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REVIEW

Neural plasticity in high-level visual cortex underlying object perceptual learning

Taiyong BI (✉)[1], Fang FANG[1,2,3]

[1] Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China
[2] Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, China
[3] PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China

Abstract **With intensive training, human can achieve impressive behavioral improvement on various perceptual tasks. This phenomenon, termed perceptual learning, has long been considered as a hallmark of the plasticity of sensory neural system. Not surprisingly, high-level vision, such as object perception, can also be improved by perceptual learning. Here we review recent psychophysical, electrophysiological, and neuroimaging studies investigating the effects of training on object selective cortex, such as monkey inferior temporal cortex and human lateral occipital area. Evidences show that learning leads to an increase in object selectivity at the single neuron level and/or the neuronal population level. These findings indicate that high-level visual cortex in humans is highly plastic and visual experience can strongly shape neural functions of these areas. At the end of the review, we discuss several important future directions in this area.**

Keywords plasticity, object perceptual learning, neural mechanism, inferior temporal cortex, lateral occipital

Introduction

Instead of a hard-wired system, our brain is plastic and is adapting to the dynamic world constantly. Such neural plasticity is prominent when the brain is immature (Hubel and Wiesel, 1970) or damaged (Kaas et al., 1990). However, even healthy adult brain can show impressive plasticity under certain circumstances. Some changes are short-lived for just a few seconds or minutes, such as neural suppression after visual adaptation (Blakemore and Campbell, 1969). One of the most stable and long-term changes is perceptual learning, which results from intensive training on a perceptual task (Gilbert et al., 2001). Training is shown to improve various visual performances, ranging from discriminating elementary visual features such as orientation (Schoups et al., 1995), contrast (Yu et al., 2004), and motion direction (Ball and Sekuler, 1987), to identifying shapes (Sigman and Gilbert, 2000) and objects (Furmanski and Engel, 2000). Such improvements from perceptual learning usually last for months, even years (Karni and Sagi, 1993).

The training-induced improvement on visual abilities is considered to be closely related to plasticity in visual cortical areas. A significant characteristic of perceptual learning is its specificity to the trained attribute, the trained position, and even the eye of origin. For example, training with an orientation discrimination task leads to a dramatic improvement in the discriminating ability around the trained orientation (Schoups et al., 2001). The specificities of perceptual learning effects have usually been taken as an implication of modification in the primary visual cortex (V1) where neurons are tuned for low-level features such as orientation, spatial frequency, retinal location etc.

Studies have been conducted to identify the neural correlates of perceptual learning. Several of them indeed found changes in neuronal tuning or cortical response magnitude in the primary visual cortex. For example, training monkeys to discriminate grating orientation leads to a sharpening of the tuning curve of V1 neurons (Schoups et al., 2001). In human imaging studies, it has been shown that training with a texture discrimination task or an orientation detection task leads to an enhancement in V1 response (Schwartz et al., 2002; Furmanski et al., 2004; Yotsumoto et al., 2008; Bao et al., 2010). These findings support that

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Correspondence: Taiyong BI
E-mail: bitaiyong@pku.edu.cn

training changes the coding of the trained attributes in the task-relevant sensory cortex.

Compared to learning of elementary visual features, object learning is far less investigated. Yet the ability to identify visual objects in a crowded environment is of greater biological significance for surviving. Could our ability to recognize objects be improved by training? A lot of studies have shown that training could lead to a better performance on recognizing complex stimuli, ranging from computer generated novel shapes (Op de Beeck et al., 2003), to common objects (Gauthier and Tarr, 1997; Furmanski and Engel, 2000), to human faces (Gold et al., 1999; Goldstone et al., 2001; Hussain et al., 2008). These improvements indicate that the neural processing of object information could be modified. It is known that visual objects, as well as complex shapes, are encoded by neurons in monkey inferotemporal (IT) cortex (Gross, 1992) and its human homolog, lateral occipital (LO) area. Neural activity in these cortical areas has a close relationship with object recognition performance (Grill-Spector et al., 2000). Because object perceptual learning shows tolerance to size and position changes of trained stimuli which are the characteristics of IT neurons (Gross, 1992; Grill-Spector et al., 1999), it thus has been suggested that the most plausible neural locus of object perceptual learning is IT or LO.

In the past decades, a large number of psychophysical and neurophysiological explorations have been made to investigate the neural mechanisms underlying object perceptual learning. Here we review psychophysical evidence on the characteristics of object perceptual learning, as well as evidence on the neural substrates of the learning. A wide range of forms of object learning are included, such as discrimination, categorization, matching, as well as passive viewing. All these kinds of learning usually exhibit typical characteristics of perceptual learning, such as specificity and persistency. As the neural locus of object learning has been speculated to be object selective cortex such as monkey IT or human lateral occipital area, we mainly review evidence showing learning related changes in these areas. Since some researchers proposed that learning may take place at a more central site which is related to attention and decision making (Mollon and Danilova, 1996), in this review, we pay special attention to evidence supporting or against the critical role of sensory cortex plasticity in object perceptual learning.

Psychophysical evidence: specificity and generalization in object perceptual learning

Furmanski and Engel (2000) studied the behavioral consequences of object learning. Subjects were trained for five days with an object recognition task. In each trial, a gray-scale object image was presented briefly and followed by a mask image (Fig. 1A). The object exposure time was controlled by a staircase procedure and subjects performed a naming task. An adaptive procedure was adopted to estimate the threshold exposure time for object recognition. Training gradually reduced the threshold exposure time, indicating a facilitated recognition performance. Importantly, this facilitation effect was specific to the trained objects and persisted after a long period of break (Fig. 1B), which is typical to perceptual learning. Furthermore, this learning effect transferred nearly completely to stimuli with a different size (Fig. 1C). These results agree well with the proposal that learning modifies neurons in object selective cortex whose response shows a large tolerance to image size variance.

A more detailed study concerning face view discrimination learning systematically examined conditions under which learning could transfer or not (Bi et al., 2010). A complete transfer of learning effect was found between trained and test stimuli that were different in size, local information, identity or retinal position (Fig. 2A–2D). However, when the configural face information was disrupted by inverting the face or when the test face was replaced with a paperclip-like object, the learning effect could no longer transfer (Fig. 2E–2F). These results provided strong evidence that face view learning takes place at cortical areas containing neurons sensitive to face view and tolerant to size, local information, position and identity changes. Such neurons were found in monkey IT area (Desimone et al., 1984), as well as superior temporal sulcus (STS) area (Perrett et al., 1985; De Souza et al., 2005). Human imaging studies also revealed that face view information is processed in higher level visual cortex including fusiform face area (FFA), occipital face area (OFA) and STS (Andrews and Ewbank, 2004; Fang et al., 2007). Therefore, the psychophysical results strongly suggest that learning modified neuronal function in these areas.

The high specificity of learning effect to the trained objects and the substantial transfer to stimuli containing only low-level property changes indicate higher level object selective areas as the neural locus of object learning. These findings thus suggest that, to reveal the neural mechanisms of object perceptual learning, it is reasonable to focus on the neural changes induced by object learning in object selective cortex such as monkey IT or human LO areas.

Electrophysiological evidence

Growing evidence suggests that object learning occurs at object selective areas. Researchers paid more attention to these areas than low level visual areas such as V1. For this reason, most of the electrophysiological studies concern neuronal activity in monkey IT area. A central question is how learning changes the representation of objects in this area.

A straightforward idea is to examine the influence of training on neuronal firing rate to the trained objects. For example, Sakai and Miyashita (1994) found that training with a form matching task could lead to a larger response to the

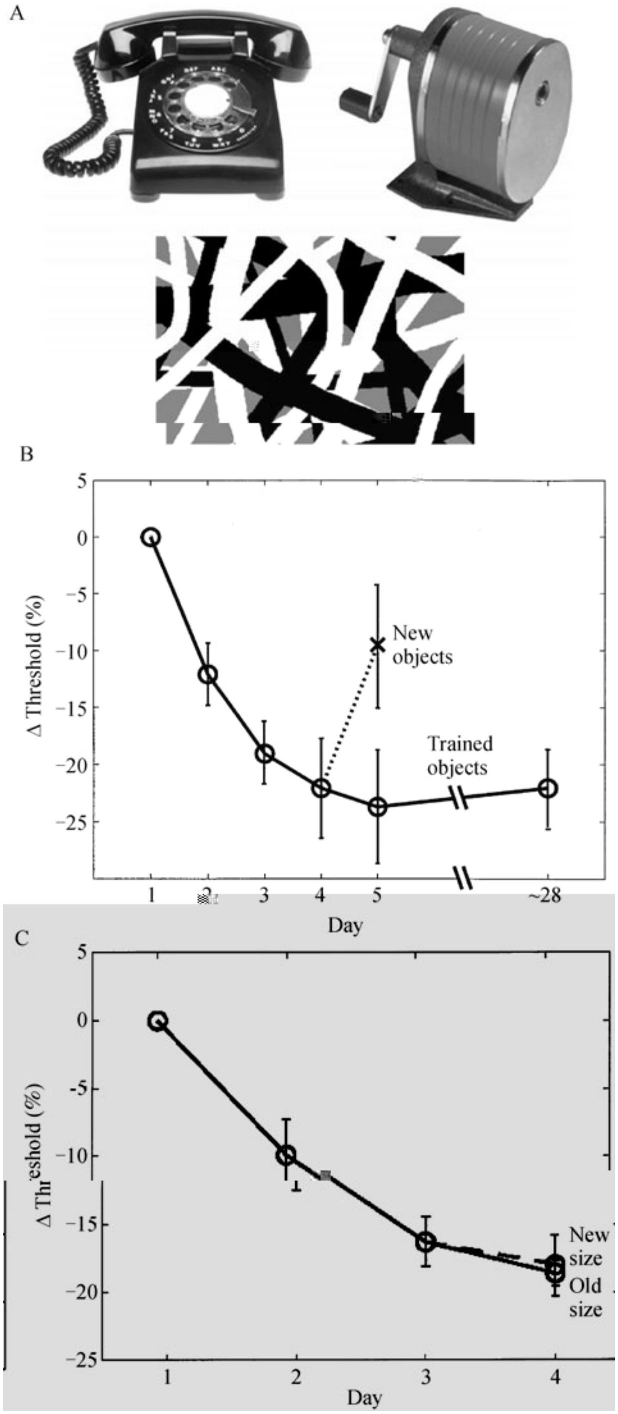

Figure 1 Learning of object identification: specificity and transfer. (A) Two examples of the stimuli used for training. Objects were presented for a short period and followed by a mask. Subjects were instructed to name the object. (B) The threshold exposure time of objects decreased gradually with training. Learning was specific to the trained objects and could persist up to 20 days after training. (C) Learning

different size.

trained stimuli than the untrained stimuli. However, not all the studies are consistent with this finding. Instead, some studies showed a decrease in firing rate (Freedman et al., 2006) or an unchanged response (Baker et al., 2002; Cox and DiCarlo, 2008).

The discrepancy among the findings concerning neuronal firing rate may stem from the different tasks or stimuli, indicating that there may not be a common mechanism of different kinds of object learning. However, different from the studies focusing on response magnitude, many studies consistently found that neuronal selectivity could be enhanced after training (Baker et al., 2002; Sigala and Logothetis, 2002; Freedman et al., 2006; Op de Beeck et al., 2007; Cox and DiCarlo, 2008; De Baene et al., 2008; Woloszyn and Sheinberg, 2012). The enhancement of selectivity was observed across different training tasks and stimuli. Thus, it is likely that selectivity change is a common and crucial neural correlate of object learning.

Selectivity is an intrinsic property of neurons in sensory cortex. For example, neurons in IT area are selective for complex shapes or objects. A neuron may fire intensively when seeing an apple, but it remains silent when seeing a pear. Selectivity refers to the difference of responses to different stimuli. The larger the selectivity, the more sensitive neurons are to specific stimulus attributes, which may in turn result in a better behavioral performance. Therefore, in addition to response change, selectivity change is also a potential mechanism underlying perceptual learning. A typical way to measure neuronal selectivity is to compute the "selectivity index". Assume a neuron responds to a set of stimuli. This neuron fires most when stimulus A is presented, but it fires least when stimulus B is presented. The selectivity index of this neuron to this set of stimuli is defined as $(R_A - R_B)/(R_A + R_B)$, where R_X means the response to stimulus X.

Sigala and Logothetis (2002) studied how neuronal selectivity changes in monkey temporal cortex after practicing a face categorization task. A series of cartoon faces varied in four features, including eye height, eye separation, nose length and mouth height (Fig. 3A). Monkeys were trained to categorize faces into two categories using the information of two features (Fig. 3B). A selectivity index could be computed for each of the four features (Fig. 3C). The results showed that selectivity indices of features useful for categorization task (diagnostic features) were significantly larger than those not useful for categorization task (non-diagnostic features) (Fig. 3D), indicating an enhancement in selectivity as a result of training.

Such an enhancement in selectivity could result from either

inhibition to non-preferred stimulus, or both. This may explain the disagreement among previous studies regarding whether the neuronal response could be increased (Woloszyn and Sheinberg, 2012), decreased (Freedman et al., 2006) or unchanged (Baker et al., 2002; Cox and DiCarlo, 2008). Yet

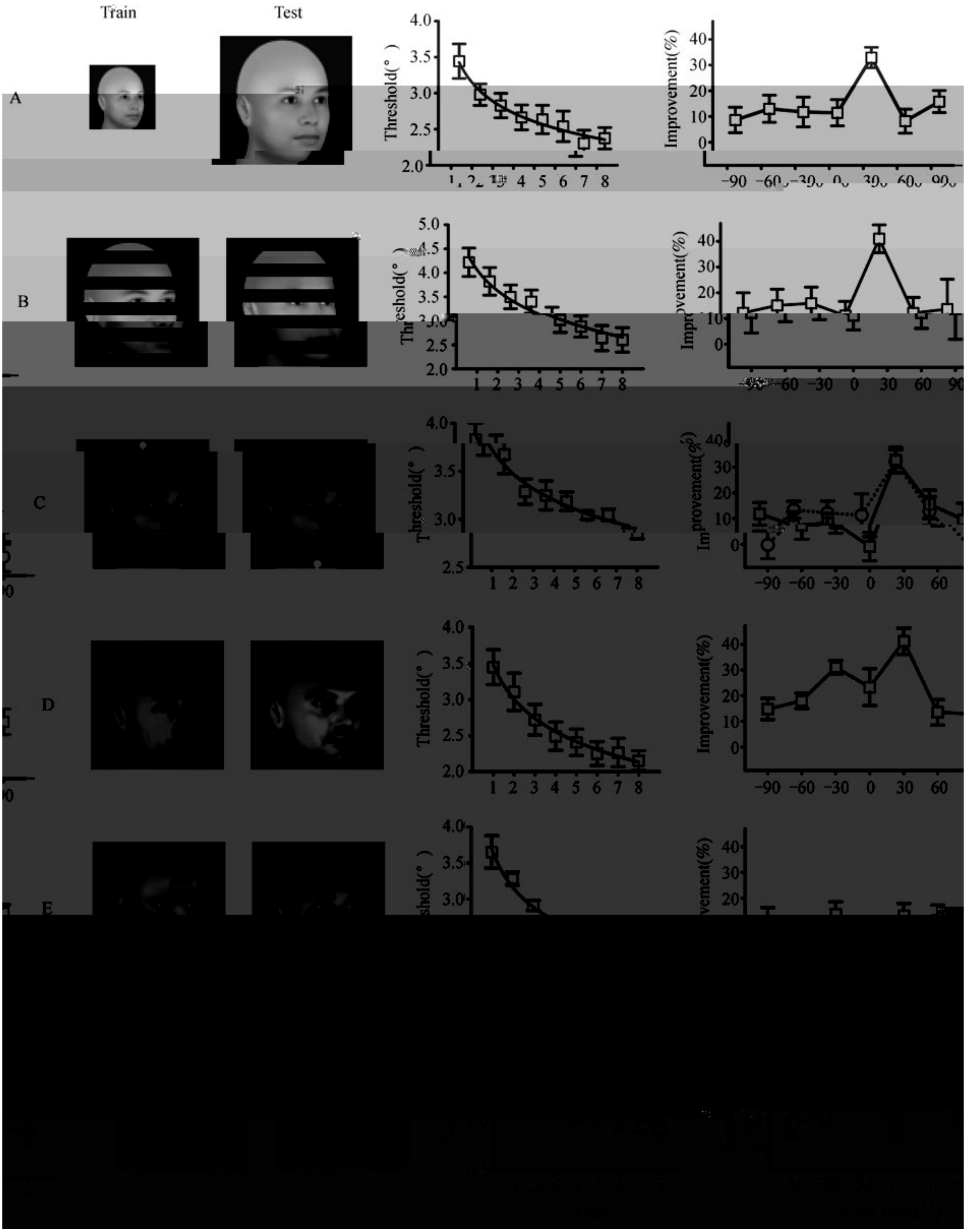

Figure 2 Face view perceptual learning. First column denotes the stimuli for training. Subjects were asked to discriminate two side views of a stimulus around a 30° view angle. The second column denotes the stimuli for testing the transfer of the learned view discrimination ability to untrained stimuli. The test stimuli were different from the trained stimuli in size (A), part (B), identity (C), visual field (D), configural information (E), and face information (F).View discrimination performances at seven view angles (one was the trained view, others were the untrained views) were tested before and after training. The third column denotes the learning curve of each stimulus in the first column. The discrimination threshold decreased gradually along an eight-day training course for all the stimuli. The fourth column denotes the percent improvement of view discrimination performance on the test stimuli in the second column. The learning effects in A–D transferred to the test stimuli in a view specific manner. However, the learning effects of inverted face and non-face objects (E and F) could not transfer to the upright face stimuli.

the selectivity was consistently found enhanced. Importantly, selectivity enhancement has been found across a wide range of tasks, including categorizing objects or shapes (Sigala and Logothetis, 2002; Freedman et al., 2006; De Baene et al., 2008), discriminating objects (Baker et al., 2002; Cox and DiCarlo, 2008), recognizing objects (Op de Beeck et al., 2007), and even when passively viewing objects (Woloszyn and Sheinberg, 2012). It is thus plausible that neuronal selectivity enhancement is the common mechanism underlying different types of object perceptual learning.

Despite the extremely high spatial and temporal resolution in electrophysiological signals, lack of examination at the neuronal population level is an evident shortage of single neuron studies. The species difference between monkey and

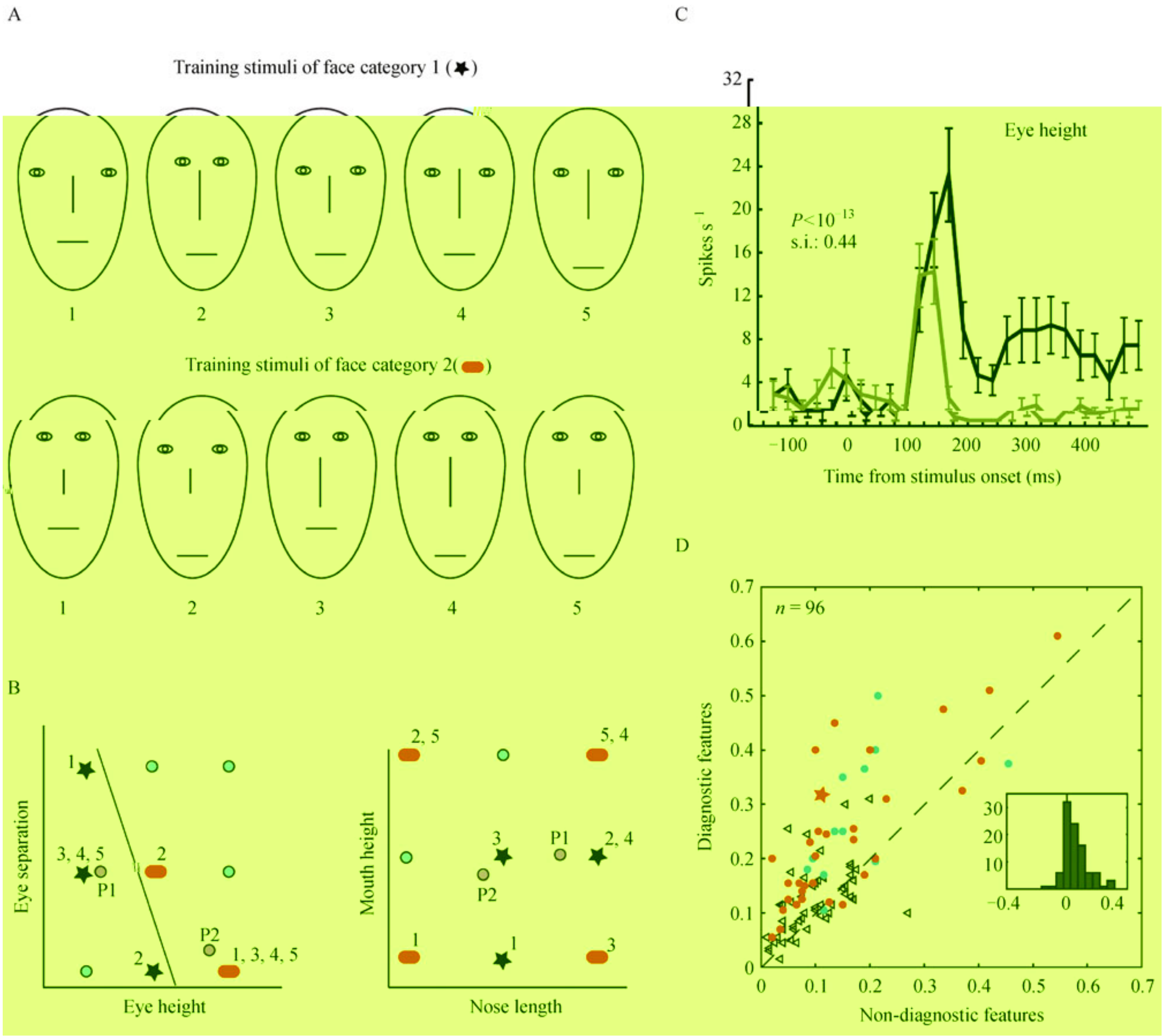

Figure 3 Neural selectivity changes with categorization learning. (A) Stimuli and categories. The stimulus set consisted of line drawings of faces with four varying features: eye height, eye separation, nose length and mouth height. (B) Two-dimensional representation of the stimulus space. Monkeys were trained to categorize faces to two categories based on two of the four varying features. Dark line denotes the category boundary. Black stars represent the stimuli of the first category and red ovals represent the stimuli of the second category. Each number indicates the position of one corresponding stimulus from panel A. (C) Example of a neuron showing feature selectivity. Black traces indicate the responses of the neuron to the best feature value; gray traces indicate responses to the worst feature value. s.i. denotes the selectivity index. For each feature, one s.i. could be computed for each neuron. (D) Plots of the average selectivity index of each neuron for the diagnostic versus the non-diagnostic features. Each point represents one neuron. Red circles represent neurons with statistically significant selectivity for diagnostic features only. Blue circles represent neurons with statistically significant selectivity for both diagnostic and non-diagnostic features. Black triangles represent neurons with no significant selectivity. Insert diagram shows the distribution (numbers of neurons) of the selectivity index for the diagnostic features after subtraction of the selectivity index for the non-diagnostic features.

human also made it difficult to completely generalize these findings to humans. Brain imaging techniques like functional magnetic resonance imaging (fMRI) and electroencephalography (EEG), which enable scientists to directly investigate human neural system at a population level, have greatly overcome the shortage of single neuron studies. With these methods, it is possible to track neural changes over a long period of learning course. For these reasons, it was proposed that "some of the most interesting studies of brain plasticity or reorganisation simply could not be done without brain scans" (Anstis, 2010).

Brain imaging evidence

The blood-oxygen-level-dependent (BOLD) signal of fMRI is thought to reflect neural activity at a neuronal population level. Using fMRI, researchers found that human cortical response could be modulated by long-term visual experience. For example, the visual word form area (VWFA) in the left temporal cortex was found to respond more vigorously to words of subjects' native language than words of other language (Baker et al., 2007). Other instances come from visual expertise researches. It is reported that activity in the right hemispherical fusiform gyrus was strongly correlated with the level of expertise on bird, car, or radiological diagnosis (Gauthier et al., 2000; Xu, 2005; Harley et al., 2009). These findings revealed that long-term visual experience could enhance the neural activity in high-level cortical areas.

Importantly, restricted experience in laboratory was shown to be sufficient to elicit stronger activity in visual areas. van der Linden et al.(2008) found that a three-day training on a categorization task of bird led to response enhancement in right fusiform gyrus region. Moore et al. (2006) found that the response enhancement in LO induced by object learning was correlated with the behavioral expertise effect. These findings support that the human occipital-temporal area is crucial in object perceptual learning. Furthermore, double dissociation of learning effect with different training tasks indicates that LO is only critical in object training task. Song et al. (2010) trained subjects to either discriminate objects or associate objects with some words. Their results showed that training with the object discrimination task led to response enhancement in LO area while training with word association led to response enhancement in VWFA. Other studies also showed that if the training task related to the low-level properties of object (e.g., visual searching task), early visual cortex but not LO area showed consistently enhanced response after training (Sigman et al., 2005; Wong et al., 2012). These evidences together indicate that human occipital-temporal cortex is susceptible to visual experience on object recognition, in line with electrophysiological findings.

Most fMRI studies examined the signal amplitude change. Since BOLD signal in a voxel is thought to represent the pooled activity of many neurons, the result of response change is not comparable to selectivity change at the single neuron level. However, using some fMRI experimental paradigms such as fMRI adaptation, we could infer the tuning property of a cortical area to a visual feature or object.

FMRI adaptation refers to the decrease of neural response when the stimuli are repetitively presented(Grill-Spector and Malach, 2001; Grill-Spector et al., 2006). Adaptation effect has been reported both at the single neuron level and the population level measured by BOLD fMRI. For example, as Fig. 4A illustrated, subjects were presented with 32 pictures in a scanning cycle. In *Same* condition, all the pictures were the same, while in *Different* condition, all the pictures contained different objects. Other conditions include different numbers of object types. Figure 4B shows the neural response in LO to these stimuli in different scanning cycles with different conditions. Response increased monotonically with the number of object types, indicating a strong suppression when the same picture was presented repeatedly.

This selective suppression effect is an indicator of neuronal selectivity in a specific cortical area. If an area shows an adaptation effect to one feature of a stimulus, it's likely that this area contains neurons tuned to this feature. For example, Fang et al. (2005) found that V1 showed a strong orientation adaptation effect which was dependent on the orientation difference between adapting and test stimuli. That is, the smaller the orientation difference between two subsequently presented gratings, the weaker the neural response in V1. This result indicates that V1 contains orientation selective neurons whose response is dependent on the difference between stimulus and its preferred orientation. Therefore, if the neural representations of two stimuli are more similar, the neural response should be smaller when the two stimuli are presented successively.

Jiang et al. (2007) found that training a car categorization task could reduce the adaption effect in the LO area. Specifically, before training, the neural responses to two successively presented cars were similar between the identical-car condition and the different-car condition. After training on categorizing these cars, neural response to the different cars was significantly higher than that to the identical cars, indicating a larger representation difference between the two different cars. This result is in accordance with the enhancement of neuronal selectivity in single cell studies. Further studies showed that this reduction on adaptation effect was specific to the trained object(Gillebert et al., 2009) and the trained feature dimension (Folstein et al., 2012). These findings indicate that neural selectivity in the human LO area could also be enhanced by perceptual learning.

FMRI studies revealed a critical role of human occipital-temporal area on object perceptual learning. However, fMRI cannot tell us about the timing property of neural response induced by learning because of the low temporal resolution of fMRI BOLD signal (on a second level). EEG signals, on the

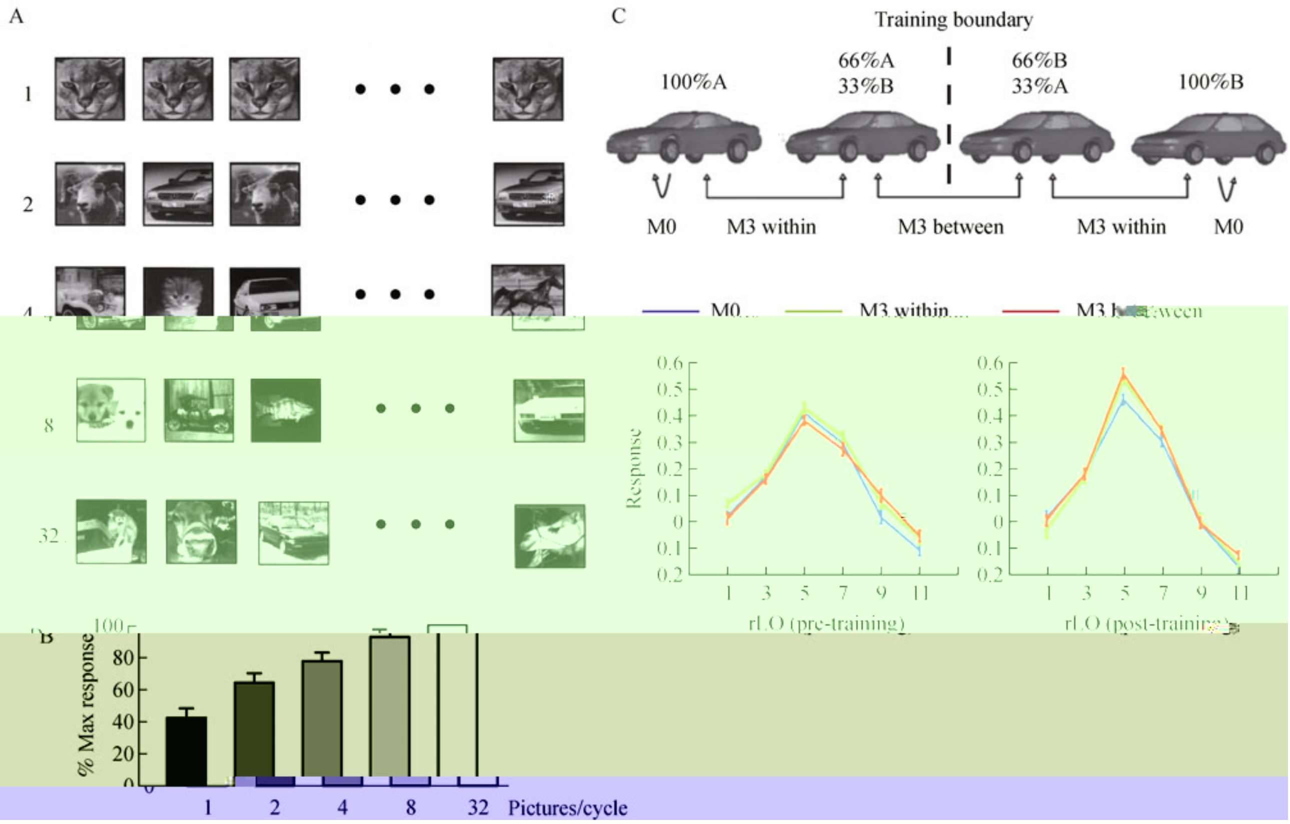

Figure 4 Example of an fMRI adaptation experiment and the learning effect on fMRI adaptation. (A) An illustration of the sequence of object images presented during an fMRI adaptation experiment. 32 pictures were sequentially presented in a repeating cycle. The number of different objects in each cycle is given on the left, ranging from 1 (the same object picture presented repeatedly) to 32 (32 different images). (B) Relative LOC signal of each repetition condition compared to the maximal activation (condition 32) as a function of number of different pictures in the cycle. Note the fMRI signal decreased monotonically as the repetition frequency increased. (C) The stimuli and result of an fMRI study on car categorization training. Subjects were trained to categorize morphed cars into two categories. Before and after training, subjects were scanned while viewing three kinds of stimuli. In condition M0, stimuli in a trial are always two identical cars which are one of the two prototypes. In condition M3, stimuli are two morphed car which are different from each other for 33% of each prototype. *Within* and *between* refer to within the same category and between different categories respectively. Before training, LO responses in three conditions were similar, indicating no difference on the neural representation of different cars. However, after training, the response for different cars was significantly higher than that for identical car, revealing a release from adaptation after training.

other hand, provide an excellent time precision (on a millisecond level) and thus have been widely used to realize this purpose. Su et al. (2012) found that training to discriminate face views shortened the latency of an event-related potential (ERP) component called "N170." N170 is a negative potential peaked around 170ms after stimulus onset. It is well accepted as reflecting face processing (Bentin et al., 1996; Jeffreys, 1996). The result that learning shortens the latency thus indicates a facilitation effect of training on the processing of face information. Studies on object training found that either the latency of N170 could be shortened (Rossion et al., 2002) or the amplitude of N170 could be enhanced (Peissig et al., 2007). Taken together, these results suggest that learning modulates the encoding stage specific to face or object information. However, a study concerning object categorization task showed that training enhanced the amplitude of N250, an ERP component around 250ms after stimulus onset (Scott et al., 2008). More surprisingly, the modulation on N250 but not N170 could last for one week after training, indicating that the modulation of a relative late stage of processing may be the long-lasting correlate of object perceptual learning. More evidence is needed to elucidate the temporal aspect of neural mechanisms underlying object learning.

Concluding remarks

Existing evidence shows that learning could modify the neural activity in object-sensitive visual cortex, either enhancing the response or increasing the selectivity of relevant neurons. Although significant progress has been made regarding the mechanism of perceptual learning, some important issues still need to be addressed.

First, little is known about the long-term changes related to training. Some studies compared the neural activities induced by the trained objects and the untrained objects. Others compared the activities before and after training. However, very few studies investigated the long-term neural changes induced by training. In one study concerning texture discrimination training, it was found that response enhancement in V1 did not persist two weeks after training (Yotsumoto et al., 2008).This result indicates that response enhancement may be a transient change. As the behavioral improvement could last for months to years (Karni and Sagi, 1993), the long-lasting change needs to be further investigated. The same problem exists in the object learning study.

Second, objects we see in real life are often in a crowded environment or embedded in external noise, while participants in laboratory were often presented with isolated and noiseless objects. Dosher and Lu (1998) proposed that perceptual learning of orientation discrimination eliminates both external noise and internal noise. They further found that learning in a noisy display did not improve the performance in clear display (Dosher and Lu, 2005), indicating two independent processes. However, very few studies examined the effect of noise on object learning. One study (Rainer et al., 2004) found that the ability to identify a natural image could be improved only when the image was embedded in external noise. Their electrophysiological results also showed that learning enhanced the activity of the most informative neurons in V4 under the condition of the noisy display but not the clear display. These findings were consistent with the proposal that noise is excluded through channel reweighting. However, more physiological researches are required to fully understand how noise is reduced.

Third, although most studies indicate that learning of object and elementary feature lead to changes in high-level visual cortex and low-level visual cortex respectively, it is especially interesting to investigate if there is common mechanism underlying these two different kinds of learning. Recently, some modeling and psychophysical works suggested that perceptual learning of elementary feature is related to changes beyond the visual cortex (Dosher and Lu, 1998; Xiao et al., 2008). Consistent with this hypothesis, human imaging studies found that orientation discrimination learning was related to the neural changes in the anterior cingulate cortex which is a higher decision-making area (Kahnt et al., 2011). Results in other human imaging and electrophysiological studies also implied the involvement of other higher-order areas, such as human attention-related regions and monkey lateral intraparietal area, in learning of contrast discrimination and motion direction discrimination (Mukai et al., 2007; Law and Gold, 2008). However, there is little evidence tapping similar issues in object learning. Future studies bridging different kinds of learning would help to improve our understanding of perceptual learning as a whole.

Finally, in additional to regional changes of brain activity, training was found to modify many other characteristics of the brain. For example, motor learning changes the functional connectivity among motor-related cortical areas (Ma et al., 2010). This result suggests that the functional change induced by training may not be restricted to some specific regions, but exists in a brain network level. In addition to functional changes, evidence also shows that brain structure is also susceptible to experience (Zatorre et al., 2012). For example, memory training could change the cortical thickness of specific regions (Engvig et al., 2010). Surprisingly, even white matter was found to be modified by training of a visual-motor skill (Scholz et al., 2009). Examining these issues could provide insight to perceptual learning from different perspectives, yet very few of such work have been done in object perceptual learning. Future works in these directions will make a whole picture of brain plasticity clearer.

Compliance with ethics requirements

Taiyong Bi and Fang Fang declare that they have no conflict of interest. This manuscript is a review article and does not involve a research protocol requiring approval by the relevant institutional review board or ethics committee.

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