food substance that used to be associated with a good experience can be devalued and avoided by subjects after earlier rewards fail to be repeated. However, this change does not happen with subjects that have damage to the orbitofrontal. Lateral and central areas of the orbitofrontal receive projections mainly from the sensory cortex, which could explain the sensitivity to devalued rewards. The medial orbitofrontal is linked more to regions with a motor function such as the anterior cingulate. There was considerable variability in the function of single neurons. Given three decision variables, some neurons coded for the value of a single option, some for two-out-of-three possibilities and some for all three possibilities. The authors found no evidence that any of the three frontal areas studied were specialised for dealing with particular decisions. However, single neurons in the anterior cingulate could encode up to at least three decision variables, suggesting that this brain region might integrate the values of different components of a decision. The lateral prefrontal increased activation for reward probability and magnitude and their combined value, and also integrated the levels of value and risk attached to an action. The medial orbitofrontal processes reward probability and the lateral orbitofrontal processes risk. The anterior cingulate appears to be particularly related to assessing the cost as opposed to the potential value of actions. The authors see the orbitofrontal as relating to expectancies for the outcomes of particular sensory stimuli, while the anterior cingulate relates to the value of actions. The anterior cingulate and the lateral prefrontal project to the pre-motor area, while the orbitofrontal is most notable for inputs from the sensory areas. Some single-neurons adapt their rate of firing to the range of possible outcomes and also to the type of outcome being assessed. These neurons have been identified in the orbitofrontal and to striatal and dopamine producing regions, and there is also some evidence for this type of firing in the anterior cingulate. The authors speculate as to whether this type of range sensitivity could be more widespread.

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Chapter 6 : Decision making in frontal cortex: from single units to fMRI - CORE

[et al.] -- *Neural circuits of reward and decision making: integrative networks across cortico-basal ganglia loops* / Haber -- *Neurochemistry of performance monitoring* / Ullsperger -- *Contributions of ventromedial prefrontal and frontal polar cortex to reinforcement learning and value-based choice* / Boorman and Noonan -- *Decision-making in*.

Find articles by Steven W. Walton Find articles by Mark E. For non-commercial, education and research purposes, users may access, download, copy, display, and redistribute this article or manuscript as well as adapt, translate, or data and text mine the content contained in this document. For any such use of this document, appropriate attribution or bibliographic citation must be given. Users should not delete any copyright notices or disclaimers. For more information or to obtain permission beyond that granted here, visit <http://> This article has been cited by other articles in PMC. Abstract Patients with damage to the prefrontal cortex PFC “especially the ventral and medial parts of PFC” often show a marked inability to make choices that meet their needs and goals. These decision-making impairments often reflect both a deficit in learning concerning the consequences of a choice, as well as deficits in the ability to adapt future choices based on experienced value of the current choice. Thus, areas of PFC must support some value computations that are necessary for optimal choice. However, recent frameworks of decision making have highlighted that optimal and adaptive decision making does not simply rest on a single computation, but a number of different value computations may be necessary. Using this framework as a guide, we summarize evidence from both lesion studies and single-neuron physiology for the representation of different value computations across PFC areas. However, in real life, patients with such frontal lobe brain damage are far from normal; they live disorganized lives, tend to be impatient, vacillate when making decisions, often invest their money in risky ventures and exhibit socially inappropriate behavior e. In other words, their defining feature is that they consistently make poor choices. This implies that we should be able to discover something fundamentally special about the functions of these three PFC areas to allow them to support appropriate decision making. They found that neurons in both regions were modulated by whether the animal received a reward, and some only when receiving reward in the context of a correct response. Years later it was found that LPFC neurons not only differentiated multiple rewards, but the value scale encoded by LPFC neurons reflected the subjective reward preferences of the animal Watanabe, Still, in all of these cases, neuronal activity was recorded in the absence of any direct choice between possible outcomes of positive value i. It was not until Shima and Tanji documented that single neurons in ACC were sensitive to reductions in reinforcement value concomitant with a change in behavioral response, that we had clear evidence of a neuronal correlate in PFC or ACC that might reflect a decision-making process. Nonetheless, at the very end of the 20th century we had evidence that single neurons in PFC encoded the value of outcomes and conveyed information about when to adapt decision making, representations which might provide a functional explanation for the decision-making deficits present in patients with ventral and medial PFC damage. However, as interest in this field grew in the 21st century, we discovered a new confounding issue; many if not all areas within the frontal cortex encode to some degree a signal that correlates with decision value. This was elegantly demonstrated by Roesch and Olson who recorded from multiple brain areas spanning both the prefrontal and premotor cortices and found that the encoding of reward value was most commonly found in premotor areas. What was notable about this finding was that damage to premotor cortex does not typically induce decision-making deficits per se. This emphasized that importance of having converging evidence from both correlative and interference techniques when trying to infer function. So we are now at a new junction; neuropsychological studies suggest decision making occurs in the PFC yet neurophysiological studies implicated almost the whole brain in representing a value signal. How do we reconcile the findings from these different methodologies and how do we determine if different brain areas support specialized functions in decision-making? The strategy that we have used in the current review is to try to find converging evidence from studies using neurophysiological and

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neuropsychological techniques in the same frontal lobe areas to address the issue of functional specialization among PFC areas. The former has unique spatial and temporal resolution, thus allowing us to identify not only in which value is represented, but also at what time course, how it changes with learning or behavioral state, and the encoding scheme in which value is represented. This is particularly important in PFC because many neurons encode value with opposing encoding schemes that when averaged across populations of neurons e. Indeed, as will become clear below, it is notable that restricted frontal lobe lesions often cause surprisingly selective impairments in value-based decision making, suggesting that these regions may only be required for a subset of such choices. As focal lesions of single PFC regions are relatively rare in humans, we mainly concentrate on the effects of circumscribed lesions of specific regions of ACC and OFC in animal models. Our review is necessarily not an exhaustive survey of the whole of PFC. For example, there have been few recording studies to date in areas 9, 10, 14, 32, and 25 cf. We also do not give as much attention to the neuroimaging literature as it deserves, and instead direct the interested reader toward reviews on this topic e. Instead, we review ACC, LPFC, and OFC function based on single neuron electrophysiology and focal lesion studies and attempt to place these functions into recent frameworks of decision making. We use an anatomical nomenclature to help synthesize results across studies and techniques. In ACC, we largely focus on the cingulate sulcus as this is the area in which most neurophysiological recordings have taken place. However, we include studies that have recorded from or lesioned the dorsal bank of the cingulate sulcus in our ACC nomenclature, even though they may include parts of areas 9 and 6. However, it is important to note that there may not be clear homologues of primate granular frontal lobe regions in the rodent brain, many of which are the targets of lesion and recording studies that we discuss. On the one hand, this is very interesting because such a signal might contribute to the process of decision making. However, which decision-making process? Many of the decisions that humans and animals face on a daily basis require a consideration of multiple-decision variables, each of which may have separate effects on the neural representation of value in a particular brain region. Even the routine decision of where to shop or forage for food is likely to be influenced by a number of disparate factors. And the choices we make today may differ substantially from the ones we made yesterday or tomorrow, as our current needs and goals change and as we learn from the choices we have made in the past. Thus, optimal decision making is likely to rest on a number of valuation processes and it is critical that we develop a framework of possible valuation processes so that we can begin to identify the unique functional roles different areas contribute to decision making. First, the brain needs to represent what alternatives are available and determine the current and predicted future internal state e. Second, given these states, the brain must then evaluate the external variables that will influence the value of the outcome e. Third, the brain needs to determine the value of the action that would obtain the different outcomes, and discount the outcome based on the expected physical costs e. Optimal selection would then be based on comparison of these action values. Finally, once the choice has been made the brain must compute the value of the obtained outcome. Depending on whether the obtained outcome matched the predicted value of that alternative, a prediction error signal can be generated to modify the value of the alternatives thereby ensuring that future choices are adaptive. It should be noted that we are largely focusing on goal-directed types of behavior in our discussion of PFC function. Representation of Internal States Representation of Incentive Value Arguably the starting point of any decision for an organism is an evaluation of its internal needs given the current state of the environment, as well as an evaluation of what outcomes might satisfy those needs. These parameters are present implicitly in almost all behavioral experiments as most tasks with animals and many with humans involve an element of incentive to motivate the subjects to attend and work. Thus OFC is in a particularly strong anatomical position to evaluate the incentive value, or preference, of different rewards. Interestingly however, in a task that required the animal to remember the sensory characteristics and identity of different rewards across delays to make a subsequent discrimination rather than use reward preference to guide decision making, we found little evidence that OFC neurons encoded reward preference Lara et al. Both medial and lateral parts of OFC, along with the ACC and subcortical regions such as the amygdala and ventral striatum,

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also seem to carry representations of the qualities of foods such as the texture, temperature, and flavor Rolls, Adaptive Coding of Incentive Value OFC therefore has a potentially rich representation of the incentive value of an anticipated outcome associated with predictive stimuli. One solution would be to have a contextually based relative valuation scale. Such adaptive coding is efficient because it allows for maximum discrimination between each distribution of possible outcomes, and it allows flexibility to encode values across decision contexts that may differ substantially in value e. However, it is also important not simply to judge value based on relative context. Interestingly, the majority of outcome sensitive OFC neurons actually do not adapt their firing rates to the range or type of outcomes available, instead encoding value on a fixed scale Kobayashi et al. Thus, as a population, OFC expresses both range adaptation and value transitivity, indicating two fundamental traits necessary for optimal choice. It therefore remains an open question whether range adaptation in frontal cortex is a unique trait of OFC neurons. However, neuroimaging studies have shown relative value activation in ACC Coricelli et al. Subjects are taught that one of two distinct reward types i. Subsequently, in a test session, subjects are presented with pairs of options, one associated with the receipt of each reward type, meaning that they have to make their decisions based on the updated values of the expected outcomes prior to re-experiencing the outcomes i. This is true whether lesions were made prior to initial stimulus-outcome training or following training. Importantly, this impairment is only present when selecting between objects associated with the devalued reward, rather than when selecting between the two foods directly Izquierdo et al. Without such associative representations, they argued, it was not possible to generate appropriate error signals following breaks of expectation to guide learning. The former may contribute to the process of making the current decision, whereas the latter signal may have multiple functions, which will be addressed in later sections of this review. Importantly, these two representations often occur in very close temporal proximity i. Although we showed that some of the same PFC neurons encode information about decision variables e. Thus, it is not simply what value information is encoded i. At first glance it would appear as though there is no particular specialization within PFC for the encoding of decision value. Single neurons across most of the brainâ€”but especially within ACC, LPFC, and OFCâ€”are modulated by almost every decision variable investigators have used to manipulate the expected value of an outcome. With respect to single neuron electrophysiology studies, the overlap of these signals across frontal areas highlights the difficulty in inferring functional specialization by comparing across studies. For example, neurons in ACC, LPFC, and OFC all encode reward magnitude but it is very difficult to infer a functional hierarchy by simply comparing which area has more neurons that encode reward magnitude because different investigators use different paradigms, record activity in different training or behavioral states and often use very different analytical methods. One resolution to this issue is to examine the activity of neurons in multiple-brain areas simultaneously. We Kennerley et al. Monkeys were trained to make choices based on conditioned stimuli that indicated different behavioral outcomes that varied in terms of either reward probability, reward magnitude, or physical effort Kennerley et al. We recorded from OFC, ACC, and LPFC simultaneously, thus allowing us to directly pit these three frontal areas against each other in animals in the same behavioral state using the same analytical methods. We found that neurons encoded value across the different decision variables in diverse ways. For example, some neurons encoded the value of just a single decision variable, others encoded the value of choices for two of the variables but not the third, while still others encoded value across all three decision variables Figure 1C, D. We found no evidence that any of the three frontal areas were specialized for encoding any particular decision variable Figure 1E.

Chapter 7 : - NLM Catalog Result

Neural basis of motivational and cognitive control. and Noonan --Decision-making in frontal cortex: from single-units to fMRI / Kennerley and Tobler --A.

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Chapter 8 : Decision Making and Reward in Frontal Cortex

Patients with damage to the prefrontal cortex (PFC)â€”especially the ventral and medial parts of PFCâ€”often show a marked inability to make choices that meet their needs and goals. These decision-making impairments often reflect both a deficit in learning concerning the consequences of a choice, as.

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