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Neural systems for perceptual skill learning

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## **Abstract**

Recent studies have begun to use functional neuroimaging techniques to examine the changes in brain activity that occur as humans learn new skills. This review outlines results from a number of imaging studies examining visual perceptual skill learning.

Although the regions engaged during skill learning differ across tasks, a common finding has been increasing activation in the inferior temporal and fusiform gyri as skill is acquired, and activation of the caudate nucleus in association with learning.

Neuroimaging has great promise for the understanding of learning at the level of large neural populations, but further work is necessary to understand the specificity of learning-related changes and their relation to underlying neurophysiological plasticity.

The ability to acquire novel highly skilled behaviors is one of the most impressive features of human cognition, and understanding its neural basis is a critical challenge for cognitive neuroscience. Study of this issue has recently been undertaken using the tools of functional neuroimaging, including positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). In this review I will outline the challenges involved in using neuroimaging to understand skill acquisition, particularly in context of the acquisition of visual perceptual skills, and provide a review of recent work that has begun to address these challenges. These studies provide an initial glimpse of the dynamic changes in neural processing associated with perceptual skill acquisition.

## **Challenges of imaging skill acquisition**

Although neuroimaging offers a powerful window into the neural processes engaged in skill learning, the imaging of skill acquisition involves a challenging set of conceptual and methodological issues (these issues are reviewed in Poldrack, 2000). Conceptually, drawing conclusions about cognitive processes from functional neuroimaging data is difficult because the mapping is heavily underdetermined; any particular change in signal could arise from any of a large number of underlying processes. This suggests that imaging of skill learning requires strong theoretical guidance if the experiments are to have significant impact on our understanding of the

underlying processes. Methodologically, there are a number of issues in data analysis that arise in the context of skill learning. For example, skill learning is invariably associated with changes in the details of task performance such as time on task, and it is known that these factors have an influence on imaging signals (e.g., D'Esposito et al., 1997). Thus, it will be difficult to determine whether a particular change in brain activity reflects learning-related changes in the engagement of a particular brain system versus performance-driven modulation of a system that is constantly engaged throughout learning. Although these issues pose difficulties for interpretation of imaging data, the studies reviewed here demonstrate that it is possible to use fMRI to extract information about the underlying functional anatomy of behavior as it changes with skill acquisition.

It is critical to note that brain imaging and neuropsychological (lesion) studies have a complementary set of strengths and weaknesses in attributing cognitive function to neural structure. Neuropsychological studies can demonstrate that a particular brain region is necessary for performance of a particular task. Imaging, on the other hand, can only demonstrate that a particular set of regions is active in the context of a particular task (or more precisely, a particular contrast between task conditions). There are well-known examples of task-related activation in regions that are known not to be necessary for performance of the particular task. For example, activity in the hippocampus is observed during delay eyeblink conditioning using PET in humans (Blaxton et al., 1996) and neurophysiology in rabbits (Berger, Rinaldi, Weisz, & Thompson, 1983), but humans

with lesions to the medial temporal lobe exhibit normal conditioning in the same paradigm (Gabrieli et al., 1995a). Such findings highlight the need to interpret imaging data in the context of neuropsychological findings or of findings using transcranial magnetic stimulation, which can create short-lived “virtual lesions” (Pascual-Leone et al., 1999; Walsh, Ashbridge, & Cowey, 1998).

The strength of imaging approaches in the context of skill learning is that they provide a window into the dynamic changes in neural processing that occur during skill learning in healthy normal humans. That is, imaging can provide a “musical score” describing the engagement and disengagement of various neural systems across the timecourse of normal skill learning. Lesion studies, in comparison, can provide only a snapshot of the role of a particular structure for learning a particular task, and they rely upon the assumption that the lesion does not alter the function of other unlesioned systems. Furthermore, imaging can provide evidence about individual differences in the neural basis of learning in normal individuals, telling us which brain regions are engaged in association with better or poorer learning (e.g., Seger et al., 2000).

### **Perceptual skill learning: Reading transformed text**

Perceptual skill learning is generally examined using paradigms that involve processing of novel classes of perceptual stimuli, or tasks that require novel perceptual-

motor mappings. Perhaps the most heavily studied perceptual skill paradigm is the mirror-reading task, in which subjects learn to read text that has been geometrically transformed (as if it were being read through a mirror). This paradigm was examined extensively in normal subjects by Paul Kolers and colleagues (Kolers, 1968; Kolers, 1975; Kolers, 1976), but interest in the task amongst cognitive neuroscientists was driven by the classic study of Cohen and Squire (1980). This study examined the performance of amnesic patients on the mirror-reading task and found that they were able to learn to read mirror-reversed text as well as normal controls, despite having impaired explicit memory for the practice episodes and the practiced stimuli. Subsequent studies have replicated this effect in other groups of amnesic patients (Martone, Butters, Payne, Becker, & Sax, 1984; Schmidtke, Handschu, & Vollmer, 1996). Studies of mirror-reading in patients with Parkinson's disease (PD) and Huntington's Disease (HD) have found mixed results. Patients with HD are mildly impaired at learning the mirror-reading task (Martone et al., 1984). Some studies of patients with PD have found impaired learning (Koenig, Thomas-Anterion, & Laurent, 1999; Roncacci, Troisi, Carlesimo, Nocentini, & Caltagirone, 1996; Yamadori, Yoshida, Mori, & Yamashita, 1996) whereas others have found intact learning (Bondi & Kaszniak, 1991; Harrington, Haaland, Yeo, & Marder, 1990). Because both PD and HD are associated with dysfunction of the basal ganglia, these data provide at least some suggestion that learning on this task may be

dependent upon the basal ganglia. See Figure 1 for a depiction of the basal ganglia and other important brain regions for skill learning.

----- Figure 1 about here -----

Skill learning on the mirror-reading task has been examined using fMRI in three studies, and additional studies have examined the neural basis of unskilled mirror-reading. Poldrack et al. (1998) compared performance of a lexical decision task on mirror-reversed compared to plain text stimuli before and after training on the mirror-reading task. Lexical decision was used in order to obtain responses without requiring speech in the scanner. Initial (unskilled) performance was associated with extensive activation of the bilateral occipital, parietal, and temporal cortices and cerebellum; a similar pattern of posterior activation has been reported by Goebel et al. (1998) and Kassubek et al. (2001) for alphabetic orthography and Dong et al. (2000) for Japanese Kana. Skill acquisition was associated with decreasing activation in regions including the bilateral occipital and right superior parietal cortices, and increasing activation in regions including the left inferior temporal cortex. On the basis of these data, Poldrack et al (1998) proposed that learning to read mirror-reversed text was associated with a transition from visuospatial transformation of the mirror-reversed stimuli to direct recognition of reversed letters and letter clusters (as initially proposed by Masson, 1986). The decrease in occipital/parietal activation reflected decreasing engagement of the dorsal visual path for visuospatial processing, and the increasing inferior temporal

activation reflected increasing engagement of the ventral visual path for object recognition (Ungerleider & Mishkin, 1982). Because the study by Poldrack et al. (1998) only imaged the rear portion of the brain, it was not possible to assess the engagement of the basal ganglia.

A subsequent study (Poldrack & Gabrieli, 2001) investigated several questions arising from the initial study by Poldrack et al. (1998) using whole-brain fMRI. In the follow-up study, subjects were presented with both novel and repeated mirror-reversed stimuli along with novel plain text items before and after training on the mirror-reading task. In addition, subjects were presented with stimuli that were geometrically transformed using transformations other than the trained mirror-reversal. One stimulus set was both inverted and mirror-reversed, and the other was spelled backwards out of normally oriented letters (see Figure 2). This study found that the caudate was active during initial mirror-reading and showed a significant learning-related increase in activation, consistent with the reported impairment of HD/PD patients at learning the mirror-reading task. (Although PD is a disorder affecting primarily the substantia nigra, it does result in significant dysfunction in the caudate and putamen as well.) Similarly, Dong et al. (2000) found activation of the caudate nucleus during unskilled reading of mirror-reversed Japanese Kana but did not examine learning-related activations. The caudate nucleus could play one (or more) of several roles in mirror-reading. One possibility is that the caudate subserves switching between the use of different task

strategies (such as visuospatial transformation versus object recognition). This would be consistent with the role of the caudate in set-shifting that has been previously suggested (Owen et al., 1992). Alternatively, the caudate may be involved in the learning of new stimulus-response associations, but it is unclear exactly how such a habit learning process would produce improved performance on new items in the mirror-reading task.

----- Figure 2 about here -----

This study also replicated the inferior temporal increase with skill learning found by Poldrack et al., (1998). However, the results of the transfer manipulation disconfirmed the item-specific learning hypothesis advanced by Poldrack et al. (1998). The increase in inferior temporal activation occurred to the same degree both for mirror-reversed items (whose orthography had been trained) and for inverted-reversed items (whose orthography had not been studied) and for spelled-backwards items (which were constructed from familiar letters but read in an unfamiliar direction). This is inconsistent with the notion that increased engagement of the left inferior temporal cortex reflected engagement of item-specific object recognition processes. Several alternative explanations can account for the transfer data. For example, the increased activation could reflect attentional modulation of visual processing, which is known to modulate activation in extrastriate visual cortices (Moran & Desimone, 1985; Nobre, Allison, & McCarthy, 1998). Alternatively, it is possible that the increased activation reflects data-driven activity associated with increased accessibility of visual letter- and word-forms.

A study by Kassubek et al. (2001) examined learning using vertically-inverted words (which are read from left to right) compared to plain text. Subjects read the stimuli silently during scanning, and word length was varied between transformed and plain-text conditions in order to equate difficulty; however, behavioral data were not collected during scanning so the effects of this manipulation are unclear. Kassubek et al. (2001) found decreasing activation in the premotor and superior parietal cortices bilaterally in association with skill learning on the task. No significant increases in activation with learning were observed; however, because the full extent of inferior temporal cortex was not imaged in this study, the impact of this null finding is unclear.

### **Perceptual skill learning: Object recognition**

Whereas studies of mirror-reading have examined the processes involved in recognition of familiar stimuli under novel transformations, other studies have examined the effects of practice on recognition of other particular classes of objects. A study by Gauthier et al. (1999) examined changes in activation as subjects learned to recognize novel objects known as “Greebles” (see Figure 2). This study found increased activation in the fusiform gyri as subjects learned to recognize these objects; in particular, regions that were initially responsive to faces but not to Greebles became sensitive to both classes of stimuli after Greeble training. Because imaging was limited to the occipital and

temporal cortices, it is unknown whether other regions also showed learning-related changes in activity. Another study by Gauthier and colleagues (Gauthier, Skudlarski, Gore, & Anderson, 2000) examined activation for expert versus novice object recognition by imaging experts at either car recognition or bird recognition while they perceived cars, birds, faces, and other objects. Using a region of interest focused on the face-responsive area in the fusiform gyrus (the so-called “fusiform face area” or FFA : Kanwisher, McDermott, & Chun, 1997), this study found that increased activation in the FFA was associated with expertise. That is, car experts exhibited activation of this region for cars but not birds compared to other objects, and bird experts for birds but not cars compared to other objects. Thus, these studies are consistent with the mirror-reading studies in showing increased activation in inferior temporal cortex with increased object recognition skill.

### **Perceptual skill learning: Simple psychophysical tasks**

There is a long tradition of study of perceptual learning in the psychophysical literature, particular for visual tasks (Gibson, 1969; Goldstone, 1998). The tasks used in perceptual learning studies differ from tasks such as mirror-reading or object recognition in that they are strongly data-driven, and also in that learning often occurs more slowly (over course of many days or weeks of training). Perceptual learning has not been

extensively investigated in neuropsychological patients, but a number of studies have used clever task manipulations in conjunction with knowledge about visual system physiology to infer the neural substrates of perceptual learning (Karni & Bertini, 1997). For example, it has been shown that perceptual learning in a texture discrimination task does not transfer to the untrained eye or to untrained retinal locations (Karni & Sagi, 1991), suggesting that the plasticity supporting perceptual learning occurs in early visual cortical regions where the visual representation is specific for these characteristics.

More recently, functional neuroimaging has been used to examine changes in neural activity related to learning on simple psychophysical tasks. Schiltz et al. (1999) imaged subjects using PET while they performed an orientation discrimination task on visual gratings (see Figure 2). Imaging was performed both before and after 10 sessions of training on the task. Subjects were trained on discrimination at one orientation (either +45 or -45 degrees), but were tested on both orientations along with a detection task, allowing examination of both training-specific and nonspecific learning-related changes. Specific learning-related decreases (i.e., decreases occurring only for the practiced orientation) were observed bilaterally in the striate and extrastriate cortices, whereas further nonspecific decreases were observed in bilateral occipital cortex, left fusiform gyrus, and cerebellum. No significant learning-related increases were observed, though power to find such increases may have been limited by the small sample size (6 subjects). A second study by Schiltz and colleagues (Schiltz, Bodart, Michel, & Crommelinck,

2001) also used PET to examine changes associated with learning of orientation discrimination skill. This study found a similar pattern of learning-related decreases as Schiltz et al. (1999), including cerebellum, right precentral, and bilateral fusiform gyri. However, Schiltz et al. (2001) also found a learning-related increase in the body of the right caudate nucleus. The finding of changes in caudate nucleus activity in relation to simple perceptual learning highlights the generality of striatal involvement in skill learning.

## **Skill learning and repetition priming**

In comparison to the small number of imaging studies that have examined skill learning, there has been extensive investigation of the neural basis of repetition priming using neuroimaging. The distinction between repetition priming and skill learning has generally been based on whether learning is measured for a specific item on a task (defined as repetition priming) or whether learning is measured for novel items on a task (defined as skill learning) (Poldrack, Selco, Field, & Cohen, 1999b; Schwartz & Hashtroudi, 1991). Imaging studies have found consistently across a wide range of tasks that repetition priming is associated with learning-related reductions in activation in task-relevant cortical regions (e.g., Buckner et al., 1995; Demb et al., 1995). Studies of visual categorization have also found decreased activation related to learning of new categorical

stimuli (Reber, Stark, & Squire, 1998). These results contrast with the findings of increased activation in studies of skill learning as reviewed above.

Although the findings of priming-related decreases and learning-related increases may appear contradictory, this conflict may be resolved by viewing skill learning and repetition priming as mirror-reflections of a common learning mechanism (Poldrack et al., 1998; Poldrack & Gabrieli, 2001; Poldrack et al., 1999b). On this view, the skill learning-related increases observed for novel stimuli reflect the building of cortical representations for the novel stimulus space. Priming-related decreases, on the other hand, represent facilitation due to repeated engagement of these cortical representations, either for novel or familiar stimuli. This view predicts that regions showing skill-related increases in activation should also show increasing priming effects (i.e., reductions) as skill is acquired. Evidence for this prediction comes from the study of mirror-reading by Poldrack and Gabrieli (2001). Repetition priming was examined both before and after training, and priming effects were examined in regions showing learning-related increases in activation. With one exception, all regions that showed learning-related increases in activation also demonstrated increasing repetition priming effects after training. Poldrack et al. (1998) also found priming-related reductions that overlapped with regions in the left inferior temporal cortex that showed learning-related increases in activation. Together these data suggest that, when examined within the same task, skill learning and repetition priming occur in a common set of neural networks.

## **Relation to neurophysiological studies of skill learning**

The imaging studies reviewed here suggest that acquisition of visual perceptual skill is particularly associated with changes in the response of occipital and inferior temporal cortices. Lesion studies in monkeys have confirmed the importance of these regions for learning of new object discriminations (e.g., Phillips, Malamut, Bachevalier, & Mishkin, 1988). Neurophysiological studies in primates have examined the nature of these changes more directly, and provide direct evidence for plasticity of neural responses related to perceptual learning. Kobatake et al. (1998) trained adult monkeys to discriminate a set of novel shapes, and compared the response of neurons in IT between trained and untrained monkeys. The trained monkeys exhibited significantly greater responses to the learned stimuli compared to untrained monkeys, demonstrating experience-dependent increases in neural response following training. Analysis of the multidimensional response space of the recorded neurons showed that distances between stimuli were greater in trained than untrained monkeys, whereas individual neurons did not respond preferentially to individual stimuli, suggesting that learning occurred at the population level by increasing the response differentiation between similar stimuli. Similar increases in IT response following training with novel objects have been found

by Sakai and Miyashita (1994) and by Logothetis et al. (1995). These findings suggest that the changes in inferior temporal activation observed in human imaging studies relate directly to alterations in the response characteristics of neurons in these regions, but the exact nature of these changes remains unknown. In particular, there is a need for studies examining the specificity of these changes in neural response. Future work combining neurophysiological recording with fMRI in primates (e.g., Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) offers the possibility of directly mapping changes in fMRI activation to changes in neurophysiological characteristics such as receptive fields.

Neurophysiological and lesion studies have also provided evidence regarding the nature of learning-related changes in the basal ganglia. Activity in the striatum of rats was examined during acquisition of an auditory-cued T-maze task by Jog et al. (1999), who recorded from multiple tetrodes over the course of 2-3 weeks. Learning was associated with substantial recruitment of novel unit responses in the striatum. In addition, the nature of striatal responses changed with learning, from initial predominance of units responding to the turning event at the T-junction to later predominance of units responding to the onset of the trial. These responses were maintained over a period of overlearning, suggesting that they represent a long-term representation of the acquired habit. More relevant to the present focus on perceptual skills, two lesion studies have reported impairment of monkeys with caudate lesions on a concurrent visual discrimination task, which requires learning of a

large number of objects over the course of successive days of training (Fernandez-Ruiz, Wang, Aigner, & Mishkin, 2001; Teng, Stefanacci, Squire, & Zola, 2000). Together these data confirm the imaging data by suggesting the importance of the striatum for skill learning, but the precise nature of the striatal contribution to perceptual skill acquisition remains to be characterized.

## **Relation of skill learning to declarative memory**

Much of the previous work on the neural basis of skill learning has been interpreted with respect to the multiple memory systems framework. According to this framework (Cohen & Eichenbaum, 1993; Squire, 1992), there are multiple systems in the brain that support different forms of memory and that are both cognitively and neurally independent. *Declarative memory* relies upon the medial temporal lobe (hippocampus and related structures) and supports explicit, conscious memory for events and facts. *Nondeclarative (or procedural) memory* relies upon a diverse set of cortical and subcortical regions, and supports such implicit memory phenomena as repetition priming, skill learning, and conditioning. Evidence for independence of these memory systems has come from double dissociations between memory tests thought to rely upon these systems. Patients with amnesia due to medial temporal lobe damage are impaired on direct tests of explicit memory such as recall but can exhibit normal skill learning and

repetition priming, whereas patients with cortical lesions exhibit impaired repetition priming in the face of normal explicit memory (Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995b; Keane, Gabrieli, Mapstone, Johnson, & Corkin, 1995).

Double dissociations are often taken as strong evidence for independence between systems (though see Dunn & Kirsner, 1988; Weiskrantz, 1968), but other findings suggest that the declarative and nondeclarative memory systems may interact during normal learning. The first suggestion of an interaction between memory systems came from a set of animal lesion studies, which found that animals with lesions to the medial temporal lobe performed better than control (sham-lesioned) animals on tasks that require the striatum (Eichenbaum, Fagan, Mathews, & Cohen, 1988; Packard, Hirsh, & White, 1989). These findings suggested that the medial temporal lobe may compete with the striatum during learning on certain tasks.

Interaction between the MTL (a putative substrate of declarative memory) and the striatum (a putative substrate of nondeclarative memory) has been further suggested by neuroimaging findings of deactivation in the MTL during some forms of skill learning. Studies of both motor skill learning (Jenkins, Brooks, Nixon, Frackowiak, & et, 1994) and cognitive skill learning (Poldrack, Prabakaran, Seger, & Gabrieli, 1999a) have found deactivation of the medial temporal lobe in conjunction with activation of the striatum during skill learning. More relevant to the current focus on perceptual skill, Poldrack and Gabrieli (2001) found deactivation of the medial temporal lobe after skill

had been acquired on the mirror-reading task but not before, in conjunction with increasing activation in the caudate nucleus. More recent work (Poldrack et al., submitted) has demonstrated a negative correlation between striatal activity and MTL activity during learning of a cognitive skill, consistent with a competitive influence between these structures. Together these data suggest an expansion of the multiple memory systems framework to allow for interaction between memory systems (cf. Kim & Baxter, 2001). A note of caution is necessary, however, because at present there is little knowledge regarding the neurophysiological correlates of these deactivations. In particular, it is not known whether inhibitory synaptic activity is associated with increased or decreased fMRI signal, or how changes in fMRI signal are related changes in neuronal population activity such as sharpened activation of more specific neuronal subpopulations.

## **Conclusions**

Whereas until recently knowledge about the neural basis of skill learning came primarily from studies of patients with brain lesions, neuroimaging has begun to provide a picture of the dynamic changes in neural activity that accompany skill acquisition. Two consistent findings occur across different forms of perceptual skill learning. First, perceptual skill learning has been associated with increased activity in the inferior

temporal and fusiform gyri. The role of these regions in skill learning had not been previously identified in neuropsychological patients. Second, perceptual skill learning has been associated with activity in the basal ganglia during skill learning and more particularly with increasing activity in the body of the caudate nucleus as skill is acquired. This finding confirms the several studies that have found impairments of perceptual skill learning in patients with basal ganglia disorders. Together these results highlight the power of neuroimaging techniques to both confirm and extend the results of neuropsychological investigations.

Although a number of consistent learning-related changes in brain activity can be identified using neuroimaging, the functional nature of these changes is not fully understood. For example, it is unknown whether increasing activity in inferior temporal cortex is related to attentional modulation of visual processing versus development of novel visual object representations. Further studies will undoubtedly address this and other outstanding issues. In addition, imaging techniques such as fMRI and PET have relatively low temporal resolution (on the order of seconds), so they cannot determine whether the timecourse of processing (on the order of milliseconds) changes with learning. This problem can likely be addressed using multimodal imaging approaches (e.g., Dale et al., 2000) that combine the high spatial resolution of fMRI with the high temporal resolution of magnetoencephalography/ electroencephalography (MEG/EEG). These techniques allow characterization of both the spatial and temporal characteristics

of task-related neural activity, and should provide additional leverage for understanding learning-related neural plasticity.

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## Figure Captions

Figure 1. Depiction of brain regions important for skill learning. The left image is an axial slice through a normal adult brain at the level of the caudate nucleus. The right image is a rendering of the left hemisphere cortical surface.

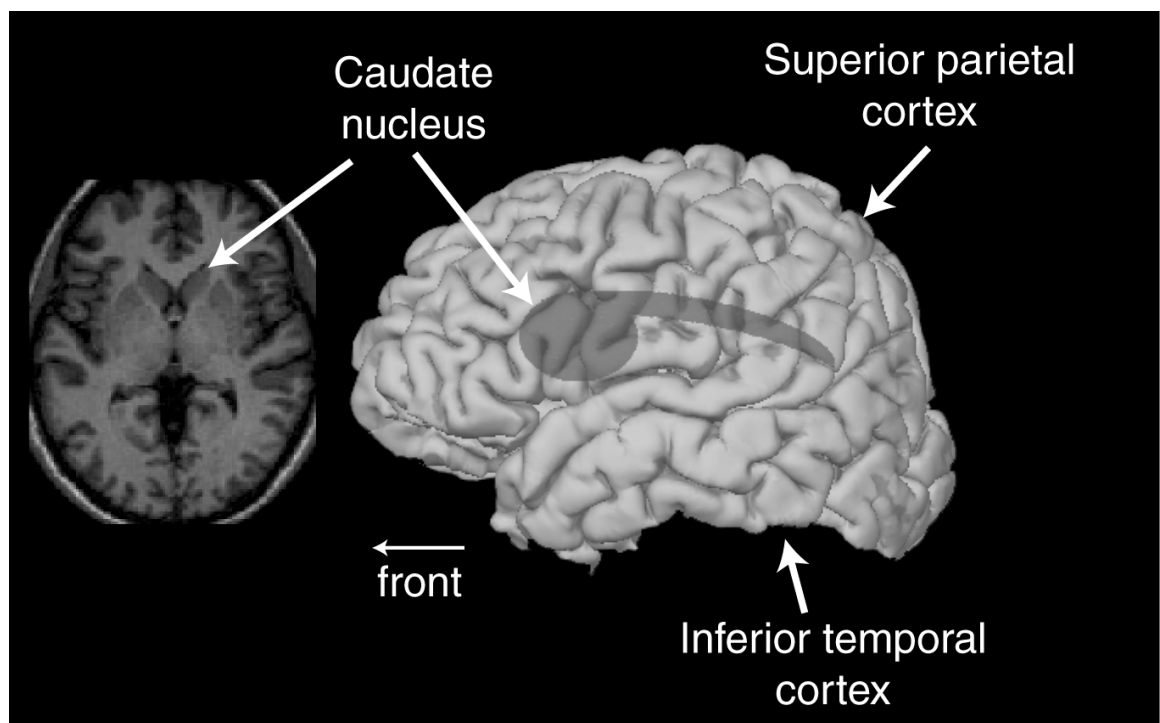


Figure 2. Examples of stimuli used in studies of perceptual skill learning. A) Various forms of geometrically-transformed text (after Poldrack & Gabrieli, 2001), B.) Greebles (Images provided courtesy of Michael J Tarr, Brown University, Providence RI). C.) Orientation gratings (from Schiltz et al., 1999).

