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REVIEW 2

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BETWEEN THE PRIMATE AND 'REPTILIAN' BRAIN: RODENT MODELS 3 DEMONSTRATE THE ROLE OF CORTICOSTRIATAL CIRCUITS IN л **5 O1 DECISION MAKING**

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- 14 Abstract—Decision making can be defined as the flexible integration and transformation of information from the external world into action. Recently, the development of novel genetic tools and new behavioral paradigms has made it attractive to study behavior of all kinds in rodents. By some perspectives, rodents are not an acceptable model for the study of decision making due to their simpler behavior often attributed to their less extensive cortical development when compared to non-human primates. We argue that decision making can be approached with a common framework across species. We review insights from comparative anatomy that suggest the expansion of cortical-striatal connectivity is a key development in evolutionary increases in behavioral flexibility. We briefly review studies that establish a role for corticostriatal circuits in integrative decision making. Finally, we provide an overview of a few recent, highly complementary rodent decision-making studies using genetic tools, revealing with new cellular and temporal resolution how, when and where information can be integrated and compared in striatal circuits to influence choice.

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Q6 Key words: rodents, corticostriatal circuit, striatum, action selection, decision-making, optogenetics.

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Abbreviations: AAV, adeno-associated virus; ChR2, Channelrhodopsin-05 2; HSV-1, herpes simplex 1; MSNs, medium spiny neurons; PINP, positively identify neural populations.

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INTRODUCTION

Decision making is an information integration and Q7 32 comparison problem in which diverse sources of 33 information from sensory, reward and memory systems 34 must be brought together in order to evaluate choices. 35 Formal accounts of decision making in diverse fields 36 such as economics, psychology, and computer science 37 model it as a two-step process (Rangel et al., 2008). In 38 the first step, values are assigned to particular actions 39 through a process of learning. In the second step, the rel-40 ative values of available actions are compared to deter-41 mine the probability of executing a particular motor 42 response (Sugrue et al., 2005; Kable and Glimcher, 43 2009; Lee et al., 2012). Decision making in this way can 44 be thought of as a process of dimensionality reduction, 45 wherein multiple streams of information are mapped onto 46 a single axis of value (Sugrue et al., 2005; Kable and 47 Glimcher, 2009; Lee et al., 2012). 48

Much of what we know about the neural substrates of 49 decision making derives from studies using non-human 50 primates as a model system. These studies build on our 51 extensive knowledge of sensory and motor systems of 52 primates (Wurtz, 1968; Wurtz and Goldberg, 1972; 53 Newsome et al., 1989; Salzman et al., 1990; Shadlen 54 and Newsome, 1996), and make use of sophisticated 55 quantitative methods for relating neural activity to 56 behavior. 57

Recently, the rodent has emerged as a useful 58 experimental model system for understanding the neural 59

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basis of decision making. Part of the appeal of using 60 rodents is the growing availability of sophisticated 61 molecular and genetic tools for monitoring and 62 manipulating neural activity in identified cell types and 63 subcircuits (Luo et al., 2008; Scanziani and Hausser, 64 2009; Kramer et al., 2013; Deisseroth, 2014). Other advan-65 tages include higher throughput, lower cost, and ethical 66 67 arguments. By applying the quantitative methods and conceptual tools historically associated with primate studies of 68 decision making, the rodent preparation has the potential 69 to offer the best of both worlds. 70

71 Although much of the work on decision making in 72 primates has focused on the role of the neocortex, there 73 is arowing evidence for the importance of the striatum. The striatum, sometimes inappropriately referred to as 74 the "reptilian brain" is a more ancient structure in the 75 timeline of evolution (MacLean, 1990), making it seem 76 an unlikely candidate for understanding higher forms of 77 cognition. Here we review arguments that suggest this 78 view is misinformed. The striatum receives convergent 79 input from the neocortex and other structures, positioning 80 it ideally to act as a central arbiter for comparing the value 81 of different choices. The role of the striatum in decision 82 83 making appears to predate the evolution of the neocortex. 84 Below we discuss how, in the evolution from amphibians 85 to reptiles the elaboration of pallial-striatal connectivity 86 may have enhanced behavioral flexibility. This elaboration 87 of cortical-striatal connectivity continued in mammals, along with increased routing of sensory information 88 through the cortex to the striatum. 89

Our review is organized in six subsections. The first 90 describes how studies of orienting behavior provide a 91 common experimental framework for study of decision 92 making across primate and rodent. Second, we review 93 literature suggesting the anatomical convergence of 94 inputs into the striatum may enable evaluation of 95 96 choices, and highlight how these cortical-striatal 97 afferents have become elaborated during evolution. Third, we briefly review studies that establish that value 98 and choice signals can be observed in striatal activity in 99 both primates and rodents. Fourth, we highlight how the 100 ability to independently study and manipulate the direct 101 and indirect pathways in the rodent using genetic tools 102 has permitted advances in understanding how these 103 pathways regulate goal directed orienting. Fifth, we 104 show how changing activity in cortical-striatal synapses 105 from a primary sensory region is sufficient to alter action 106 selection. And sixth, we lay out future directions for 107 research. 108

COMPARABLE CIRCUITS FOR ORIENTING IN 109 **PRIMATES AND RODENTS** 110

111 In animal studies of decision making, subjects must be trained to report their choices non-verbally. In primate 112 studies, subjects can be trained to report their choices 113 using a saccadic eye movement (Wurtz and Mohler, 114 1974; Sugrue et al., 2005; Gold and Shadlen, 2007; 115 Kable and Glimcher, 2009; Lee et al., 2012). In rodent 116 studies, subjects can report their choices by selecting 117 the left or right port of a 3-port behavior box (Uchida 118 and Mainen, 2003; Kepecs et al., 2008; Otazu et al., 119

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2009; Erlich et al., 2011; Huberman and Niell, 2011; 120 Meier et al., 2011; Carandini and Churchland, 2013) 121 (see Fig. 1).

Interestingly, primate saccadic eye movements and 123 rodent choice port selection seem to recruit readily 124 comparable neural circuits. These circuits, which 125 originally evolved to control whole head and body 126 orienting movements, have been conserved throughout 127 vertebrate evolution, and provide a unified framework 128 for understanding how decisions are mapped onto motor 129 responses across species (Grillner et al., 2008). Rodent 130 head and body orienting behaviors, and primate saccadic 131 eye movements, can both be induced by stimulating the 132 superior colliculus (Wurtz and Goldberg, 1972; Stryker 133 and Schiller, 1975; Dean et al., 1989). Upstream struc-134 tures, including the cortical frontal eve fields (FEF) and 135 lateral intraparietal area (LIP), which control eye move-136 ments in non-human primates, have rodent homologs 137 with apparently similar function (Erlich et al., 2011). Sim-138 ilar parallels have been identified in areas such as the 139 orbitofrontal (Feierstein et al., 2006), anterior cingulate 140 (Kvitsiani et al., 2013), and medial frontal cortex (Sul 141 et al., 2010; Rodgers and DeWeese, 2014). 142

THE EVOLVING ROLE OF THE STRIATUM IN DECISION MAKING

A complex network of brain areas are involved in decision making (Sugrue et al., 2005; Gold and Shadlen, 2007; Kable and Glimcher, 2009; Lee et al., 2012). In mammals, key areas include the prefrontal and motor cortex. However, there is growing evidence that the purely corticocentric approach is incomplete, and that other structures, including the basal ganglia, also play a central role.

The basal ganglia are set of subcortical nuclei present throughout the vertebrate phylogeny. Recent comparative anatomical studies have demonstrated that the organization of the basal ganglia has remained largely unchanged from the lamprey to reptiles and primates, a degree of conservation in the vertebrate line that spans 560-million years of evolution (Grillner et al., 2013; Robertson et al., 2014). This collection of subcortical nuclei control basic motor programs for fundamental behaviors such as orienting within the superior colliculus/ tectum that are present in all vertebrates. By contrast, many vertebrate species lack a well-developed, six-layered neocortex.

The basal ganglia are made up of a collection of 165 connected brain regions including the striatum, pallidum, 166 subthalamic nucleus and substantia nigra as well as dopaminergic modulation from the midbrain (Albin et al., 168 1989a; Kreitzer and Malenka, 2008; Gerfen and 169 Surmeier, 2011). The basic components of the basal gan-170 glia are found across vertebrate species, from lamprey to 171 primates (Grillner et al., 2008; Stephenson-Jones et al., 172 2012). The primary input structure of the basal ganglia 173 is the striatum. The striatum can be sub-divided into the 174 dorsal and ventral portions, which project to dorsal and 175 ventral pallidal structures, respectively, as well as the 176 substantia nigra. The main cells of the striatum are the 177 medium spiny neurons (MSNs), which fall into two clas-178 ses that differ in their pattern of anatomical projections 179

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