

## Category Learning

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### Introduction

Category learning broadly is the ability of organisms to learn to classify items into groups, often on the basis of perceptual similarity. Categorization provides a foundation for the ability to choose appropriate behavior and generalize from past experiences. This article will emphasize what we have learned about the neural basis of category learning from neuroimaging studies; for a broader review across multiple neuroscience methodologies, see Seger and Miller (2010).

As in many areas of research, in cognitive neuroimaging, researchers began to study category learning in exploratory studies that utilized theoretical distinctions and tasks developed in the fields of cognitive psychology and cognitive neuropsychology; research often focused on identifying neural systems that supported nondeliberative forms of category learning that neuropsychologists had shown were preserved in patients with hippocampal amnesia (Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Reber, Stark, & Squire, 1998a).

In the years since, the field has developed; category learning research now addresses a variety of aspects of categorization. In the succeeding text, we review four important active areas of neuroimaging research in category learning. First is research examining the role of higher-order perceptual cortex in the acquisition of categories. The second area concerns how multiple learning and memory systems contribute to category learning, with a focus on the corticostriatal and corticohippocampal systems. Third, we review studies that address how neural networks underlying cognitive control, particularly those of the frontoparietal system, participate in performing category learning tasks. The final section addresses the question of how neural systems change across time during category learning and how skilled or automatic performance differs from early learning. Throughout, we focus on how methodological advances in the field have contributed to advancing research in category learning, including the use of model-based fMRI approaches to more carefully characterize the computational functions of different regions, multivoxel pattern analysis (MVPA) and repetition suppression to identify finer grained patterns of activity within larger neural regions, and functional connectivity methods to examine how distributed neural systems interact during categorization.

### Perceptual Contributions in Category Learning

Early category learning neuroimaging research often reported activity in extrastriate occipital and inferotemporal regions during categorization (Patalano, Smith, Jonides, & Koeppe, 2001) and often reported that this activity changed during categorization learning (Seger et al., 2000; van der Linden, Murre, & van Turenout, 2008) or differed for category members in comparison with nonmembers (Aizenstein et al., 2000;

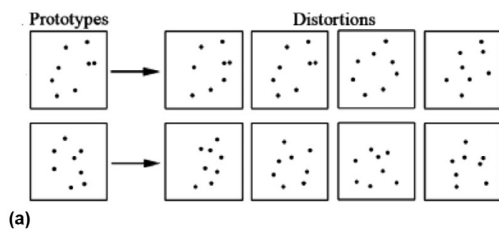
Reber, Gitelman, Parrish, & Mesulam, 2003; Reber, Stark, & Squire, 1998b; Reber et al., 1998a). Although this research was intriguing, it was unclear whether this activity was due to actual modification of the tuning of the representations in these regions or due to changes in top-down influences on perceptual regions during learning. Although most research to date has focused on visual categorization and we focus below on the visual modality, it should be noted that recent studies have begun to address whether similar learning related changes can be found in higher-order auditory processing regions (Ley et al., 2012; Myers & Swan, 2012).

One early study (Reber et al., 1998a) used the dot pattern classification task (see Figure 1(a)) and found a region of early visual cortex (approximately BA18 or V3) that showed reduced activity for category members compared with nonmembers after relatively brief amounts of training. Follow-up studies found that this pattern was reversed when explicit memory for the stimuli was probed, with greater activity for category members (Aizenstein et al., 2000; Reber et al., 1998b, 2003). Later studies indicated that this pattern may be due to differences in processing during study (Gureckis, James, & Nosofsky, 2010) or differences in response criterion at test, with categorization tasks generally using a more lenient criterion and explicit recognition of a strict criterion (Nosofsky, Little, & James, 2012). It is likely that the modulation of this early visual cortical region is due to top-down differences in strategy at study or test rather than inherent plasticity within this visual region, which is consistent with research suggesting that early visual system plasticity requires extensive training (Sabel & Kastner, 2000).

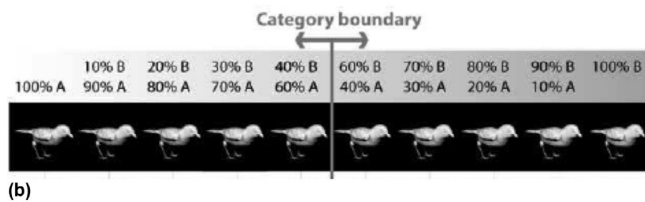
Researchers focusing on perceptual processing in categorization have developed a number of specialized methods to more precisely characterize perceptual contributions to categorization. They usually target a region of extrastriate visual cortex that they expect will perform basic perceptual processing for the object type of interest (e.g., the lateral occipital complex for structural processing of objects or the fusiform face area for faces) and then develop new categorically structured items by forming visual prototype objects and morphing them to form intermediate items. A typical stimulus set is illustrated in Figure 1(b) (van der Linden et al., 2008). Subjects are given extensive training with these novel stimuli to maximize the chance of finding plastic changes in the corresponding perceptual processing regions. Studies often use a transfer task in which subjects do not explicitly categorize stimuli to minimize top-down influences from the categorization task and to isolate bottom-up changes in perceptual processing resulting from the category learning. These studies often use a repetition suppression or adaptation method (Grill-Spector, Henson, & Martin, 2006) in which items are presented repeatedly; decreases in activity are interpreted as indicating similarity of processing at the neural level and increases in activity as differences in processing. The results with adaptation studies have been mixed. One study reported changes in item-specific

### Prototype structures:

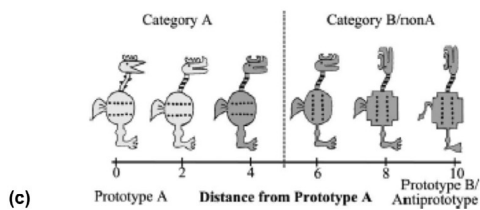
#### Variations of a single prototype



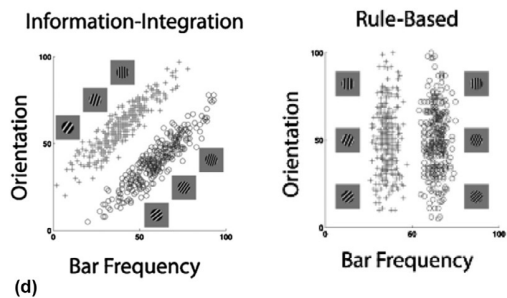
#### Continuous variation between prototypes



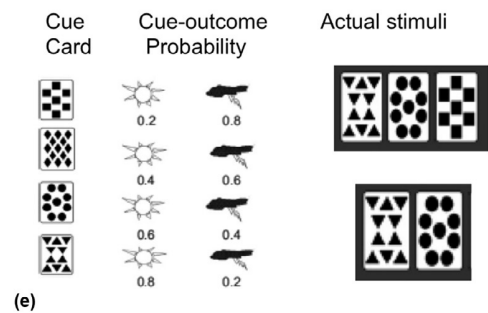
#### Discrete feature variation between prototypes



### Information integration and rule based decision bounds



### Probabilistic classification



**Figure 1** Illustration of commonly used category structures in neuroimaging studies of category learning. (a) Prototype learning using the Posner and Keele dot pattern task. (b) Continuous morphed stimuli based on two prototypes. (c) Continuum between two prototypes formed by manipulation of discrete features. (d) Information-integration and rule-based tasks. (e) Probabilistic classification or 'weather prediction' task. (b) is adapted from van der Linden, M., van Turennout, M., & Indefrey, P. (2010). Formation of category representations in superior temporal sulcus. *Journal of Cognitive Neuroscience*, 22, 1270–1282; (c) from Zeithamova, D., Maddox, W. T., & Schyns, P. D. (2008). Dissociable prototype learning systems: Evidence from brain imaging and behavior. *Journal of Neuroscience*, 28, 13194–13201; and (d) from Smith, J. D., Berg, M. E., Cook, R. G., Murphy, M. S., Crossley, M. J., Boomer, J., et al. (2012). Implicit and explicit categorization: A tale of four species. *Neuroscience and Biobehavioral Reviews*, 36, 2355–2369.

repetition suppression in extrastriate regions, but no changes in amount of adaptation related to category membership (Jiang et al., 2007). Other studies have found changes in repetition suppression for items containing learned category relevant features, with a greater release from suppression for items on opposite sides of the category boundary than would be expected due to mere visual similarity independent of category membership (Folstein, Palmeri, & Gauthier, 2012; van der Linden, van Turennout, & Indefrey, 2010). Folstein, Gauthier, and Palmeri (2012) argued that these discrepant results could be due to subtle differences in how the categories in each study were structured.

Another popular method is to use MVPA to identify any fine-grained changes on the voxel level. Studies using MVPA have found voxels in perceptual regions sensitive to relevant perceptual features (Li, Ostwald, Giese, & Kourtzi, 2007) and voxels that change in activity in a category-specific manner during passive viewing of stimuli after learning a categorical

decision bound (Li, Mayhew, & Kourtzi, 2009, 2012; Mayhew, Li, Storrar, Tsvetanov, & Kourtzi, 2010).

### Learning and Memory Systems: The Hippocampus and the Basal Ganglia

The theoretical grounding of many category learning studies is in the multiple memory systems approach, which argues that different types of material are learned or remembered via different neural systems. Categorization tasks were thought to be implicit or nondeliberative tasks that should be independent of medial temporal lobe involvement and instead rely on other neural systems—in the case of category learning, the basal ganglia. An influential series of experiments used the probabilistic categorization or 'weather prediction' task, illustrated in Figure 1(e) (Aron et al., 2004; Aron, Gluck, & Poldrack, 2006; Poldrack et al., 1999, 2001; see also Shohamy, Myers, Kalanithi, &

Gluck, 2008 for a review). This research found overall below baseline hippocampal activity accompanied by increased basal ganglia activity during learning, which was interpreted as evidence for competition between the two memory systems.

The emphasis of more recent research has shifted from identifying dissociations to more carefully characterizing the specific contributions of each neural system to learning and broadening the scope of potential interactions between systems to identify when systems might work independently and cooperatively. For example, Foerde, Knowlton, and Poldrack (2006) found that when learned under single-task conditions, subjects recruited hippocampal regions for probabilistic classification, but during dual-task conditions, subjects relied on the basal ganglia. Overall, research has found that these systems may play multiple roles and contribute to different task demands.

For the basal ganglia, studies indicate that different regions make different contributions to categorization. The anterior striatum is sensitive to feedback processing when learning via trial and error (Cincotta & Seger, 2007; Lopez-Paniagua & Seger, 2011; Seger & Cincotta, 2005). The putamen is active when making a motor response indicating category membership (Peterson & Seger, 2013) and is more active for correct than incorrect responses (Daniel & Pollmann, 2010). The body and tail of the caudate are active during stimulus processing, when subjects are determining category membership (Seger, Peterson, Cincotta, Lopez-Paniagua, & Anderson, 2010), and activity in this region also correlates with accuracy (Lopez-Paniagua & Seger, 2011; Nomura et al., 2007; Seger & Cincotta, 2005). Trial and error category learning has a stimulus-response-feedback structure that makes it very similar to instrumental learning, and these roles of the basal ganglia in category learning may be characteristic of all forms of basal ganglia-mediated learning (Seger, 2009). One approach to characterizing these functions computationally comes from the field of reinforcement learning, after the finding that modulatory dopaminergic projections to the basal ganglia code for reward receipt, in particular the presence of unanticipated rewards and the absence of anticipated rewards. This measure is referred to a reward prediction error. Estimates of reward prediction and reward prediction error derived from individual subjects' learning behavior have been shown to well characterize activity in the basal ganglia in studies using these measures as regressors in model-based fMRI analyses (Daniel & Pollmann, 2012; Schonberg, Daw, Joel, & O'Doherty, 2007; Seger & Peterson, 2013; Seger et al., 2010).

Evidence for the role of the hippocampus in category learning has been mixed. As described in the preceding text, initial studies using the probabilistic classification task found that the hippocampus was at below baseline levels of activity or showed a transient spike in activity at the beginning of learning, followed by a reduction to below baseline levels (Poldrack et al., 2001). More recently, Seger, Dennison, Lopez-Paniagua, Peterson, and Roark (2011) identified two roles for the hippocampus in categorization learning: first, in processing novel stimuli (a region in anterior hippocampus was active for novel stimuli only, with below baseline activity for repeated stimuli) and second in contributing to categorization based on episodic memory (a posterior region of the hippocampus was active during categorization on trials when subjects reported their decision was based on episodic memory). Davis and colleagues

found that the hippocampus is active when categorizing stimuli that are exceptions to the overall rule or pattern; episodic memory for individual stimuli is important for this function (Davis, Love, & Preston, 2012a).

Current studies are often based on the assumption that systems can be active in parallel, and try to identify what the conditions and computational demands are that lead to hippocampal recruitment. Davis and colleagues found that basal ganglia and hippocampus were both active during categorization but that some subregions of each structure were best fit by measures of recognition strength and other subregions best fit by measures of entropy or uncertainty (Davis, Love, & Preston, 2012b). Recruitment of basal ganglia versus hippocampal systems may also depend on the strategies used by subjects. Hammer et al. (2010) found that both systems were more active when subjects were led to focus on between-category differences as opposed to within-category similarities. Zeithamova, Maddox, and Schnyer (2008) found greater activity in the basal ganglia when subjects were trained to make decisions about whether stimuli were category members or nonmembers, in comparison with greater hippocampal activity when learning to categorize the same stimuli into two different categories.

### Frontoparietal Rule Learning and Cognitive Control Mechanisms

Early research clearly found that category learning, like most demanding cognitive tasks, recruited a broad and distributed neural network including frontoparietal cognitive control systems. For example, Poldrack and Foerde (2008) did a meta-analysis combining results from four probabilistic classification studies (task illustrated in Figure 1(e)) and found common activity in the bilateral inferior frontal/anterior insula, bilateral middle frontal, bilateral parietal, medial frontal/anterior cingulate, and bilateral striatum. This has led to the realization that category learning likely recruits and relies upon these mechanisms to meet the categorization task demands.

One important role of frontoparietal systems in categorization is to support alternative strategies involving rule learning and application. These processes involve frontoparietal systems for generation of potential hypothesis, working memory for the hypothesis, feedback processing, and shifting to a new hypothesis if the current one is not supported (Seger & Cincotta, 2006). A powerful approach to understanding how rule learning differs from more implicit forms of categorization was pioneered by Ashby and colleagues. They developed tasks that use the same stimuli but different category decision bounds and thus require different strategies from the subjects (Ashby & Maddox, 2005). In the implicit version of their task, referred to as information integration (see Figure 1(d)), they use a diagonal decision bound that requires subjects to integrate information from both dimensions. This is very difficult to do via hypothesis testing and subjects typically are not able to verbalize a rule. In comparison, rule learning versions of this task used the same types of stimuli but with a vertical or horizontal decision bound that subjects can learn as a simple verbalizable rule referring to a single dimension (e.g., thick bars are in category A and thin bars in category B). Rule learning tasks

have been found to have greater activation in the prefrontal cortex (PFC), in particular in the lateral PFC, during learning (Helie, Roeder, & Ashby, 2010; Koenig et al., 2005; Soto, Waldschmidt, Helie, & Ashby, 2013). They also sometimes have higher hippocampal activity (Nomura et al., 2007) possibly due to encoding and retrieval of episodic memory for the rule.

In addition to rule-based categorization learning, the frontoparietal networks likely provide general support for executive and decision processes drawn upon during category learning. One example is systems important for resolving uncertainty and conflict. In categorization, stimuli can often have at least a partial information overlap with more than one category option, which means the brain needs to resolve the conflict between options when deciding to go with one over the other. Recent studies that have manipulated the uncertainty over stimulus category membership have found widespread recruitment of medial frontal regions that are thought to mediate conflict generally (Daniel et al., 2011; Grinband, Hirsch, & Ferrera, 2006; Summerfield, Behrens, & Koechlin, 2011).

Another example is the presence of intermediate representations in frontal and parietal cortex that appear to serve an integrative function of adding together the net amount of evidence for a decision, whether it be in the domain of perception or memory. Categorization may recruit these processes as well (Seger & Peterson, 2013). For example, Nosofsky et al. (2012) found different amounts of activity in cortical regions commonly associated with information accumulation when subjects performed a categorization task using a strict threshold versus a lenient threshold for assessing category membership.

### Automaticity and Changes Across Time

Behavioral and neuroimaging results suggest that category representations change as categorization performance becomes automatic. Studies using prototype structured stimuli have reported changes in connectivity or breadth of activity across training. DeGutis and D'Esposito (2009) found increased functional connectivity between perceptual cortex, motor cortex, and the hippocampus after extensive training on a prototype learning task similar to the one illustrated in Figure 1(b). Little and colleagues (Little, Klein, Shobat, McClure, & Thulborn, 2004; Little & Thulborn, 2006) examined learning of dot pattern prototypes (illustrated in Figure 1(a)) across extensive training and found a network consisting of the frontal eye fields, inferior and superior parietal lobules, and visual cortex that initially increased in activity, then decreased, and became more focal.

Automaticity has also been examined through parallel studies of information-integration and rule-based categorization tasks (see Figure 1(d)). Ashby, Ennis, and Spiering (2007) and Ashby, Turner, and Horvitz (2010) argued that automatic categorization responses are selected via direct projections from sensory to motor regions. Several neuroimaging results support this conjecture. Helie et al. (2010) scanned participants as they gained experience with a rule-based categorization task. Early categorization accuracy was correlated with activity in the PFC, anterior cingulate, head of the caudate, and areas within the medial temporal lobe. These regions shifted with training, such

that after extensive training, only premotor regions correlated with behavioral accuracy. In a similar experiment involving an information-integration category learning task, Waldschmidt and Ashby (2011) found that activity in the putamen was correlated with behavioral accuracy early in training but that these regions shifted to the supplementary and presupplementary motor areas after extensive training.

These results suggest that distinct networks may support early rule-based and information-integration category learning, but that category representations across structures may become more similar with extensive training. Using MVPA, Soto et al. (2013) investigated changes in rule-based and information-integration category representations across training. A classifier designed to identify regions predictive of stimulus category across category structure indicated that both basal ganglia and motor regions predicted stimulus category early in training. After extensive training, however, only motor regions were predictive of stimulus category across structure. Additionally, regions reflecting categorical representations within each structure became more similar across tasks.

### Conclusion

A common theme in category learning neuroimaging studies has been the realization that categorization shares neural and cognitive processes with other tasks and that using category learning tasks to investigate these shared factors can be very fruitful. Researchers exploring similarities between category learning and instrumental learning have identified neural systems involved in component processes such as feedback and reward processing (Aron et al., 2004; Daniel & Pollmann, 2010; Shohamy et al., 2008) and mapping between stimuli and responses (Seger, 2009). Categorization furthermore has a number of features in common with perceptual and economic decision making, including how to adjust for uncertainty, value decision options, integrate evidence from multiple sources, and generalize to novel stimuli and situations (Seger & Peterson, 2013). Category learning therefore not only is a fascinating domain of learning in and of itself but also provides a powerful model system for the exploration of many fundamental aspects of cognition.

See also: [INTRODUCTION TO ANATOMY AND PHYSIOLOGY](#): Basal Ganglia; Lateral and Dorsomedial Prefrontal Cortex and the Control of Cognition; Topographic Layout of Monkey Extrastriate Visual Cortex; [INTRODUCTION TO COGNITIVE NEUROSCIENCE](#): Motor Decision-Making; Neural Correlates of Motor Skill Acquisition and Consolidation; Neuroimaging Studies of Reinforcement-Learning; Perceptual Decision Making: Prediction and Expectation; Reward Processing; Rule Representation; Statistical Learning; Uncertainty; [INTRODUCTION TO METHODS AND MODELING](#): Methodological Issues in fMRI Functional Connectivity and Network Analysis; Multi-voxel Pattern Analysis; Resting-State Functional Connectivity; [INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE](#): Exploring the Brain Dynamics of Racial Stereotyping and Prejudice; [INTRODUCTION TO SYSTEMS](#): Expertise and Object Recognition.



## References

- Aizenstein, H. J., MacDonald, A. W., Stenger, V. A., Nebes, R. D., Larson, J. K., Ursu, S., et al. (2000). Complementary category learning systems identified using event-related functional MRI. *Journal of Cognitive Neuroscience*, 12, 977–987.
- Aron, A. R., Gluck, M. A., & Poldrack, R. A. (2006). Long-term test-retest reliability of functional MRI in a classification learning task. *NeuroImage*, 29, 1000–1006.
- Aron, A. R., Shohamy, D., Clark, J., Myers, C., Gluck, M. A., & Poldrack, R. A. (2004). Human midbrain sensitivity to cognitive feedback and uncertainty during classification learning. *Journal of Neurophysiology*, 92, 1144–1152.
- Ashby, F. G., Ennis, J. M., & Spiering, B. J. (2007). A neurobiological theory of automaticity in perceptual categorization. *Psychological Review*, 114, 632–656.
- Ashby, F. G., & Maddox, W. T. (2005). Human category learning. *Annual Review of Psychology*, 56, 149–178.
- Ashby, F. G., Turner, B. O., & Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity. *Trends in Cognitive Sciences*, 14, 208–215.
- Cinotta, C. M., & Seger, C. A. (2007). Dissociation between striatal regions while learning to categorize via feedback and via observation. *Journal of Cognitive Neuroscience*, 19, 249–265.
- Daniël, R., & Pollmann, S. (2010). Comparing the neural basis of monetary reward and cognitive feedback during information-integration category learning. *Journal of Neuroscience*, 30, 47–55.
- Daniël, R., & Pollmann, S. (2012). Striatal activations signal prediction errors on confidence in the absence of external feedback. *NeuroImage*, 59, 3457–3467.
- Daniël, R., Wagner, G., Koch, K., Reichenbach, J. R., Sauer, H., & Schlösser, R. G. (2011). Assessing the neural basis of uncertainty in perceptual category learning through varying levels of distortion. *Journal of Cognitive Neuroscience*, 23, 1781–1793.
- Davis, T., Love, B. C., & Preston, A. R. (2012a). Learning the exception to the rule: Model-based fMRI reveals specialized representations for surprising category members. *Cerebral Cortex*, 22, 260–273.
- Davis, T., Love, B. C., & Preston, A. R. (2012b). Striatal and hippocampal entropy and recognition signals in category learning: Simultaneous processes revealed by model-based fMRI. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 38, 821–839.
- DeGutis, J., & D'Esposito, M. (2009). Network changes in the transition from initial learning to well-practiced visual categorization. *Frontiers in Human Neuroscience*, 3, 44.
- Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11778–11783.
- Folstein, J. R., Gauthier, I., & Palmeri, T. J. (2012). How category learning affects object representations: Not all morphospaces stretch alike. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 38, 807–820.
- Folstein, J. R., Palmeri, T. J., & Gauthier, I. (2012). Category learning increases discriminability of relevant object dimensions in visual cortex. *Cerebral Cortex*, 23(4), 814–823.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1), 14–23.
- Grinband, J., Hirsch, J., & Ferrera, V. P. (2006). A neural representation of categorization uncertainty in the human brain. *Neuron*, 49, 757–763.
- Gureckis, T. M., James, T. W., & Nosofsky, R. M. (2010). Re-evaluating dissociations between implicit and explicit category learning: An event-related fMRI study. *Journal of Cognitive Neuroscience*, 23(7), 1697–1709.
- Hammer, R., Brechmann, A., Chi, F., Weirshall, D., & Hochstein, S. (2010). Differential category learning processes: The neural basis of comparison-based learning and induction. *NeuroImage*, 52, 699–709.
- Helie, S., Roeder, J. L., & Ashby, F. G. (2010). Evidence for cortical automaticity in rule-based categorization. *Journal of Neuroscience*, 30, 14225–14234.
- Jiang, X., Bradley, E., Rini, R. A., Zeffiro, T., Vanmeter, J., & Reserhuber, M. (2007). Categorization training results in shape- and category-selective human neural plasticity. *Neuron*, 53, 891–903.
- Koenig, P., Smith, E. E., Glosser, G., DeVita, C., Moore, P., McMillan, C., et al. (2005). The neural basis for novel semantic categorization. *NeuroImage*, 24, 369–383.
- Ley, A., Vroomen, J., Hausfeld, L., Valente, G., DeWeerd, P., & Formisano, E. (2012). Learning of new sound categories shapes neural response patterns in human auditory cortex. *Journal of Neuroscience*, 32, 13273–13280.
- Li, S., Mayhew, S. D., & Kourtzi, Z. (2009). Learning shapes the representation of behavioral choice in the human brain. *Neuron*, 62, 441–452.
- Li, S., Mayhew, S. D., & Kourtzi, Z. (2012). Learning shapes spatiotemporal brain patterns for flexible categorical decisions. *Cerebral Cortex*, 22, 2322–2335.
- Li, S., Ostwald, D., Giese, M., & Kourtzi, Z. (2007). Flexible coding for categorical decisions in the human brain. *Journal of Neuroscience*, 27, 12321–12330.
- Little, D. M., Klein, R., Shohat, D. M., McClure, E. D., & Thulborn, K. R. (2004). Changing patterns of brain activation during category learning revealed by functional MRI. *Cognitive Brain Research*, 22, 84–93.
- Little, D. M., & Thulborn, K. R. (2006). Prototype-distortion category learning: A two-phase learning process across a distributed network. *Brain and Cognition*, 60, 233–243.
- Lopez-Panigua, D., & Seger, C. A. (2011). Interactions within and between corticostriatal loops during component processes of category learning. *Journal of Cognitive Neuroscience*, 23, 3068–3083.
- Mayhew, S. D., Li, S., Storror, J. K., Tsvetanov, K. A., & Kourtzi, Z. (2010). Learning shapes the representation of visual categories in the aging human brain. *Journal of Cognitive Neuroscience*, 22, 2899–2912.
- Myers, E. B., & Swan, K. (2012). Effects of category learning on neural sensitivity to non-native phonetic categories. *Journal of Cognitive Neuroscience*, 24, 1695–1708.
- Nomura, E. M., Maddox, W. T., Filoteo, J. V., Ing, A. D., Gitelman, D. R., Parrish, T. B., et al. (2007). Neural correlates of rule-based and information-integration visual category learning. *Cerebral Cortex*, 17, 37–43.
- Nosofsky, R. M., Little, D. R., & James, T. W. (2012). Activation in the neural network responsible for categorization and recognition reflects parameter changes. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 333–338.
- Patalano, A. L., Smith, E. E., Jonides, J., & Koeppe, R. A. (2001). PET evidence for multiple strategies of categorization. *Cognitive, Affective, & Behavioral Neuroscience*, 1, 360–370.
- Peterson, E. J., & Seger, C. A. (2013). Many hats: Intra-trial and reward-level dependent BOLD activity in the striatum and prefrontal cortex. *Journal of Neurophysiology*, 110(7), 1689–1702.
- Poldrack, R. A., Clark, J., Pare-Blagoev, E. J., Shohamy, D., Creso, M. J., Myers, C., et al. (2001). Interactive memory systems in the human brain. *Nature*, 414, 546–550.
- Poldrack, R. A., & Forde, K. (2008). Category learning and the memory systems debate. *Neuroscience and Biobehavioral Reviews*, 32, 197–205.
- Poldrack, R. A., Prabhakaran, V., Seger, C. A., & Gabrieli, J. D. E. (1999). Striatal activation during acquisition of a cognitive skill. *Neuropsychology*, 13, 564–574.
- Reber, P. J., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2003). Dissociating explicit and implicit category knowledge with fMRI. *Journal of Cognitive Neuroscience*, 15, 574–583.
- Reber, P. J., Stark, C. E., & Squire, L. R. (1998a). Cortical areas supporting category learning identified using functional MRI. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 747–750.
- Reber, P., Stark, C., & Squire, L. (1998b). Contrasting cortical activity associated with category memory and recognition memory. *Learning and Memory*, 5, 420–428.
- Sabel, B. A., & Kasten, E. (2000). Restoration of vision by training of residual functions. *Current Opinion in Ophthalmology*, 11(6), 430–436.
- Schönberg, T., Daw, N. D., Joel, D., & O'Doherty, J. P. (2007). Reinforcement learning signals in the human striatum distinguish learners from nonlearners during reward-based decision making. *Journal of Neuroscience*, 27, 12860–12867.
- Seger, C. A. (2009). The involvement of corticostriatal loops in learning across tasks, species, and methodologies. *Basal Ganglia IX: Proceedings of the International Basal Ganglia Society*. Springer.
- Seger, C. A., & Cinotta, C. M. (2005). The roles of the caudate nucleus in human classification learning. *Journal of Neuroscience*, 25, 2941–2951.
- Seger, C. A., & Cinotta, C. M. (2006). Dynamics of frontal, striatal, and hippocampal systems during rule learning. *Cerebral Cortex*, 16, 1546–1555.
- Seger, C. A., Dennison, C. S., Lopez-Panigua, D., Peterson, E. J., & Roark, A. A. (2011). Dissociating hippocampal and basal ganglia contributions to category learning using stimulus novelty and subjective judgments. *NeuroImage*, 55, 1739–1753.
- Seger, C. A., & Miller, E. K. (2010). Category learning in the brain. *Annual Review of Neuroscience*, 33, 203–219.
- Seger, C. A., & Peterson, E. J. (2013). Categorization and decision making: generalization. *Neuroscience and Biobehavioral Reviews*, 37, 1187–1200.
- Seger, C. A., Peterson, E. J., Cinotta, C. M., Lopez-Panigua, D., & Anderson, C. W. (2010). Dissociating the contributions of independent corticostriatal systems to visual categorization learning through the use of reinforcement learning modeling and Granger causality modeling. *NeuroImage*, 50, 644–656.
- Seger, C. A., Poldrack, R. A., Prabhakaran, V., Zhao, M., Glover, G. H., & Gabrieli, J. D. E. (2000). Hemispheric asymmetries and individual differences in visual concept learning as measured by functional MRI. *Neuropsychologia*, 38, 1316–1324.

- Shohamy, D., Myers, C. E., Kalanithi, J., & Gluck, M. A. (2008). Basal ganglia and dopamine contributions to probabilistic category learning. *Neuroscience and Biobehavioral Reviews*, 32, 219–236.
- Smith, J. D., Berg, M. E., Cook, R. G., Murphy, M. S., Crossley, M. J., Boomer, J., et al. (2012). Implicit and explicit categorization: A tale of four species. *Neuroscience and Biobehavioral Reviews*, 36, 2355–2369.
- Soto, F. A., Woldschmidt, J. G., Helie, S., & Ashby, F. G. (2013). Brain activity across the development of automatic categorization: A comparison of categorization tasks using multi-voxel pattern analysis. *NeuroImage*, 71, 284–297.
- Summerfield, C., Behrens, T. E., & Koehlin, E. (2011). Perceptual classification in a rapidly changing environment. *Neuron*, 71, 725–736.
- van der Linden, M., Murre, J. M., & van Turenmout, M. (2008). Birds of a feather flock together: Experience-driven formation of visual object categories in human ventral temporal cortex. *PLoS One*, 3, e3995.
- van der Linden, M., van Turenmout, M., & Indefrey, P. (2010). Formation of category representations in superior temporal sulcus. *Journal of Cognitive Neuroscience*, 22, 1270–1282.
- Woldschmidt, J. G., & Ashby, F. G. (2011). Cortical and striatal contributions to automaticity in information-integration categorization. *NeuroImage*, 56, 1791–1802.
- Zeithamova, D., Maddox, W. T., & Schyns, P. D. (2008). Dissociable prototype learning systems: Evidence from brain imaging and behavior. *Journal of Neuroscience*, 28, 13194–13201.