



# Visual learning for perceptual and categorical decisions in the human brain

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## ABSTRACT

Successful actions and interactions in the complex environments we inhabit entail making fast and optimal perceptual decisions. Extracting the key features from our sensory experiences and deciding how to interpret them is a computationally challenging task that is far from understood. Accumulating evidence suggests that the brain may solve this challenge by combining sensory information and previous knowledge about the environment acquired through evolution, development, and everyday experience. Here, we review the role of visual learning and experience-dependent plasticity in shaping decisions. We propose that learning plays an important role in translating sensory experiences to decisions and actions by shaping neural representations across cortical circuits in a task-dependent manner.

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## 1. Introduction

Successful everyday actions rely on the brain extracting a robust estimate of the current state of the environment given noisy sensory signals and judging the rewards and risks associated with a particular decision (Platt & Huettel, 2008; Rushworth & Behrens, 2008; Schultz et al., 2008; Yu & Dayan, 2005). Recent theoretical and experimental work suggests ways that the primate brain meets this challenge by taking into account knowledge from previous experience (Daw & Doya, 2006; Sutton & Barto, 1998). Here, we focus on the role of learning in shaping processes related to the detection of objects in cluttered scenes and their assignment to meaningful categories. We propose that the brain learns to exploit flexibly the statistics of the environment, extract the image features relevant for perceptual decisions and assign objects into meaningful categories in an adaptive manner.

## 2. Learning to detect targets in cluttered scenes

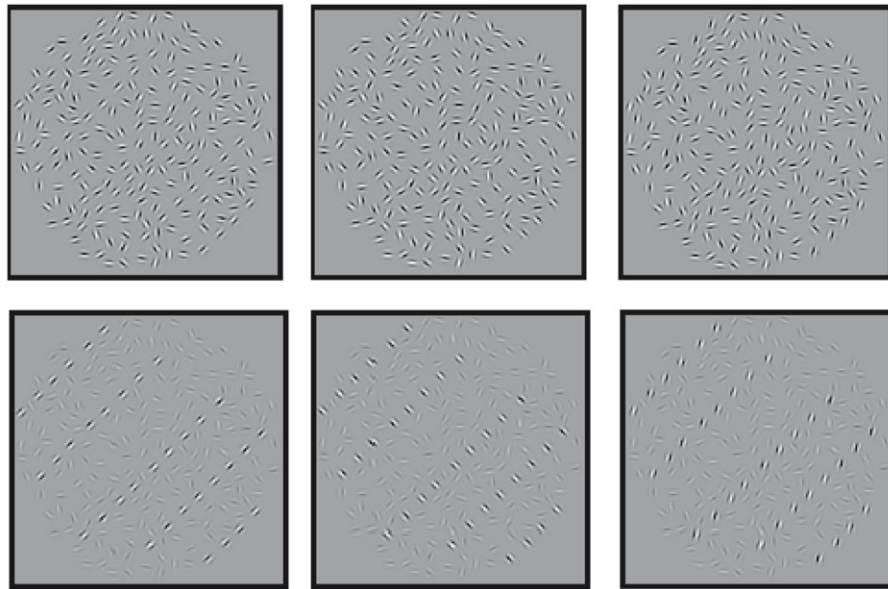
The ability to detect and identify targets in cluttered scenes is a skill critical for many of our interactions in the complex environments we inhabit: identifying predators and prey in natural scenes, recognizing friends in the crowd, detecting objects in medical or security images. Evolution and development have been proposed to shape the organization of the visual system and facilitate visual recognition in cluttered scenes (Gilbert, Sigman, & Crist, 2001; Simoncelli & Olshausen, 2001). For example, recent studies suggest that regularities (e.g. orientation similarity for neighboring

elements) are characteristic of natural scenes and the primate brain has developed a network of connections that mediate integration of features based on these correlations (Geisler, Perry, Super, & Gallogly, 2001; Gilbert, 1992; Sigman, Cecchi, Gilbert, & Magnasco, 2001).

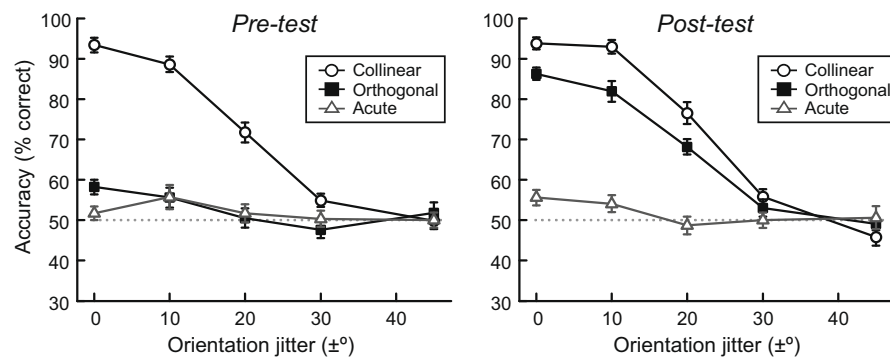
However, learning through everyday experiences has also been shown to be a key facilitator in the detection and recognition of targets in cluttered scenes (Brady & Kersten, 2003; Doshier & Lu, 1998; Gilbert, Sigman, & Crist, 2001; Gold, Bennett, & Sekuler, 1999; Goldstone, 1998; Kovacs, Kozma, Feher, & Benedek, 1999; Schyns, Goldstone, & Thibaut, 1998; Sigman & Gilbert, 2000) by enhancing the integration of relevant object features and their segmentation from clutter. For example, observers are shown to learn distinctive target features by using image regularities in natural scenes more efficiently and by suppressing background noise (Brady & Kersten, 2003; Doshier & Lu, 1998; Eckstein, Abbey, Pham, & Shimozaki, 2004; Gold et al., 1999; Li, Levi, & Klein, 2004). In particular, learning has been suggested to enhance the correlations between neurons responding to the features of target patterns while de-correlating neural responses to target and background patterns. As a result, redundancy in the physical input is reduced and target salience is enhanced (Jagadeesh, Chelazzi, Mishkin, & Desimone, 2001) supporting efficient detection and identification of objects in cluttered scenes (Barlow, 1990). Further, our recent behavioral studies show that short-term experience in adulthood may modify the behavioral relevance (i.e. utility) of atypical contour statistics for the interpretation of natural scenes (Schwarzkopf & Kourtzi, 2008). In particular, observers learn to use discontinuities typically associated with surface boundaries (orthogonal alignments) for contour linking and detection, suggesting flexible learning for perceptual decisions (Fig. 1).

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### A. Stimuli



### B. Training on orthogonal contours



**Fig. 1.** Learning to detect targets in cluttered scenes. (A) Examples of stimuli: collinear contours in which elements are aligned along the contour path, orthogonal contours in which elements are oriented at  $90^\circ$  to the contour path, and acute contours in which elements are oriented at  $30^\circ$  to the contour path. For demonstration purposes the same stimuli are shown with the contrast of the background elements reduced. Stimuli contained five parallel global contours, but their orientation was randomized between  $15^\circ$  and  $165^\circ$  in steps of  $30^\circ$ . (B) Psychometric curves for contour detection performance (percent correct) plotted as a function of local orientation jitter. Average performance across observers is shown before (pre-test left panel) and after training (post-test right panel) on orthogonal contours with feedback. Before training observers were more sensitive to collinear than orthogonal or acute alignments. Only after training was the observers' sensitivity to the regularities present in orthogonal stimuli enhanced and their performance in detecting contours was similar for orthogonal and collinear stimuli. In contrast, learning did not transfer to acute or collinear contours on which the observers were not trained, that is, performance for these contours remained close to pre-training levels.

### 3. Neural signatures of visual learning in the primate brain

Recent computational work proposes that learning may occur across different stages of visual analysis from orientation detectors in the primary visual cortex to occipitotemporal neurons tuned to object parts and views (Poggio & Edelman, 1990; Riesenhuber & Poggio, 2000; Wallis & Rolls, 1997). Numerous behavioral studies have shown learning-dependent changes in the processing of simple visual features such as oriented lines and gratings (Fahle, 2004) and complex objects (Fine & Jacobs, 2002). But what are the neural signatures of learning across stages of visual analysis in the primate brain?

Recent neurophysiological and functional magnetic resonance imaging (fMRI) investigations have focused on elucidating the loci of brain plasticity and changes in neuronal responses that underlie visual learning (for reviews, Gilbert et al., 2001; Kourtzi & DiCarlo, 2006). Further, human evoked potential studies suggest that learning of visual features and objects occurs within the first 200 ms after stimulus onset and correlates with behavioral improvement

after training (Ding, Song, Fan, Qu, & Chen, 2003; Fahle & Skrandies, 1994; Rossion, Collins, Goffaux, & Curran, 2007; Shoji & Skrandies, 2006; Skrandies, Jedynak, & Fahle, 2001; Song et al., 2007).

Perceptual learning of basic visual features (e.g. orientation) has been suggested to result in experience-dependent changes at early stages of visual analysis, as this learning is somewhat confined to the trained retinal location (Crist, Li, & Gilbert, 2001; Fahle, 2004; Schoups, Vogels, & Orban, 1995). That is, changes in the receptive field tuning properties of neurons in the primary visual cortex (V1) might account for the specificity of learning effects for the stimulus position in the visual field and the trained stimulus attribute. Recent imaging studies (Furmanski, Schluppeck, & Engel, 2004; Schiltz et al., 1999; Schwartz, Maquet, & Frith, 2002) provide evidence for the involvement of V1 in feature learning. However, neurophysiological evidence for the contribution of V1 in behavioral improvement after training on visual discrimination, remains controversial (Ghose, Yang, & Maunsell, 2002; Schoups, Vogels, Qian, & Orban, 2001). There is some evidence for sharpening of ori-

entation-tuning after training (Schoups et al., 2001), but no evidence for changes in the size of the cortical representation or the receptive field properties of neurons in V1 (Crist, Li, & Gilbert, 2001; Ghose et al., 2002). Training-dependent changes on orientation-tuning are shown to be more pronounced in V4 (Raiguel, Vogels, Mysore, & Orban, 2006; Yang & Maunsell, 2004), while effects in V1 are shown to be task-dependent and may engage top-down facilitation mechanisms (Crist et al., 2001; Li, Piech, & Gilbert, 2004; Li, Piech, & Gilbert, 2008; Sigman et al., 2005). For example, a recent study (Li et al., 2008) showed enhanced delayed V1 responses after training for collinear contours in accordance with the perceptual salience of these contours (Li et al., 2008). These learning-dependent modulations were absent under anesthesia and were reduced by tasks diverting attention away from the stimulus. These findings are consistent with attention-gated top-down mechanisms that may modulate responses in V1 in a task-dependent manner (Gilbert et al., 2001; Li et al., 2004) by retuning read out signals rather than changing the neural encoding (Law & Gold, 2008).

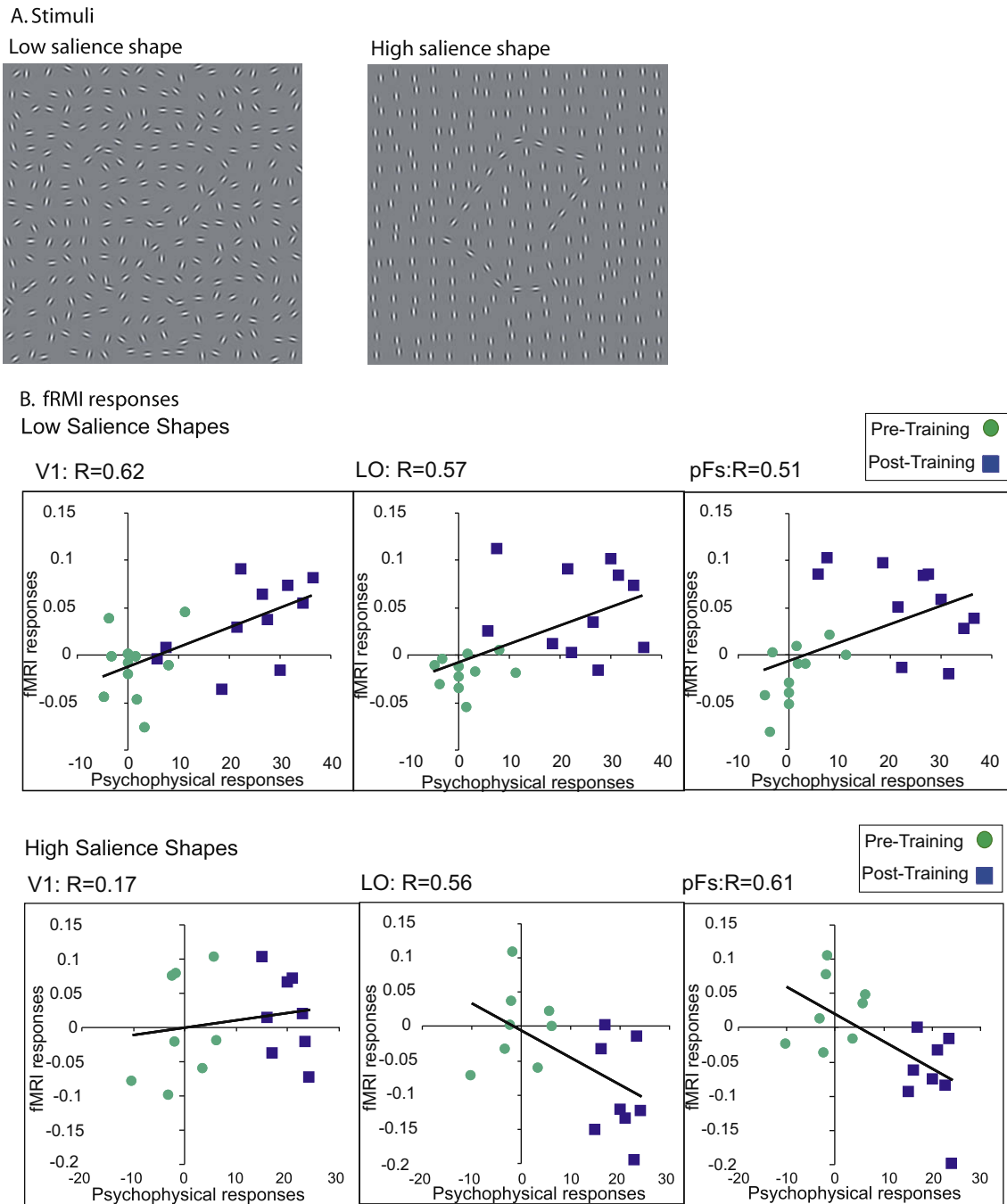
In contrast, studies investigating the neural basis of object learning have focused on higher stages of visual (inferior temporal cortex) and cognitive processing (prefrontal cortex). Numerous neurophysiological (Baker, Behrmann, & Olson, 2002; Freedman, Riesenhuber, Poggio, & Miller, 2003; Logothetis, Pauls, & Poggio, 1995; Op de Beeck, Wagemans, & Vogels, 2003; Rolls, 1995; Rolls, Aggelopoulos, & Zheng, 2003; Sakai & Miyashita, 1991; Sheinberg & Logothetis, 2001; Sigala & Logothetis, 2002) and imaging (Chao, Weisberg, & Martin, 2002; Dolan et al., 1997; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Grill-Spector, Kushnir, Hendler, & Malach, 2000) studies provide evidence that the representations of shape features in temporal and frontal areas are modulated by learning. Recent fMRI studies (Kourtzi, Betts, Sarkheil, & Welchman, 2005; Sigman et al., 2005) provide evidence for recurrent mechanisms of visual learning that tune processing in early visual areas via feedback connections from higher cortical circuits (Roelfsema, 2006; Roelfsema & van Ooyen, 2005). These findings are consistent with the proposal that learning begins at higher visual areas for easy tasks and proceeds to early retinotopic areas that have higher resolution for finer and more difficult discriminations (Ahissar & Hochstein, 2004). In particular, neuroimaging studies suggest that learning may enhance the functional interactions between occipitotemporal areas that encode physical stimulus experiences and parieto-frontal circuits that represent our perceptual interpretations (Büchel, Coull, & Friston, 1999; Dolan et al., 1997; McIntosh, Rajah, & Lobaugh, 1999). For example, Sigman et al. (2005) suggest that shape representation may shift from higher to early visual areas to support rapid and automatic search of visual targets in cluttered scenes independent of attentional control. Thus, these fMRI studies suggest that learning shapes object representations not only by enhancing the processing of feature detectors with increasing complexity along the stages of visual analysis in a bottom-up manner but also in a top-down manner taking into account the relevant task dimensions and demands.

Further, recent fMRI studies (Kourtzi et al., 2005) provide evidence that these recurrent plasticity mechanisms are adaptable to natural image regularities which determine the salience of targets in cluttered scenes (Fig. 2). In particular, these studies suggest that opportunistic learning (Brady & Kersten, 2003) of salient targets in natural scenes is mediated by sparser feature coding at higher stages of visual analysis, whereas learning of camouflaged targets is implemented by bootstrapped mechanisms (Brady & Kersten, 2003) that enhance the segmentation and recognition of ambiguous targets in both early and higher visual areas. Specifically, observers were instructed to discriminate between two shapes consisting of contours defined by aligned Gabor elements and embedded in a field of randomly oriented and positioned Gabors. Before training, no significant differences were observed in

the performance and fMRI responses for a set of shapes on which the observers were to be trained and a set of shapes that were to remain untrained. In contrast, after training, when the shapes appeared camouflaged in a background of randomly oriented and positioned Gabors (low-salience shapes), fMRI responses were higher for trained than untrained shapes, suggesting enhanced representations of the trained shapes. However, when shapes popped-out from a background of uniformly oriented Gabors (high-salience shapes) decreased fMRI responses were observed for trained shapes, suggesting sparser coding after training. Interestingly, this learning-dependent plasticity was distributed across early and higher visual areas for low-salience shapes, but restricted to higher occipitotemporal areas for high-salience shapes. These findings are consistent with the notion that training with low salience targets in cluttered scenes may increase neuronal sensitivity to the target features and suppress the background noise. Specifically, the learning of low salience target shapes resulted in stronger responses to trained than untrained shapes in both early and higher visual areas. This increased neuronal sensitivity during perceptual learning (Kobatake, Wang, & Tanaka, 1998; Logothetis et al., 1995; Sakai & Miyashita, 1991; Vaina, Belliveau, des Rozières, & Zeffiro, 1998) has been suggested to involve increased recruitment of neurons with enhanced responses to similar features of the trained stimuli. As a result, the signal-to-noise ratio in the neural responses is increased for trained compared to untrained shapes. This process may enhance the salience of the target features, facilitating their segmentation from the background and enhancing the global integration that is important for the detection and recognition of visual targets in noise. In contrast, when targets appear in uniform backgrounds they are easily segmented and can be searched more efficiently (Treisman, Vieira, & Hayes, 1992; Wolfe, Cave, & Franzel, 1989). The lower fMRI responses observed for trained than untrained high-salience shapes are consistent with the idea that training with these pop-out targets engages smaller neural ensembles that increase their selectivity for features unique to the stimulus but most relevant for its discrimination in the context of a task. This mechanism results in sparser but more efficient representations of the trained stimuli or features that are important for prompt and successful object categorization and recognition.

Interestingly, a range of fMRI studies using learning or repetition suppression paradigms (i.e. when a stimulus is presented repeatedly) show similar effects for long-term training, rapid learning and priming that depend on the nature of the stimulus representation. In particular, enhanced responses have been observed when learning engages processes necessary for the formation of new representations, as in the case of unfamiliar (Gauthier et al., 1999; Henson, Shallice, & Dolan, 2000; Schacter et al., 1995), degraded (Dolan et al., 1997; George et al., 1999; Tovee, Rolls, & Ramachandran, 1996) masked unrecognizable (Grill-Spector et al., 2000; James, Humphrey, Gati, Menon, & Goodale, 2000) or noise-embedded (Rainer, Lee, & Logothetis, 2004; Schwartz et al., 2002; Vaina et al., 1998) targets. In contrast, when the stimulus perception is unambiguous (e.g. familiar, undegraded, recognizable targets presented in isolation), training results in more efficient processing of the stimulus features indicated by attenuated neural responses (Chao et al., 2002; Henson et al., 2000; James et al., 2000; Jiang, Haxby, Martin, Ungerleider, & Parasuraman, 2000; Koutstaal et al., 2001; Schiltz et al., 1999; van Turennout, Ellmore, & Martin, 2000).

However, when interpreting these imaging findings it is important to note that experience-dependent fMRI activations could be the result of changes in the number, the gain or the tuning of neurons recruited for processing of a stimulus in the context of a task. As imaging studies measure activation at the large scale of neural populations rather than the single neuron, it is difficult to discern these different neural plasticity mechanisms. Recent neurophysiological studies (Rainer & Miller, 2000; Rainer et al., 2004) shed light



**Fig. 2.** fMRI signatures of learning for target detection. (A) Examples of low- and high-salience shapes defined by collinear Gabor elements and embedded in a background of randomly oriented and positioned elements (low salience) or a homogeneous background of elements of the same orientation (high salience). (B) Relationship between psychophysical and fMRI learning effects: fMRI data and the corresponding psychophysical response for low-salience and high-salience shapes. For each individual subject, we plotted a behavioral learning index (percent correct for trained minus percent correct for untrained stimuli) and an fMRI learning index (percent signal change for trained minus percent signal change for untrained stimuli) after training. Positive values indicate stronger responses for trained than untrained shapes, whereas negative values indicate lower responses for trained than untrained shapes. For low-salience shapes the regression analysis showed that responses across early (e.g. V1) and higher (LO, pFs) visual areas was higher for trained than untrained shapes. In contrast, for high-salience shapes the regression was significant only in the LOC subregions (LO, pFs) but not in the early visual areas (e.g. V1). Interestingly, decreased fMRI responses were observed in the LOC for trained than untrained high-salience shapes.

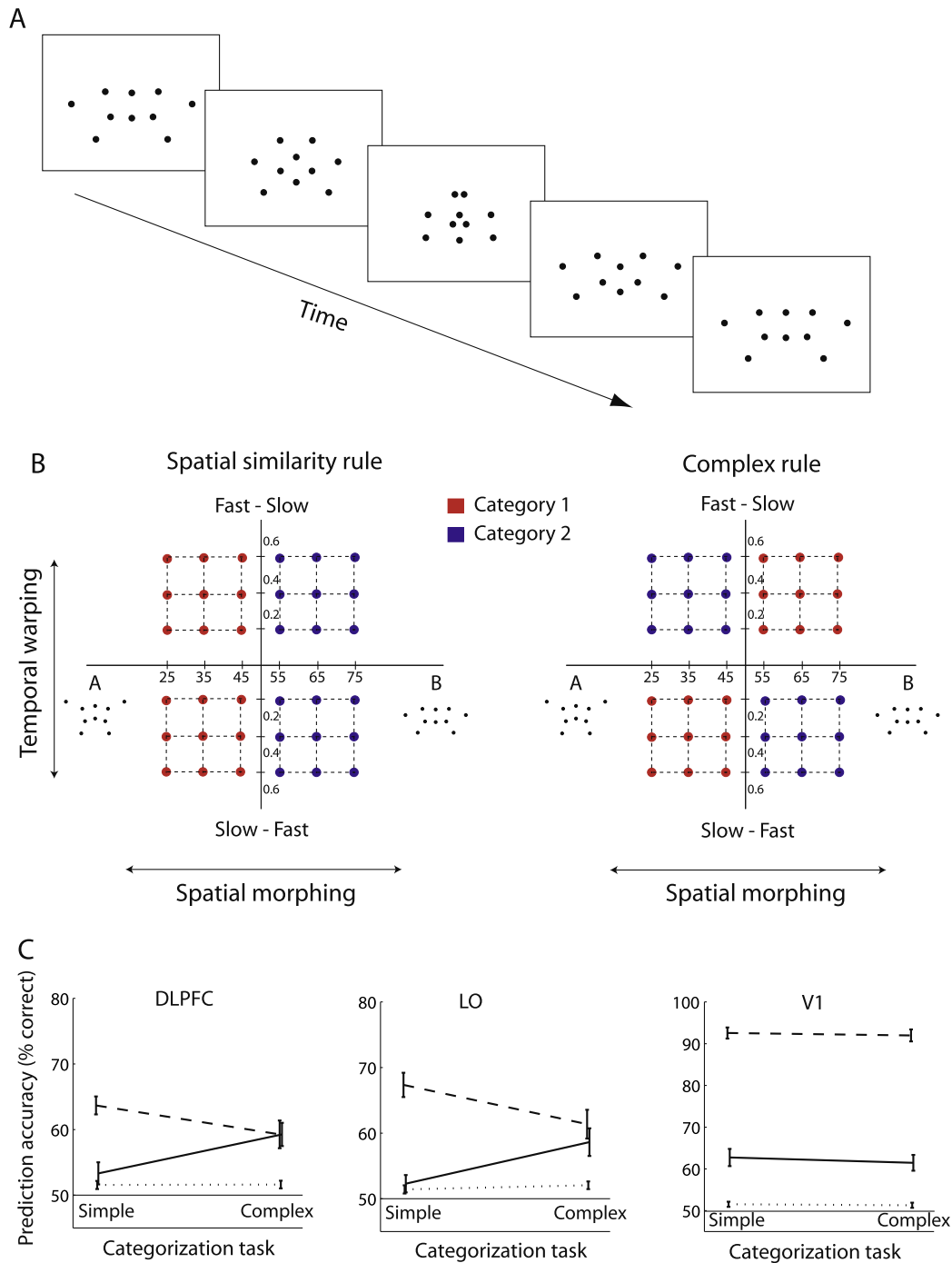
to cortical reorganization mechanisms at the level of the single neuron when monkeys learn to discriminate images of natural scenes presented in noise. These studies suggest that learning enhances the selective processing of critical features in early occipitotemporal areas, while efficient processing independent of background noise in the prefrontal cortex. These findings suggest that learning in different cortical areas bolsters functions that are important for different tasks ranging from the bottom-up detection

of target features across visual occipitotemporal areas to the top-down selection of familiar objects in the prefrontal cortex.

In sum, the current experimental evidence suggests that brain plasticity underlying visual learning is distributed across cortical circuits rather than confined to a single locus. These findings are consistent with computational approaches proposing that associations between features that mediate the recognition of familiar objects may occur across stages of visual analysis from

orientation detectors in the primary visual cortex to occipitotemporal neurons tuned to object parts and views (Poggio, 1990; Riesenhuber & Poggio, 1999; Wallis & Rolls, 1997). Such changes in the connectivity of visual analysis circuits may be adaptive and

efficient compared to changes in core feed forward visual processing (e.g. receptive fields) that may have catastrophic consequences for the visual processing of the trained stimuli in another context or task.



**Fig. 3.** fMRI signatures of learning for categorical decisions. (A) *Stimuli*: Five sample frames of a prototypical stimulus depicting a dynamic figure. Each stimulus comprised ten dots that were configured in a skeleton arrangement and moved in a biologically plausible manner (i.e. sinusoidal motion trajectories). (B) *Stimulus space and categorization tasks*: Stimuli were generated by applying spatial morphing (steps of percent stimulus B) between prototypical trajectories (e.g. A–B) and temporal warping (steps of time warping constant). Stimuli were assigned to one of four groups: A fast-slow (AFS), A slow-fast (ASF), B fast-slow (BFS) and B slow-fast (BSF). For the simple categorization task (left panel) the stimuli were categorized according to their spatial similarity: Category 1 (red dots) consisted of AFS, ASF and Category 2 (blue dots) of BFS, BSF. For the complex task (right panel) the stimuli were categorized based on their spatial and temporal similarity: Category 1 (red dots) consisted of ASF, BFS, and Category 2 (blue dots) of AFS, BSF. (C) *Multivariate pattern analysis of fMRI data*: Prediction accuracy (i.e. probability with which we correctly predict the presented and perceived stimuli from brain activation patterns) for the spatial similarity and complex classification schemes across categorization tasks (simple, complex task). Prediction accuracies for these MVPA rules are compared to accuracy for the shuffling rule (baseline prediction accuracy, dotted line). Interactions of prediction accuracy across tasks in DLPFC and LO indicate that the categories perceived by the observers are reliably decoded from fMRI responses in these areas. In contrast, the lack of interaction in V1 shows that the stimuli are represented based on their physical similarity rather than the rule used by the observers for categorization. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 4. Learning to form visual categories

Our ability to group diverse sensory events and assign novel input into meaningful categories is a cognitive skill critical for adaptive behavior and survival in a dynamic, complex world (Miller & Cohen, 2001). Extensive behavioral work on visual categorization (Goldstone, Lippa, & Shiffrin, 2001; Nosofsky, 1986; Schyns et al., 1998) suggests that the brain solves this challenging task by representing the relevance of visual features for categorical decisions rather than similarity in the sensory input (i.e. retinal image properties). Recent neuropsychological and imaging studies have identified distinct networks of cortical and subcortical areas in the human brain that are involved in visual categorization (for reviews, Ashby & Maddox, 2005; Keri, 2003). These studies have implicated different brain regions in category learning depending on the structure of visual categories. In particular, areas in the prefrontal cortex and basal ganglia have been implicated in rule-based tasks in which the category structure is determined by a single stimulus dimension. This is consistent with physiology and imaging studies showing that the prefrontal cortex guides visual attention to select behaviorally relevant information (Desimone, 1998; Desimone & Duncan, 1995; Maunsell & Treue, 2006; Reynolds & Chelazzi, 2004) and represents the task-relevant features (for reviews, Duncan, 2001; Miller, 2000; Miller & D'Esposito, 2005). In contrast, the basal ganglia have been primarily implicated in information-integration tasks that require combining information from different stimulus dimensions for making a categorical decision. Further, the medial temporal cortex has been implicated in category learning tasks that rely on memorization. Finally, prototype-distortion tasks during which participants compare category exemplars to prototypical visual stimuli have been shown to engage occipito-temporal regions. Interestingly, the role of temporal cortex in categorical decisions remains controversial. Some neurophysiological studies propose that the temporal cortex represents primarily the visual similarity between stimuli (Freedman et al., 2003; Op de Beeck, Wagemans, & Vogels, 2001; Thomas, Van Hulle, & Vogels, 2001), while others show that it represents learned stimulus features and categories (Freedman, Riesenhuber, Poggio, & Miller, 2006; Freedman et al., 2003; Meyers, Freedman, Kreiman, Miller, & Poggio, 2008), diagnostic dimensions for categorization (Mirabella et al., 2007; Sigala & Logothetis, 2002) and is modulated by task demands (Koida & Komatsu, 2007) and experience (e.g. Baker et al., 2002; Booth & Rolls, 1998; Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Kobatake et al., 1998; Kourtzi et al., 2005; Logothetis et al., 1995; Miyashita & Chang, 1988; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006).

It is important to note that using neuroimaging to isolate this flexible code for translating sensory information to perceptual categories in the human brain is limited as the typical fMRI resolution does not allow us to discern selectivity for features represented by overlapping neural populations. Using multivariate methods for the analysis of neuroimaging data (Cox & Savoy, 2003; Haynes & Rees, 2006; Norman, Polyn, Detre, & Haxby, 2006) has been proposed as a more sensitive approach than conventional analysis methods and has revealed a distributed pattern of activations for object categories in the temporal cortex (Hanson, Matsuka, & Haxby, 2004; Haxby et al., 2001; O'Toole, Jiang, Abdi & Haxby, 2005; Williams, Dang, & Kanwisher, 2007). Using this approach (i.e. multi-voxel pattern analysis) Li, Ostwald, Giese, and Kourtzi (2007) showed that we can successfully determine human brain regions that carry information about the diagnostic stimulus features for the different categorization tasks (Goldstone et al., 2001; Nosofsky, 1986; Palmeri & Gauthier, 2004; Schyns et al., 1998; Sigala, Gabbiani, & Logothetis, 2002; Smith & Ratcliff, 2004). That is, multivariate methods allow us to decode fMRI selectivity for visual features that is shaped by

task context and feature-based attention (i.e. whether the observers attend and categorize the stimuli based on single or combined stimulus dimensions) rather than features fixed by low-level processes (i.e. similarity in the physical input). In particular, observers were presented with a space of dynamic displays comprising synthetic movements rendered with dots placed in a skeleton; the structure of these movements was unfamiliar but their trajectories followed biological constraints. This stimulus space was generated by linear morphing between prototypical movement configurations (spatial dimension) and temporal warping of their speed profile (temporal dimension). Observers were instructed to categorize these stimuli based on the spatial or temporal dimension. Further, observers were trained to learn an abstract rule for stimulus classification that entailed taking into account both dimensions. The results showed that fMRI signals in brain areas encoding behaviorally relevant information were decoded more reliably when brain responses for stimulus categories were classified based on the categorization rule used by the observers rather than a rule that did not match the perceived stimulus categories (Fig. 3). These findings demonstrate that adaptive coding is implemented in the human brain by shaping neural representations in a network of areas with dissociable roles in visual categorization. Specifically, temporal and parietal areas were shown to encode the perceived form and motion similarity respectively, consistent with previous studies showing categorical representations in these regions (Freedman & Assad, 2006; Freedman et al., 2003). In contrast, frontal areas and the striatum were shown to represent task-relevant conjunctions of spatio-temporal features critical for complex categorization tasks. That is, neural representations in these areas are shaped by the behavioral relevance of sensory features and previous experience to reflect the perceptual (categorical) rather than the physical similarity between stimuli. Further, recent work (Li, Mayhew, & Kourtzi, 2009) comparing behavioral choices of human observers with those of a pattern classifier based on multi-voxel single-trial fMRI signals showed that category learning shapes decision-related processes in frontal and higher occipitotemporal regions rather than signal detection or response execution in primary visual or motor areas. In particular, in prefrontal circuits learning shapes the estimation of the decision criterion only in the context of the categorization task. In contrast, in higher occipitotemporal regions the representations of perceived categories are sustained after training independent of the task and may serve as selective readout signals for optimal decisions.

These findings are consistent with neurophysiological evidence for recurrent processes in visual categorization. It is possible that information about spatio-temporal stimulus properties in higher temporal and parietal cortex is combined with motor responses to form associations and representations of meaningful categories in the striatum and frontal cortex (Muhammad, Wallis, & Miller, 2006; Toni, Rushworth, & Passingham, 2001). In turn, these category formation and decision processes modulate selectivity for perceptual categories along the behaviorally relevant stimulus dimensions in a top-down manner (Freedman et al., 2003; Mirabella et al., 2007; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Smith, Gosselin, & Schyns, 2004) resulting in enhanced selectivity for form similarity in higher visual areas, whereas temporal similarity in parietal areas.

#### 5. Conclusions

Learning plays a fundamental role in the functional optimization of the adult visual system. In particular, the adult human brain appears to capitalize on natural image correlations that determine the target distinctiveness in a scene and learns to detect, categorize and identify novel objects in a flexible manner. This adaptive

behavior is implemented by experience-dependent plasticity mechanisms that reorganize processing across multiple cortical areas. That is, there does not appear to be an exclusive locus of plasticity in the visual system that underlies learning. On the contrary, learning is implemented through recurrent mechanisms that support adaptive processing of visual features depending on the task context and demands. Such processing allows the brain to combine inherently noisy and ambiguous sensory input with previous knowledge that is critical for optimal decisions and actions. An important aim for future work is to understand how learning through everyday experiences relates to long-term optimization of the visual system through evolution and development. Investigating the commonalities and/or differences between long-term optimization and shorter-term learning processes is critical for understanding the key principles that underlie adaptive behavior and designing biologically plausible artificial systems.

## References

- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, 8(10), 457–464.
- Ashby, F. G., & Maddox, W. T. (2005). Human category learning. *Annual Review of Psychology*, 56, 149.
- Baker, C. I., Behrmann, M., & Olson, C. R. (2002). Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nature Neuroscience*, 5(11), 1210–1216.
- Barlow, H. (1990). Conditions for versatile learning. Helmholtz's unconscious inference, and the task of perception. *Vision Research*, 30(11), 1561–1571.
- Booth, M. C. A., & Rolls, E. T. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cerebral Cortex*, 8, 510–523.
- Brady, M. J., & Kersten, D. (2003). Bootstrapped learning of novel objects. *Journal of Vision*, 3(6), 413–422.
- Buchel, C., Coull, J. T., & Friston, K. J. (1999). The predictive value of changes in effective connectivity for human learning. *Science*, 283(5407), 1538–1541.
- Chao, L. L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex*, 12(5), 545–551.
- Cox, D. D., & Savoy, R. L. (2003). Functional magnetic resonance imaging (fMRI) "brain reading": Detecting and classifying distributed patterns of fMRI activity in human visual cortex. *Neuroimage*, 19(2 Pt 1), 261.
- Crist, R. E., Li, W., & Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. *Nature Neuroscience*, 4(5), 519–525.
- Daw, N. D., & Doya, K. (2006). The computational neurobiology of learning and reward. *Current Opinion in Neurobiology*, 16(2), 199–204.
- Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 353(1373), 1245–1255.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Ding, Y., Song, Y., Fan, S., Qu, Z., & Chen, L. (2003). Specificity and generalization of visual perceptual learning in humans: An event-related potential study. *Neuroreport*, 14(4), 587–590.
- Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R. S., et al. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature*, 389(6651), 596–599.
- Doshier, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences USA*, 95(23), 13988–13993.
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, 2(11), 820–829.
- Eckstein, M. P., Abbey, C. K., Pham, B. T., & Shimozaki, S. S. (2004). Perceptual learning through optimization of attentional weighting: Human versus optimal Bayesian learner. *Journal of Vision*, 4(12), 1006–1019.
- Fahle, M. (2004). Perceptual learning: A case for early selection. *Journal of Vision*, 4(10), 879–890.
- Fahle, M., & Skrandies, W. (1994). An electrophysiological correlate of learning in motion perception. *German Journal of Ophthalmology*, 3(6), 427–432.
- Fine, I., & Jacobs, R. A. (2002). Comparing perceptual learning tasks: A review. *Journal of Vision*, 2(2), 190–203.
- Freedman, D. J., & Assad, J. A. (2006). Experience-dependent representation of visual categories in parietal cortex. *Nature*, 443(7107), 85–88.
- Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2003). A comparison of primate prefrontal and inferior temporal cortices during visual categorization. *Journal of Neuroscience*, 23(12), 5235–5246.
- Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2006). Experience-dependent sharpening of visual shape selectivity in inferior temporal cortex. *Cerebral Cortex*, 16(11), 1631–1644.
- Furmanski, C. S., Schluppeck, D., & Engel, S. A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, 14(7), 573–578.
- Gauthier, I., Anderson, A. W., Tarr, M. J., Skudlarski, P., & Gore, J. C. (1997). Levels of categorization in visual recognition studied using functional magnetic resonance imaging. *Current Biology*, 7(9), 645–651.
- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience*, 2(6), 568–573.
- Geisler, W. S., Perry, J. S., Super, B. J., & Gallogly, D. P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, 41(6), 711–724.
- George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience*, 2(6), 574–580.
- Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, 87(4), 1867–1888.
- Gilbert, C. D. (1992). Horizontal integration and cortical dynamics. *Neuron*, 9(1), 1–13.
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, 31(5), 681–697.
- Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature*, 402(6758), 176–178.
- Goldstone, R. L. (1998). Perceptual learning. *Annual Review of Psychology*, 49, 585–612.
- Goldstone, R. L., Lippa, Y., & Shiffrin, R. M. (2001). Altering object representations through category learning. *Cognition*, 78(1), 27–43.
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience*, 3(8), 837–843.
- Hanson, S. J., Matsuka, T., & Haxby, J. V. (2004). Combinatorial codes in ventral temporal lobe for object recognition: Haxby (2001) revisited: Is there a face area? *NeuroImage*, 23(1), 156.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293(5539), 2425–2430.
- Haynes, J. D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, 7(7), 523.
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, 287(5456), 1269–1272.
- Jagadeesh, B., Chelazzi, L., Mishkin, M., & Desimone, R. (2001). Learning increases stimulus salience in anterior inferior temporal cortex of the macaque. *Journal of Neurophysiology*, 86(1), 290–303.
- James, T. W., Humphrey, G. K., Gati, J. S., Menon, R. S., & Goodale, M. A. (2000). The effects of visual object priming on brain activation before and after recognition. *Current Biology*, 10(17), 1017–1024.
- Jiang, Y., Haxby, J. V., Martin, A., Ungerleider, L. G., & Parasuraman, R. (2000). Complementary neural mechanisms for tracking items in human working memory. *Science*, 287(5453), 643–646.
- Keri, S. (2003). The cognitive neuroscience of category learning. *Brain Research, Brain Research Reviews*, 43(1), 85.
- Kobatake, E., Wang, G., & Tanaka, K. (1998). Effects of shape-discrimination training on the selectivity of inferotemporal cells in adult monkeys. *Journal of Neurophysiology*, 80(1), 324–330.
- Koida, K., & Komatsu, H. (2007). Effects of task demands on the responses of color-selective neurons in the inferior temporal cortex. *Nature Neuroscience*, 10(1), 108–116.
- Kourtzi, Z., Betts, L. R., Sarkheil, P., & Welchman, A. E. (2005). Distributed neural plasticity for shape learning in the human visual cortex. *PLoS Biology*, 3(7), e204.
- Kourtzi, Z., & DiCarlo, J. J. (2006). Learning and neural plasticity in visual object recognition. *Current Opinion in Neurobiology*, 16(2), 152–158.
- Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, 39(2), 184–199.
- Kovacs, I., Kozma, P., Feher, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences USA*, 96(21), 12204–12209.
- Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, 11(4), 505–513.
- Li, R. W., Levi, D. M., & Klein, S. A. (2004). Perceptual learning improves efficiency by re-tuning the decision 'template' for position discrimination. *Nature Neuroscience*, 7(2), 178–183.
- Li, S., Mayhew, S. D., & Kourtzi, Z. (2009). Learning shapes the representation of behavioral choice in the human brain. *Neuron*, 62(3), 441–452.
- Li, S., Ostwald, D., Giese, M., & Kourtzi, Z. (2007). Flexible coding for categorical decisions in the human brain. *Journal of Neuroscience*, 27(45), 12321–12330.
- Li, W., Piech, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651.
- Li, W., Piech, V., & Gilbert, C. D. (2008). Learning to link visual contours. *Neuron*, 57(3), 442–451.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology*, 5(5), 552–563.
- Maunsell, J. H., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6), 317–322.
- McIntosh, A. R., Rajah, M. N., & Lobaugh, N. J. (1999). Interactions of prefrontal cortex in relation to awareness in sensory learning. *Science*, 284(5419), 1531–1533.
- Meyers, E. M., Freedman, D. J., Kreiman, G., Miller, E. K., & Poggio, T. (2008). Dynamic population coding of category information in inferior temporal and prefrontal cortex. *Journal of Neurophysiology*, 100(3), 1407–1419.

- Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience*, 1(1), 59–65.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167–202.
- Miller, B. T., & D'Esposito, M. (2005). Searching for the top in top-down control. *Neuron*, 48(4), 535–538.
- Mirabella, G., Bertini, G., Samengo, I., Kilavik, B. E., Frilli, D., Della Libera, C., et al. (2007). Neurons in area V4 of the macaque translate attended visual features into behaviorally relevant categories. *Neuron*, 54(2), 303–318.
- Miyashita, Y., & Chang, H. S. (1988). Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature*, 331(6151), 68–70.
- Muhammad, R., Wallis, J. D., & Miller, E. K. (2006). A comparison of abstract rules in the prefrontal cortex, premotor cortex, inferior temporal cortex, and striatum. *Journal of Cognitive Neuroscience*, 18(6), 974.
- Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, 10(9), 424–430.
- Nosofsky, R. M. (1986). Attention, similarity, and the identification-categorization relationship. *Journal of Experimental Psychology: General*, 115(1), 39–61.
- Op de Beek, H. P., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination training alters object representations in human extrastriate cortex. *Journal of Neuroscience*, 26(50), 13025–13036.
- Op de Beek, H., Wagemans, J., & Vogels, R. (2001). Inferotemporal neurons represent low-dimensional configurations of parameterized shapes. *Nature Neuroscience*, 4(12), 1244.
- Op de Beek, H., Wagemans, J., & Vogels, R. (2003). The effect of category learning on the representation of shape: Dimensions can be biased but not differentiated. *Journal of Experimental Psychology: General*, 132(4), 491–511.
- O'Toole, A. J., Jiang, F., Abdi, H., & Haxby, J. V. (2005). Partially distributed representations of objects and faces in ventral temporal cortex. *Trends in Cognitive Sciences*, 17(4), 580–590.
- Palmeri, T. J., & Gauthier, I. (2004). Visual object understanding. *5(4)*, 291.
- Platt, M. L., & Huettel, S. A. (2008). Risky business: The neuroeconomics of decision making under uncertainty. *Nature Neuroscience*, 11(4), 398–403.
- Poggio, T. (1990). A theory of how the brain might work. *Cold Spring Harbor Symposia on Quantitative Biology*, 55, 899–910.
- Poggio, T., & Edelman, S. (1990). A network that learns to recognize three-dimensional objects. *Nature*, 343(6255), 263–266.
- Raiguel, S., Vogels, R., Mysore, S. G., & Orban, G. A. (2006). Learning to see the difference specifically alters the most informative V4 neurons. *Journal of Neuroscience*, 26(24), 6589–6602.
- Rainer, G., Lee, H., & Logothetis, N. K. (2004). The effect of learning on the function of monkey extrastriate visual cortex. *PLoS Biology*, 2(2), E44.
- Rainer, G., & Miller, E. K. (2000). Effects of visual experience on the representation of objects in the prefrontal cortex. *Neuron*, 27(1), 179–189.
- Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, 27, 611–647.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, 2(11), 1019–1025.
- Riesenhuber, M., & Poggio, T. (2000). Models of object recognition. *Nature Neuroscience*, 3, 2(Suppl), 1199–1204.
- Roelfsema, P. R. (2006). Cortical algorithms for perceptual grouping. *Annual Review of Neuroscience*, 29, 203–227.
- Roelfsema, P. R., & van Ooyen, A. (2005). Attention-gated reinforcement learning of internal representations for classification. *Neural Computation*, 17(10), 2176–2214.
- Rolls, E. T. (1995). Learning mechanisms in the temporal lobe visual cortex. *Behavioral Brain Research*, 66(1–2), 177–185.
- Rolls, E. T., Aggelopoulos, N. C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, 23(1), 339–348.
- Rossion, B., Collins, D., Goffaux, V., & Curran, T. (2007). Long-term expertise with artificial objects increases visual competition with early face categorization processes. *Journal of Cognitive Neuroscience*, 19(3), 543–555.
- Rotshtein, P., Henson, R. N., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, 8(1), 107.
- Rushworth, M. F., & Behrens, T. E. (2008). Choice, uncertainty and value in prefrontal and cingulate cortex. *Nature Neuroscience*, 11(4), 389–397.
- Sakai, K., & Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature*, 354(6349), 152–155.
- Schacter, D. L., Reiman, E., Uecker, A., Polster, M. R., Yun, L. S., & Cooper, L. A. (1995). Brain regions associated with retrieval of structurally coherent visual information. *Nature*, 376(6541), 587–590.
- Schiltz, C., Bodart, J. M., Dubois, S., DeJardin, S., Michel, C., Roucoux, A., et al. (1999). Neuronal mechanisms of perceptual learning: Changes in human brain activity with training in orientation discrimination. *Neuroimage*, 9(1), 46–62.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology (London)*, 483(Pt 3), 797–810.
- Schoups, A. A., Vogels, R., Qian, N., & Orban, G. A. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412, 549–553.
- Schultz, W., Preusschoff, K., Camerer, C., Hsu, M., Fiorillo, C. D., Tobler, P. N., et al. (2008). Review: Explicit neural signals reflecting reward uncertainty. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 363, 3801–3811.
- Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences USA*, 99(26), 17137–17142.
- Schwarzkopf, D. S., & Kourtzi, Z. (2008). Experience shapes the utility of natural statistics for perceptual contour integration. *Current Biology*, 18(15), 1162–1167.
- Schyns, P. G., Goldstone, R. L., & Thibaut, J. P. (1998). The development of features in object concepts. *Behavioral and Brain Sciences*, 21(1), 1–17 [discussion 17–54].
- Sheinberg, D. L., & Logothetis, N. K. (2001). Noticing familiar objects in real world scenes: The role of temporal cortical neurons in natural vision. *Journal of Neuroscience*, 21(4), 1340–1350.
- Shoji, H., & Skrandies, W. (2006). ERP topography and human perceptual learning in the peripheral visual field. *International Journal of Psychophysiology*, 61(2), 179–187.
- Sigala, N., Gabbiani, F., & Logothetis, N. K. (2002). Visual categorization and object representation in monkeys and humans. *Journal of Cognitive Neuroscience*, 14(2), 187–198.
- Sigala, N., & Logothetis, N. K. (2002). Visual categorization shapes feature selectivity in the primate temporal cortex. *Nature*, 415(6869), 318–320.
- Sigman, M., Cecchi, G. A., Gilbert, C. D., & Magnasco, M. O. (2001). On a common circle: Natural scenes and Gestalt rules. *Proceedings of the National Academy of Sciences USA*, 98(4), 1935–1940.
- Sigman, M., & Gilbert, C. D. (2000). Learning to find a shape. *Nature Neuroscience*, 3(3), 264–269.
- Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D., & Gilbert, C. D. (2005). Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron*, 46(5), 823–835.
- Simoncelli, E. P., & Olshausen, B. A. (2001). Natural image statistics and neural representation. *Annual Review of Neuroscience*, 24, 1193–1216.
- Skrandies, W., Jedynak, A., & Fahle, M. (2001). Perceptual learning: Psychophysical thresholds and electrical brain topography. *International Journal of Psychophysiology*, 41(2), 119–129.
- Smith, M. L., Gosselin, F., & Schyns, P. G. (2004). Receptive fields for flexible face categorizations. *Psychological Science*, 15(11), 753–761.
- Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neuroscience*, 27(3), 161–168.
- Song, Y., Peng, D., Lu, C., Liu, C., Li, X., Liu, P., et al. (2007). An event-related potential study on perceptual learning in grating orientation discrimination. *Neuroreport*, 18(9), 945–948.
- Sutton, R., & Barto, A. G. (1998). *Reinforcement learning*. Cambridge, MA: MIT Press.
- Thomas, E., Van Hulle, M. M., & Vogels, R. (2001). Encoding of categories by noncategory-specific neurons in the inferior temporal cortex. *Journal of Cognitive Neuroscience*, 13(2), 190.
- Toni, I., Rushworth, M. F., & Passingham, R. E. (2001). Neural correlates of visuomotor associations. Spatial rules compared with arbitrary rules. *Experimental Brain Research*, 141(3), 359–369.
- Tovee, M. J., Rolls, E. T., & Ramachandran, V. S. (1996). Rapid visual learning in neurones of the primate temporal visual cortex. *Neuroreport*, 7(15–17), 2757–2760.
- Treisman, A., Vieira, A., & Hayes, A. (1992). Automaticity and preattentive processing. *American Journal of Psychology*, 105(2), 341–362.
- Vaina, L. M., Belliveau, J. W., des Roziers, E. B., & Zeffiro, T. A. (1998). Neural systems underlying learning and representation of global motion. *Proceedings of the National Academy of Sciences USA*, 95(21), 12657–12662.
- van Turenout, M., Ellmore, T., & Martin, A. (2000). Long-lasting cortical plasticity in the object naming system. *Nature Neuroscience*, 3(12), 1329–1334.
- Wallis, G., & Rolls, E. T. (1997). Invariant face and object recognition in the visual system. *Progress in Neurobiology*, 51(2), 167–194.
- Williams, M. A., Dang, S., & Kanwisher, N. G. (2007). Only some spatial patterns of fMRI response are read out in task performance. *Nature Neuroscience*, 10(6), 685–686.
- Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), 419–433.
- Yang, T., & Maunsell, J. H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24(7), 1617–1626.
- Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. *Neuron*, 46(4), 681–692.