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Category learning in the brain

Carol A. Seger¹ and Earl K. Miller²

¹Department of Psychology and Program in Molecular, Cellular, and Integrative Neurosciences, Colorado State University, Fort Collins, CO, 80523 USA

²The Picower Institute for Learning and Memory and Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139 USA

Additional Items requested by Annual Reviews:

Abstract (150 words max).

The ability to group items and events into functional categories is a fundamental characteristic of sophisticated thought. It is subserved by plasticity in many neural systems, including neocortical regions (sensory, prefrontal, parietal, and motor cortex), the medial temporal lobe, the basal ganglia and midbrain dopaminergic systems. These systems interact during category learning. Corticostriatal loops may mediate recursive, bootstrapping interactions between “fast” reward-gated plasticity in the basal ganglia and “slow”, reward-shaded, plasticity in the cortex. This can provide a balance between acquisition of details of experiences and generalization across them. Interactions between the corticostriatal loops can integrate perceptual, response, and feedback related aspects of the task and mediate the shift from novice to skilled performance. The basal ganglia and medial temporal lobe interact competitively or cooperatively, depending on the demands of the learning task.

Key words (3 to 5, not mentioned in title).

Classification, Concept learning, Memory systems,

A list of all important acronyms (up to 10) and their spell-outs.

VTA Ventral Tegmental Area
DA Dopamine
SNr Substantia Nigra, pars reticulata
SNc Substantia Nigra, pars compacta
BG Basal Ganglia
PFC Prefrontal Cortex
PMC Premotor Cortex
ITC Inferotemporal cortex
MTL Medial Temporal Lobe
fMRI functional Magnetic Resonance Imaging

A side bar (up to 200 words in length) highlighting a related topic

Side bar: Computational Factors in Category learning.

- *Generalized knowledge versus memory for specific instances.* The complementary memory systems framework notes that there is a conflict between generalized knowledge (e.g., the overall concept of a chair) and specific memories (e.g., one's own office chair) (O'Reilly & Munakata, 2000). Categorization learning emphasizes the acquisition of generalized knowledge about the world, but also requires some specific representations, for example in the situation of arbitrary categories or in representing exceptions to general rules.
- *Fast versus slow learning.* Fast learning has obvious advantages: one can learn to get to resources and avoid obstacles faster and better than competitors. But fast learning comes at a cost; it does not allow the benefits that come from generalizing over multiple experiences, so by necessity it tends to be specific and error-prone. For example, consider conditioned taste aversion: A one-trial and often erroneous aversion for a particular food. Extending learning across multiple episodes allows organisms to pick up on the regularities of predictive relationships and leave behind spurious associations and coincidences. It also allows category formation by allowing learning mechanisms to identify the commonalities across different category members. We suggest that the brain balances the advantages and disadvantages of fast vs. slow learning by having "fast" plasticity mechanisms (large changes in synaptic weights) in subcortical structures train slower plasticity (small weight changes) in cortical networks.

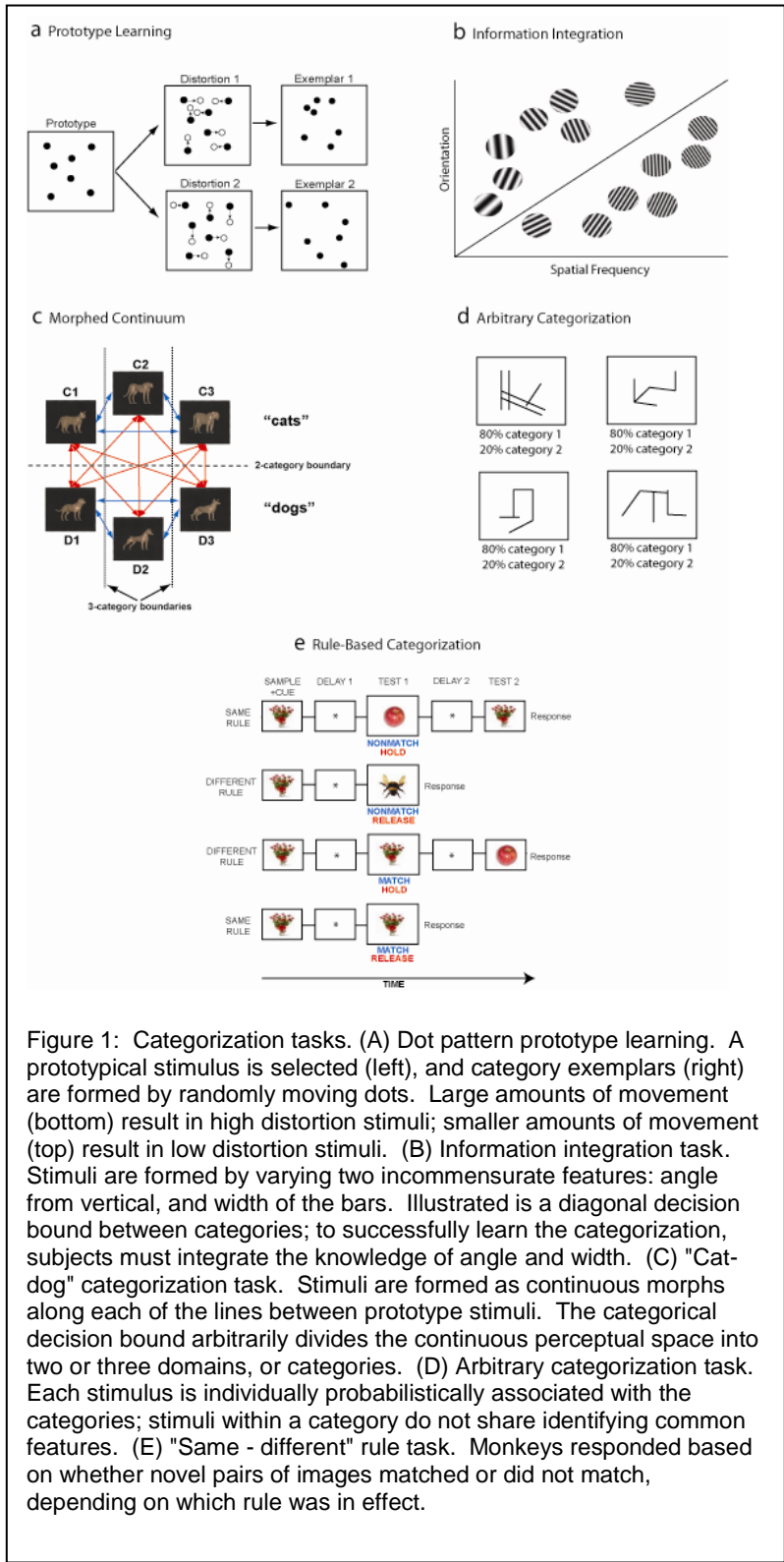
I Introduction

While our brains can store specific experiences, it is not always advantageous for us to be too literal. A brain limited to storing an independent record of each experience would require a prodigious amount of storage and bog us down with details. We have instead evolved the ability to detect the higher-level structure of experiences, the commonalities across them that allow us to group them into meaningful categories and concepts. This imbues the world with meaning. We instantly recognize and respond appropriately to objects, situations, expressions, etc. even though we have never encountered those exact examples before. It allows proactive, goal-directed thought by allowing us to generalize about – to imagine -- future situations that share fundamental elements with past experience. Imagine the mental cacophony without this. The world would lack any deeper meaning. Experiences would be fragmented and unrelated. Things would seem strange and unfamiliar if they differed even trivially from previous examples. This describes many of cognitive characteristics of neuropsychiatric disorders like autism.

Here, we review how categories are learned by the brain. We begin with a brief definition of categories, and description of how category learning is studied. We argue that categorization is not dependent on any single neural system, but rather results from the recruitment of a variety of neural systems depending on task demands. We then describe the primary brain areas involved in categorization learning: visual cortex, prefrontal and parietal cortex, the basal ganglia, and the medial temporal lobe. This leads to a discussion and hypotheses of how neural systems interact during category acquisition. This focuses on interactions within and between corticostriatal loops connecting cortex and basal ganglia, and between the basal ganglia and the medial temporal lobe. We will end by summarizing principles by which the brain learns categories and other abstractions.

Categories

Categories represent our knowledge of groupings and patterns that are not explicit in the bottom-up sensory inputs. A simple example is crickets sharply dividing a range of pure tones into “mate” versus “bat” (a predator) (Wyttenbach et al., 1996). A wide range of tones on either side of a sharp boundary (16 kHz) are treated equivalently while nearby tones that straddle it are treated differently. This grouping of experience by functional relevance occurs at many levels of processing and for a wide range of phenomena from more literal (e.g., color) to abstract (e.g., peace, love and understanding). Many categorical distinctions are innate or result from many years of experience (e.g., faces), but key to human intelligence is our ability to quickly learn new categories, even when they are multivariate and abstract (e.g., Free Jazz, gastropub). There are several



excellent reviews of innate or well-learned categories (Mahon & Caramazza 2009; Martin, 2007). We focus on category learning.

Examples of category learning tasks are shown in Figure 1. Many tasks use novel stimuli formed according to a particular perceptual manipulation and then grouped according to an experimenter-defined boundary. Some examples of stimuli used in tasks include prototypes, information integration, and stimuli morphed along a continuum, (Figure 1A-C, respectively). We can also group events and actions into categories by more abstract properties or rules, which can range from simple deterministic rules based on a single easily identified dimension to more complex situations in which rules may be probabilistic, or complex (e.g., a conjunctive or disjunctive rule), or

require identification of an abstract feature not actually present in the physical item (e.g., the rule "same" or "different" (Figure 1E). Categorization can even be

completely arbitrary (Figure 1D). For example, imagine a group of students, half of which are enrolled in one section of a course, and half in the other section. The students within each section likely do not share any particular perceptual characteristics that are not shared by students in the other section. However, this categorization scheme has great utility for predicting which students are likely to attend class in a particular room at a particular time.

II Brain areas involved in category learning

Not surprisingly given the variety of above examples, category learning likely involves many brain systems including most of the neocortex, hippocampus, and basal ganglia. We review what types of category tasks recruit each region of the brain, and describe each region's putative role. We make no claims to an exhaustive treatment; categorical representations are likely in many domains and their respective neural systems. For example, there is also evidence that the amygdala participates in generalization of knowledge about fearful or aversive types of stimuli (Barot et al. 2008).

Visual cortex

We focus on the visual system, the best-studied modality. However, similar processes are likely present in other sensory modalities, including the auditory (Vallabha et al. 2007), somatosensory (Romo & Salinas 2001), and olfactory (Howard et al. 2009) systems.

Likely candidates for visual categorization are areas at the highest levels of visual processing. One is the inferior temporal cortex (ITC), whose neurons have complex shape-selectivity (Desimone et al., 1984; Logothetis and Sheinberg, 1996; Tanaka, 1996). Neurons with category-like tuning properties have been known since the seminal work on “face cells” by Gross and colleagues (Desimone et al., 1984). The human fusiform face area (Kanwisher et al, 1997), an ITC area with a preponderance of face cells, is recruited during learning of new face categories (DeGutis & D'Esposito 2007). Inferior temporal neurons in trained monkeys are specifically activated by “trees” or “fish” and show relatively little differentiation within those categories (Vogels, 1999). Microstimulation of monkey ITC can facilitate visual classification of novel images (Kawasaki & Sheinberg 2008).

But the ITC may play less of a role in learning explicit representations of category membership and more in high-level analysis of features that contribute to categorization. ITC neurons often do not completely generalize among category members; they retain selectivity for underlying perceptual similarity between individuals (Freedman et al., 2003) (Jiang et al. 2007). At the same time, they emphasize certain critical stimuli or diagnostic features for the categories and show greater activity for stimuli near category boundaries (DeGutis & D'Esposito 2007, Freedman et al. 2003) (Sigala & Logothetis 2002).

Simple shape based perceptual categories may be acquired in earlier visual areas. A commonly used task is the dot pattern prototype learning task (see Figure 1A); subjects learn a single category (e.g., “A” vs “not A”) via simply observing category members. This type of relative simple category learning may depend on plasticity in the early visual system locus. fMRI studies show activity changes after dot pattern learning in extrastriate visual cortex, typically around BA 18/19 and roughly corresponding to visual area V2 (Aizenstein et al. 2000, Reber et al. 1998, Reber et al. 2003) . Performance on this task is preserved in persons with amnesia (Knowlton and Squire, 1993); for a comprehensive review, see Smith 2008), indicating independence from the medial temporal lobe memory system, and is preserved in Parkinson's disease (Reber and Squire, 1999), indicating independence from corticostriatal systems. However, patients with moderate severity Alzheimer's disease, which can include damage to extrastriate visual cortex, are impaired (Keri et al. 1999). Other categorization tasks, however, do recruit corticostriatal and/or medial temporal lobe systems, especially more complex category learning that involve learning via trial-and-error feedback and learning of multiple categories (Vogels et al. 2002, Little & Thulborn 2005, Casale & Ashby 2008).

Plasticity in visual cortex likely involves local changes in the strength of cortical synapses due to Hebbian learning (McClelland, 2006) subserved by mechanisms of long term potentiation. Sensory cortex typically emphasizes stability over plasticity, particularly in adults. As a result, perceptual categories, especially in early sensory cortex, do not usually result from just casual or limited amounts of passive experience with a stimulus.

Prefrontal cortex

The prefrontal cortex occupies a far greater proportion of the human cerebral cortex than in other animals, suggesting that it might contribute to those cognitive capacities that separate humans from animals (Fuster, 1995) (Miller and Cohen, 2001). It seems more modifiable by experience more readily than sensory cortex.

For example, Freedman and colleagues trained monkeys to categorize stimuli along a morphing continuum of different blends of “cats” and “dogs” (Freedman et al., 2001, 2002; Freedman et al., 2003; see Figure 1C) and found that a large proportion of randomly selected lateral PFC neurons with hallmarks of category representations: sharp differences in activity to similar-looking stimuli across a discrete category boundary yet similar activity to different-looking members of the same category. Simultaneous recording from the PFC and anterior-ventral ITC revealed weaker category effects in the ITC (they retained more selectivity for individual members) and that category signals appeared with a shorter latency in the PFC than ITC, as if it were fed back from the PFC (Freedman et al, 2003; Meyers et al. 2008). Human imaging studies found that ITC is sensitive to

perceptual features of stimuli and perceptual distance between stimuli, but only PFC represents the boundary between categories itself or crucial conjunctions between features (Jiang et al. 2007, Li et al. 2009).

PFC neurons also reflect abstract rule-based categorical distinctions. For example, Wallis and Miller (Wallis et al., 2001; Wallis and Miller, 2003; Muhammad et al., 2006) trained monkeys to apply either a “same” or “different” rule to novel pairs of pictures (see Figure 1E). Many PFC neurons conveyed which rule was in effect independent of which specific cue signalled the rule, not linked to the behavioral response, and unaffected by the exact pictures the monkeys were judging. By contrast, there was relatively little effect of the rules in the ITC, even though it is directly connected with the lateral PFC and it is critical for visual analysis of the pictures (Muhammad et al., 2006).

Parietal cortex

The parietal cortex seems to emphasize visuospatial functions and link information from perceptual cortex with potential responses. Many studies have examined its neural selectivity by having subjects discriminate the direction of motion of moving dots. Many direction-selective neurons are in extrastriate area V5 / MT (Newsome et al., 1986), which project to the lateral inferior parietal lobe and insula which integrate overall movement pattern (Ho et al. 2009; Rorie & Newsome, 2005). Freedman and Assad (2006) trained monkeys to classify 360 degrees of motion direction into two categories and found that category membership was strongly reflected in the lateral inferior parietal region, but much less so in V5 / MT. The respective roles of the parietal and frontal cortices in categorization and visual cognition in general remain to be determined, but several studies indicate a close functional link between the lateral inferior parietal lobe and the PFC (Chafee and Goldman-Rakic, 2000; Buschman and Miller, 2007).

Premotor and motor cortex

Categorical decision tasks also involve selection and execution of an appropriate behavior. This recruits premotor cortex (PMC) and primary motor cortex within the frontal lobe. Category learning can also result in plasticity in brain systems involved in attention and eye movements (Blair et al., 2009). Little and Thulborn (2005) found changes in frontal eye field and supplementary eye field activity across training in a dot pattern categorization task that likely reflected improved visual scanning of the stimuli.

As expertise is developed, reliance on motor systems increases and reliance on other systems decreases. Indeed, PFC damage preferentially affects new learning: Animals and humans can still engage in complex behaviors as long as they were well-learned before the damage (Shallice, 1982; Dias et al., 1997) (Murray et al. 2000). PFC neurons are more strongly activated during new

learning than execution of familiar tasks (Asaad et al., 1998). There are stronger signals in the dorsal PMC than the PFC when humans performed familiar versus novel classifications (Boettiger and D'Esposito, 2005) and when monkeys performed familiar abstract rules (Muhammad et al., 2006) Thus, the PFC may acquire new categories, but other areas like the premotor cortex may store them once they become familiar.

Hippocampus and the medial temporal lobe

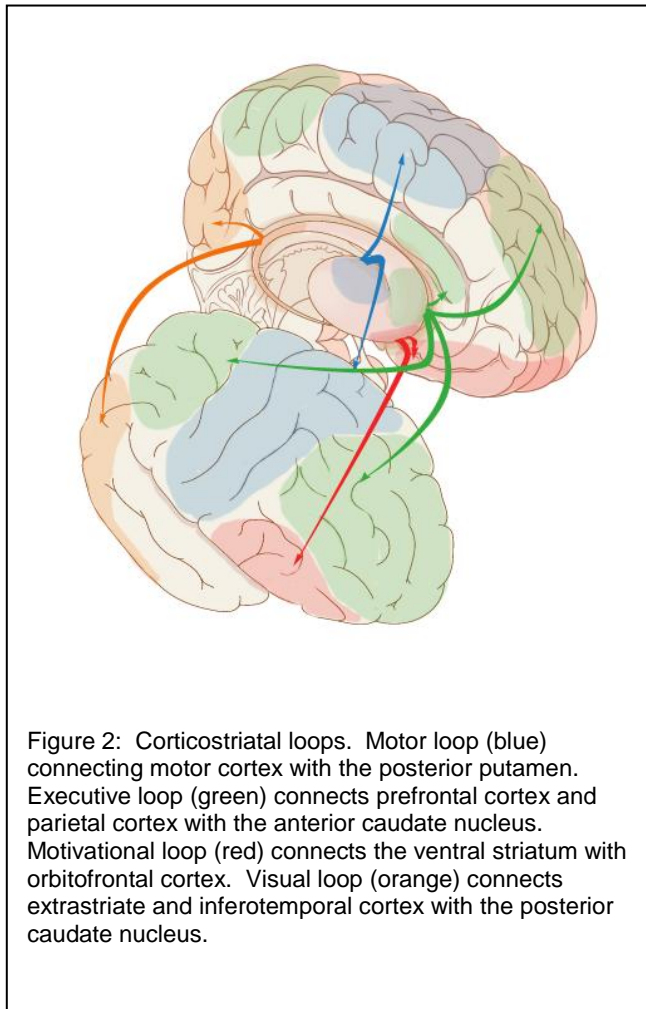
The medial temporal lobe has anatomical and functional connections with cortex and seems specialized for rapid learning of individual instances (O'Reilly and Munakata, 2000). The circuitry of the MTL and cortex forms a loop: information from broad neocortical regions across parietal, frontal, and temporal cortex projects to the entorhinal region of the parahippocampal gyrus. From entorhinal cortex, the primary projections pass to the dentate gyrus, CA3 field of the hippocampus, CA1 field, and back to entorhinal cortex. The CA3 contains autoassociative recurrent links, which allow association formation during encoding, and pattern completion during recall (Becker & Wojtowicz 2007, Gluck et al. 2003 O'Reilly and Munakata, 2000).

Several lines of evidence suggest multiple roles for the MTL in categorization. They seem to make use of the MTL's ability to learn individual instances. One task that requires instance learning is the arbitrary categorization task (Figure 1D), in which the category membership of each item must be remembered individually. fMRI studies find that MTL (among other systems, including corticostriatal systems) is often recruited during these tasks (Poldrack et al., 1999, 2001; Seger & Cincotta, 2005). Likewise, monkey neurophysiology studies found that neurons in the hippocampus and temporal cortex show category-specific activity after training to groupings of arbitrary stimuli (Hampson et al., 2004). Kreiman et al. (2000) found neurons in the human MTL that were selective for diverse pictures of familiar concepts like "Bill Clinton". The instance learning capacity of the MTL may also be invoked to store exceptions to rules and other categorical regularities (Love et al. 2004). Some degree of instance memory may be required in all categorization tasks that use novel stimuli; the MTL may be required in order to set up a memory representation of each stimulus that can then be accessed by other systems (Meeter et al. 2008).

Another important potential contribution of the MTL follows from observations that information acquired via the MTL can be transferred to new situations. One example is acquired equivalence. For example, if a subject learns that stimulus A is in categories 1 and 2, and stimulus B is in category 1, they can reasonably infer that stimulus B might also be in category 2. The MTL is involved in these tasks (Myers et al. 2003; Shohamy & Wagner 2008).

The basal ganglia and corticostriatal loops

The basal ganglia are a collection of subcortical nuclei that interact with cortex in corticostriatal "loops". Cortical inputs arrive largely via the striatum and are ultimately directed back into the cortex via the thalamus. Most of the cortex projects directly onto the striatum (Kemp and Powell, 1970)(Flaherty and Graybiel, 1991). The basal ganglia maintain a degree of topographical separation in different loops, ensuring that the output is largely to the same cortical areas that gave rise to the initial inputs to the BG (Alexander et al., 1986;



Parthasarathy et al., 1992; Hoover and Strick, 1993; Kelly and Strick, 2004). The frontal cortex receives the largest portion of BG outputs, suggesting some form of close collaboration between these structures (Middleton and Strick, 1994, 2002). However, almost all cortical regions participate in corticostriatal loops. Although there is overlap between the loops at their boundaries, it is useful to talk of four loops: executive, motivational, visual, and motor (Seger 2008; Lawrence et al., 1998), as illustrated in Figure 2. The basal ganglia exert a tonic inhibition on cortex; they selectively and phasically "release" the cortex to allow for selection of a movement (Humphreys et al., 2006), or cognitive strategy (Frank 2005). In categorization tasks, this function may be recruited to help with selection of both an

appropriate category representation and related strategies or behaviors (Seger, 2008).

The basal ganglia are active in a wide variety of categorization tasks (Nomura et al. 2007; Poldrack et al., 1999, 2001; Seger and Cincotta, 2005; Zeithamova et al., 2008), particularly those that require subjects to learn via trial and error (Merchant et al. 1997)(Cincotta & Seger 2007). Performance on these tasks is impaired in patients with compromised basal ganglia functions due to Parkinson's and Huntington's Disease (Knowlton et al., 1996; Shohamy et al., 2004; Ashby

and Maddox, 2005). The roles of individual corticostriatal loops and their interactions during categorization are discussed further below.

Midbrain dopaminergic system and reinforcement learning mechanisms

Any form of supervised (reward-based) learning, including category learning, depends on the midbrain dopaminergic brain systems (the ventral tegmental area, VTA, and the substantia nigra, pars compacta, SNc) (Schultz et al., 1992). Neurons in these areas show activity that seems to correspond to the reward prediction error signals suggested by models of animal learning (Hollerman and Schultz, 1998; Montague et al., 2004), but see (Redgrave and Gurney, 2006). They activate and release dopamine (DA) widely throughout the subcortex and cortex (especially in the frontal lobe) whenever animals are unexpectedly rewarded, and pause when an expected reward is withheld. Over time the cells learn to respond to an event that directly predicts a reward: the event 'stands in' for the reward (Schultz et al., 1993). Functional imaging has also found that the basal ganglia are sensitive to prediction error (Seymour et al. 2007).

Cortical inputs converge onto the dendrites of striatal spiny cells along with a strong input from midbrain dopaminergic neurons. Dopamine is required for strengthening or weakening of synapses in the striatum by long-term depression or potentiation, respectively (Calabresi et al., 1992; Otani et al., 1998; Kerr and Wickens, 2001). These anatomical and neurophysiological properties suggest that the striatum has an ideal infrastructure for rapid, *reward-gated*, supervised learning that quickly forms representations of the patterns of cortical connections that predict reward (Houk and Wise, 1995; Miller and Buschman, 2007). Functional imaging, neuropsychological, and computational studies suggest that feedback-based category learning via trial-and-error depends on both dopamine and the basal ganglia (Shohamy et al. 2008).

III Interaction between neural systems during category learning

Above, we discussed how categorization learning relies on multiple neural systems. For example, a visual categorization task may recruit visual cortex and medial temporal lobe to represent and memorize the individual stimuli and facilitate processing of relevant features, the prefrontal cortex to learn and represent categorization rules and strategies, and the basal ganglia, parietal lobe, and motor cortexes to make decisions and select behavioral responses on the basis of categorical information. In this section we discuss several ways that these neural systems may interact during category learning.

Interactions between fast subcortical plasticity and slower cortical plasticity

A key issue in learning is the need to balance the advantages and disadvantages of "fast" vs. "slow" plasticity (see Sidebar). Fast plasticity (large changes in

synaptic weights with each episode) in a neural network has advantages in rapid storage of relevant patterns of activity (and quick learning). But it is slow plasticity (small weight changes) that allows networks to generalize; gradual changes result in neural ensembles that are not tied to specific inputs but instead store what is common among them. One possible solution is to have fast plasticity and slow plasticity systems interact (McClelland et al., 1995; O'Reilly and Munakata, 2000). For example, McClelland et al (1995) suggested that long term memory consolidation results from fast plasticity in the hippocampus whose output trains slower plasticity cortical networks that gradually elaborates the memories and link them to others. A similar relationship between the cerebellum and cortex could underlie motor learning (Houk & Wise 1995). We suggest that an interaction between fast plasticity in the basal ganglia and slow plasticity in the cortex underlies many forms of category learning and abstraction (Miller and Buschman, 2007).

"Fast" and "slow" plasticity may arise from different applications of the dopaminergic teaching signal. Both the cortex and basal ganglia receive projections from midbrain dopaminergic neurons, but dopamine input to cortex is much lighter than that into the striatum (Lynd-Balta and Haber, 1994). Dopamine projections also show a gradient in connectivity with heavier inputs in the PFC that drop off posteriorly (Thierry et al., 1973; Goldman-Rakic et al., 1989). This may explain why the PFC seems to show a greater deal of experience-dependent selectivity than visual cortex. In the striatum, the DA influence may be greater still. DA neurons terminate near the synapse between a cortical axon and striatal spiny cell, a good position to gate plasticity between the cortex and striatum. DA neurons synapse on the dendrites of cortical neurons, and thus may have a lesser influence. Thus, while plasticity in the striatum may be fast and *reward-gated* in the cortex it may be slower and *reward-shaded*. Thus, the striatum may be better suited to learn details, the specific cues, responses, etc. that predict rewards while cortex acquires the commonalities among them that result in categories and abstractions (see Daw et al., 2005).

There is some suggestive evidence for this. Pasupathy and Miller (2005) found that during conditional visuomotor learning in monkeys, striatal neural activity showed rapid, almost bi-stable, changes compared to a much slower trend in the PFC. Seger and Cincotta (2006) found that as humans learn rules, changes in striatal activity precede those in the frontal cortex. Abstract rules are more strongly represented (more neurons and stronger effects) and appear with a shorter latency in the frontal cortex than the dorsal striatum (Muhammad et al., 2006), which is consistent with a greater cortical involvement in abstraction.

Under this view, normal learning depends on balance between the fast and slow plasticity systems. An imbalance between these systems that causes basal ganglia plasticity to become abnormally strong and overwhelm the cortex might result in an autistic-like brain that is overwhelmed with details and cannot generalize. Recent work by Bear and colleagues may provide a molecular link

(Dolen et al., 2007). They found that many psychiatric and neurological symptoms of Fragile X, including autism, can be explained by abnormally high activation of metabotropic glutamate receptor mGluR5. mGluR5 co-localizes with dopamine receptors in striatal neurons and is thought to regulate dopamine-dependent plasticity. The idea is that too much mGluR5 boosts dopaminergic plasticity mechanisms in striatum, and overwhelms the cortex, resulting in an inability to generalize and fractionated, piecemeal cognition.

Interactions within corticostriatal loops: recursive processing and bootstrapping

As noted above, the cortex forms closed anatomical loops with the BG: channels within the BG return outputs, via the thalamus, to the same cortical areas that gave rise to their initial cortical input (Hoover and Strick, 1993; Kelly and Strick, 2004). Closed loops suggest recursivity, bootstrapping operations in which the results from one iteration are fed back through the loop for further processing and elaboration. Some form of recursive processing must underlie the open-ended nature of human memory and thought. We suggest that recursive interactions between BG fast plasticity and slow cortical plasticity underlies construction of categories and abstractions. This may be reflected in a hallmark of human intelligence: it is easiest for us to understand new categories and concepts if they can be grounded first in familiar ones. We learn to multiply through serial addition and we understand quantum mechanics by constructing analogies to waves and particles.

Interactions between corticostriatal loops

Although BG - PFC connections are particularly prominent, the BG interacts with all cortical regions. Figure 2 illustrates the major patterns of projection, broken into "loops". Functional imaging has shown that all four loops are recruited during categorization learning, albeit in different roles (Seger & Cincotta 2005; Seger, 2008). The visual loop receives information from visual cortex; this information feeds forward to the executive and motor loops, providing a potential mechanism for selection of appropriate responses (Ashby et al., 1998; Ashby et al. 2007), as well as back to visual cortex where it may assist in refinement of visual processing. The executive loop is associated with functions necessary for categorization learning, including feedback processing, working memory updating, and set shifting. The motor loop is involved in selecting and executing appropriate motor behavior, including selection of the motor response used to indicate category membership. The motivational loop is involved in processing reward and feedback.

The loops interact during learning. Seger and colleagues (Seger et al., in press) examined interactions between corticostriatal loops during categorization using Granger causality modeling and found patterns consistent with directed influence from the visual loop, to the motor loop, and from the motor loop to the executive

loop. This pattern is consistent with the processes required during each step of a typical categorization trial: processing the visual stimulus, preparing and executing the motor response indicating category membership, and receiving and processing feedback.

Corticostriatal loops also interact across many experiences or trials as subjects progress from being novices to experts in a categorization domain. The executive and motivational loops are most important early, when acquisition of information is fastest and feedback processing is the most useful, whereas the motor loop rises in importance as expertise is acquired (Williams & Eskandar 2006). The anterior caudate (executive loop) is sensitive to learning rate; activity is greatest when learning is occurring most rapidly (Williams & Eskandar 2006) and there is the greatest amount of prediction error (difference between expected outcome and actual outcome) to serve as a learning signal (Haruno & Kawato 2006). In contrast, the putamen (motor loop) is more engaged late in learning, when the category membership (and associated reward or feedback) is well learned. (Seger et al., in press; Williams & Eskandar 2006) This is consistent with observations that the rodent dorsomedial striatum (equivalent to primate anterior caudate) is important for initial goal-oriented learning, whereas dorsolateral striatum (equivalent to primate posterior putamen) is important for later habit formation (Yin & Knowlton 2006).

Finally, corticostriatal loops can compete depending on the material being learned. Categories that can be learned via explicit rule based processes tend to rely on prefrontal cortex and anterior caudate regions involved in the executive loop. Other category structures (such as information integration categories, Figure 1B) that are learned via more implicit processes rely on the visual loop. The COVIS model (Ashby et al. 1998, Ashby et al. 2007) proposes that the executive and visual loops compete for dominance in controlling categorization. This is supported by studies examining individual differences in prefrontal capacity: subjects with high capacity tend to favor the rule learning system and are relatively impaired at learning an information integration task that requires the more implicit strategy to achieve optimal performance (Decaro et al. 2008).

Interactions between the Medial Temporal Lobe and Basal Ganglia

Both MTL and BG systems can form relationships between stimuli and categories. As described above, the MTL does so via explicit representation of the stimulus and its arbitrary category membership, whereas the basal ganglia maps perceptual commonalities of categories to their associated behaviors. Human imaging studies suggest competition between MTL and BG systems during category learning, as BG activity increases, MTL activity decreases (Poldrack et al. 1999, 2001). However, relative decreases in MTL activity are difficult to interpret in functional imaging studies; apparent "suppression" of the MTL may simply be due to lower activity during categorization than during the comparison tasks (Law et al. 2005). Stronger evidence for competition between

the two systems comes from lesion and pharmacological manipulations. When MTL is damaged or "turned off", the BG can take over a larger role in the control of behavior (Frank et al. 2006). Subjects with basal ganglia damage due to Parkinson's disease recruit MTL to a larger extent than controls during probabilistic classification category learning (Moody et al. 2004).

The BG and MTL may not invariably compete during categorization learning. Some studies show parallel recruitment of both systems, implying independent or cooperative contributions (Cincotta & Seger 2007). The MTL may be required initially to set up new individual item representations of stimuli (Meeter et al. 2008). These stimulus representations may then be accessible to BG systems for forming associations between stimuli and categories. Consistent with this theory, Poldrack et al (2001) found transient MTL activity at the beginning of a probabilistic classification task, which was then followed by a relative decrease in MTL activity and increase in BG activity.

It is unclear how interaction between MTL and BG is mediated. There is evidence that the relationship is bilateral: increases in BG activity lead to decreases in MTL activity and vice versa (Lee et al. 2008). Some research indicates that PFC is involved (Poldrack & Rodriguez 2004). During distraction with PFC demanding dual tasks, categorization performance becomes more strongly related to striatal activity and less to MTL (Foerde et al. 2006). In emotional situations, it appears that the amygdala can mediate the balance between systems (Wingard & Packard 2008).

Conclusion: Principles of category learning in the brain

We are only beginning to understand how the brain learns categories. But we can posit some potential principles and hypotheses.

- Categorization involves both stimulus representations (e.g., of features, central tendencies, and degree of variability) and processes (e.g. decision making processes establishing a criterion or rule for category membership) that recruit different neural systems depending on the type of category and how it is used.
- There is no single "categorization area" in the brain. Categories are represented in a distributed fashion across the brain and there are multiple neural systems involved. Many of the systems involved in categorization have been identified in the multiple memory systems framework (Ashby & O'Brien 2005, Poldrack & Foerde 2008, Smith & Grossman 2008). Categorization tasks are not "process-pure": multiple systems may be recruited to solve any given categorization problem.
- There are fundamental computational constraints on category learning. There is a tradeoff between generalizing across previous experience, and remembering specific items and events. This may be solved by having fast plasticity (large

synaptic weight changes) in subcortical systems (e.g., basal ganglia and hippocampus) train slower plasticity (smaller weight changes) in the cortex, the latter of which builds the category representations by finding the commonalities across the specifics learned by the former. Normal learning depends on balance between these mechanisms. The balance can change depending on task demands. Certain neuropsychiatric disorders, like autism, may result from an imbalance causing the faster plasticity mechanisms in the subcortex to overwhelm the slower cortical plasticity. This could result in a brain that has great difficulty generalizing.

- Category learning may depend on recursive, bootstrapping interactions within corticostriatal loops. The open-ended nature of human thought likely depends on some form of recursive processing and the closed anatomical loops the basal ganglia form with the cortex seem well-suited. Different phases of learning and different aspects of a categorization task may also involve interactions across different corticostriatal loops.

- Category learning cuts across distinctions between implicit and explicit systems, and declarative and nondeclarative memory systems. Explicit systems are those that are associated with some degree of conscious penetrability (Seger, 1994). In categorization, these include PFC systems recruited in explicit rule learning tasks, as well as MTL systems that result in consciously accessible episodic memories. Most other systems are typically considered to be implicit or unconscious (e.g., perceptual cortex), however some (notably the corticostriatal loops) can be recruited in both explicit and implicit tasks. The declarative - nondeclarative distinction differs from the explicit - implicit distinction in that it separates MTL dependent memory processes from other learning systems, respectively. Categorization tasks may recruit various combinations of implicit and/or explicit, declarative and/or nondeclarative systems. For example, simple dot pattern learning is largely implicit (in that it occurs without intention to learn or awareness of learning), and nondeclarative (in that it is independent of MTL systems). Rule learning is explicit in that subjects intend to learn and have awareness of what they have learned, and is nondeclarative in that it largely recruits prefrontal cortex and does not require the MTL.

- A major challenge in understanding category learning is determining which category learning systems are recruited in particular situations, and whether the systems function independently, cooperatively, or antagonistically. What is ultimately learned is an interaction between the structure of the information in the environment and the neural systems recruited to process the information (Zeithamova et al. 2008, Reber et al. 2003). Which systems are recruited can also depend on factors that can vary across individuals and situations, such as cognitive capacity (Decaro et al., 2008) and motivational state (Grimm et al., 2007).

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