

Perceptual Learning: Toward a Comprehensive Theory

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Abstract

Visual perceptual learning (VPL) is long-term performance increase resulting from visual perceptual experience. Task-relevant VPL of a feature results from training of a task on the feature relevant to the task. Task-irrelevant VPL arises as a result of exposure to the feature irrelevant to the trained task. At least two serious problems exist. First, there is the controversy over which stage of information processing is changed in association with task-relevant VPL. Second, no model has ever explained both task-relevant and task-irrelevant VPL. Here we propose a dual plasticity model in which feature-based plasticity is a change in a representation of the learned feature, and task-based plasticity is a change in processing of the trained task. Although the two types of plasticity underlie task-relevant VPL, only feature-based plasticity underlies task-irrelevant VPL. This model provides a new comprehensive framework in which apparently contradictory results could be explained.

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INTRODUCTION

It is well known that there is a temporal window, termed **critical period**, during which the visual system is highly plastic in one's early life and goes through a major rewiring that leads to acquisitions of important visual abilities (Hensch 2005a,b; Hubel & Wiesel 1964; Morishita & Hensch 2008). However, this does not indicate that after the critical period the visual system does not have the ability to learn or that the visual plasticity brake (inhibition of plasticity) is completely on. Extensive research findings indicate that as a result of visual experiences, an adult can acquire a new skill on a visual task and can maintain the skill for months or even years (Fahle & Poggio 2002, Fine & Jacobs 2002, Gilbert & Li 2012, Gold & Watanabe 2010, Goldstone 1998, Karmarkar & Dan 2006, Lu et al. 2011, Sagi 2011, Sagi & Tanne 1994, Sasaki & Watanabe 2012, Sasaki et al. 2010, Seitz & Dinse 2007). For example, it is extremely difficult to discriminate the sex of a chick. However, with training an adult can learn to do this extremely difficult task fairly precisely (Eagleman 2011). A radiologist can easily find cancer that most untrained observers would fail to see in an X-ray image. These examples indicate that it is possible to acquire some visual skills long after the critical period. The process and result of acquiring such visual skills is called visual perceptual learning (VPL). VPL is regarded as an important tool that can help clarify the basic mechanisms of visual and brain plasticity.

In addition, training on a visual task can significantly strengthen the visual abilities of adult patients with amblyopia and other forms of abnormal vision, which is regarded as an example of a highly successful translation of basic research findings into practical and powerful real-world applications (Andersen et al. 2010, Bennett et al. 2001, Levi & Li 2009a, Li et al. 2013, Ooi et al. 2013, Polat et al. 2004, Shibata & Watanabe 2012). Furthermore, it has been found that training of older people on a visual task leads to better performance (Andersen et al. 2010, Bower et al.

2013, Deloss et al. 2014). This raises the possibility that visual training of older people can restore or at least improve a variety of visual abilities that have declined with aging (Andersen 2012).

Thus, a clearer understanding of the mechanisms of VPL in adults should lead to new innovations in basic science and clinical intervention. For this reason, research on VPL has become increasingly popular, as evidenced by the fact that approximately 150 papers on VPL were published in 2013 alone.

In spite of the hope that a large volume of data accumulation would lead to clarification of the mechanism of VPL, which in turn would lead to the development of highly effective ways to greatly restore or improve damaged or deteriorated vision, the general tendency of the research field has been to oppose the establishment of such a mechanism. In reality, instead of different models converging on a unified view, several issues that highly relate to core mechanisms of VPL are becoming incrementally more controversial.

This review focuses on VPL of relatively primitive visual features including orientation, motion direction, and luminance contrast. Visual processing of a primitive feature has been better clarified than many other types of brain processing. Thus, a better understanding of the basic mechanism of learning of a primitive visual feature may lead to better clarification of learning of other sensory modalities, learning of more complex visual processing including visual categorization, and learning of more complex features such as objects and faces. A better understanding may also significantly contribute to the development of clinical methods to improve and/or restore visual abilities that have been damaged by diseases or have declined with aging. However, important differences exist between VPL of a primitive visual feature and these aspects of learning. Thus, interested readers should also read reviews on specialized fields, including (*a*) the learning of other sensory modalities (Beste & Dinse 2013, de Villers-Sidani & Merzenich 2011), more complex aspects (Ashby & Maddox 2011, Op de Beeck & Baker 2010), and faces (Bi et al. 2014); (*b*) the clinical applications of VPL (Levi 2012, Levi & Li 2009b); and (*c*) the effects of aging on VPL (Andersen 2012).

Active and passive natures exist in most types of learning and memory, and VPL is similarly classified into two types, task-relevant VPL and task-irrelevant VPL. Task-relevant VPL is defined as VPL of a feature that is relevant to a given task during training. Task-irrelevant VPL is defined as VPL of a feature that is irrelevant to a given task (Seitz & Watanabe 2005). We review research on task-relevant VPL, then task-irrelevant VPL, and finally propose a unified model to account for both task-relevant and task-irrelevant VPL.

TASK-RELEVANT VISUAL PERCEPTUAL LEARNING

One of the most controversial issues in task-relevant VPL is which stage/brain area of visual information processing is changed in association with task-relevant VPL. Most models of task-relevant VPL are roughly classified according to which stage/area is assumed to be associated with task-relevant VPL: the early-stage model, the mid-stage model, and the late-stage model. “Stage” is a term to be used for visual information processing, and “area” is an anatomically and/or neurophysiologically defined region in the brain. However, for simplification here we roughly regard V1 or the striate cortex (the first visual cortex, to which visual signals from the eyes are projected) as being in the earliest stage of visual cortical processing. V1 is known to process more primitive visual signals more locally, with smaller receptive fields than in higher visual areas (Hubel & Wiesel 1968, Roe & Ts'o 1995).

We regard the extrastriate areas, such as V2, V3, V4, and the middle-temporal area (MT or V5) as being in the mid stage. These areas respond to visual signals more globally than does V1. It has been suggested that V4 correlates with color constancy (Zeki 1993) and a surface

representation (Bouvier et al. 2008). MT (V5) of monkeys/humans and V3A of humans have been found to respond to global motion (Braddick et al. 2001, Koyama et al. 2005, Movshon et al. 1985, Newsome & Pare 1988, Rees et al. 2000, Tootell et al. 1997).

We regard any cortical areas that process visual signals beyond the mid stage as being the late stage. Whereas the early and mid stages consist of the visual cortex, in which visual signals from the eyes are processed and integrated, visual information beyond the visual cortex is processed in a more cognitive fashion. The late-stage areas include the lateral intraparietal sulcus (LIP) and dorsolateral prefrontal cortex. It has been found that LIP (Shadlen & Newsome 1996) and dorsolateral prefrontal cortex (Heekeren et al. 2004) correlate with visual decision.

Early-Stage Model

What is changed? This model assumes that task-relevant VPL is associated with changes in V1 (Adab & Vogels 2011; Adini et al. 2002; Bejjanki et al. 2011; Choi & Watanabe 2012; Crist et al. 1997; Dill & Fahle 1997; Fahle 2002; Fahle & Edelman 1993; Fahle & Poggio 2002; Gilbert & Li 2012; Harris & Fahle 1995; Karni & Sagi 1991, 1993; Schwartz et al. 2002; Xu et al. 2010, 2012a,b,c). A number of studies have shown that VPL is highly specific for the trained location, feature, and eye. With regard to location specificity, psychophysical studies have found that performance improvement on the trained feature that was presented in a specific location of the visual field during training is no longer observed if the same feature is presented even 1° or 2° shifted from the trained location (Ahissar & Hochstein 1997, Crist et al. 1997, Fahle & Edelman 1993, Fiorentini & Berardi 1980, Karni & Sagi 1991, McKee & Westheimer 1978, Poggio et al. 1992, Saarinen & Levi 1995, Shiu & Pashler 1992, Watanabe et al. 2002). Feature specificity has been found for visual features including orientation (Fiorentini & Berardi 1980, Poggio et al. 1992, Schoups et al. 1995) and motion direction (Ball & Sekuler 1987, Koyama et al. 2004, Vaina et al. 1998, Watanabe et al. 2002). Eye specificity indicates that VPL trained with one eye generally does not completely transfer to the other eye (Fahle & Poggio 2002; Karni & Sagi 1991, 1993), although that is not always the case (Schoups & Orban 1996). Because signals from the two different eyes are not converged until V1, incomplete transfer of VPL suggests that VPL is at least partially associated with changes before the conversion that starts in V1, although an alternate interpretation has also been proposed (Young et al. 2004).

On the basis of such specificity, it has been suggested that VPL occurs in V1, which was once thought to become hard-wired early in the human development process (i.e., so rigid that very little change occurred after an early critical period in life). It has been shown that this high specificity of a feature in VPL is in accord with neurophysiological findings that neurons in V1 tend to possess smaller receptive fields than those in higher areas (Felleman & Van Essen 1991, Zeki 1993). Orientation specificity tends to be higher in cells in low-level visual processing areas (Felleman & Van Essen 1991, Zeki 1993). In addition, it has been reported that external feedback regarding the correctness of a subject's responses (response feedback) is not necessary for VPL to occur (Fahle et al. 1995, Poggio et al. 1992). The featural specificity and lack of need for response feedback led some researchers to suggest that VPL occurs in the early visual system.

Results of some animal physiological studies suggest that changes occur in V1 in association with task-relevant VPL. As a result of training on an orientation discrimination task, slopes of the limbs of tuning curves of neurons most sensitive to differences in the discriminated orientations in monkey V1 increased (Schoups et al. 2001). In another study, although neither basic receptive field properties nor visual topography was changed in association with VPL, the influence of contextual stimuli placed outside the receptive field showed a change consistent with results of the trained discrimination (Crist et al. 2001). Perceptual learning improved contrast sensitivity in V1 neurons

DO RESPONSE CHANGES IN A BRAIN AREA SHOWN AFTER TRAINING ALWAYS INDICATE THAT PLASTICITY HAS OCCURRED IN THIS AREA?

Assume that as a result of training on a feature, responses to the feature in a cortical area (say, V1) have changed. In this case, it is premature to conclude that plasticity has occurred in V1 because at least one more possibility exists. That is, the changes in V1 could result from temporal feedback from a higher cortical area (say, V4) in which plasticity has actually occurred. In this case, the changes in V1 are not due to plasticity in V1 but merely reflect response changes in V4 due to plasticity. There are at least two ways to determine why changes have occurred. One is to test whether the response changes in V1 are correlated with response changes in any other area. If there is no correlation between response changes in V1 and any other area, it is likely that the plasticity has occurred in V1. In one study (Yotsumoto et al. 2008), BOLD signal changes in V1 observed for the first several weeks during training had no correlation with response changes in any other measured area. These results suggest that the activation changes in V1 are not likely to reflect plasticity in other measured areas. Another way to determine why changes have occurred is to examine eye specificity. This method can be applied only to cases in which plasticity has occurred in V1. Some types of VPL result from training on a stimulus presented to only one eye (trained eye) and do not transfer to the untrained eye. In such cases, response changes in V1 that are observed when tested with the trained eye yet are absent when tested with the untrained eye may suggest that plasticity related to the VPL occurred in V1 (Karni & Sagi 1991, 1993; Shibata et al. 2012b; Xu et al. 2012b), although another interpretation has been suggested (Young et al. 2004). The conjecture that plasticity was likely to have occurred in V1 is based on the fact that most monocular cells are found in V1, and feedback from an area higher than V1 does not specifically affect the V1 neurons that respond to signals from one eye.

in cats (Hua et al. 2010). By means of optogenetics, a cutting-edge technique in which specific neurons are sensitized by light, activation of a specific subtype of cortical inhibitory interneurons was induced. This activation led the mouse V1 to sharpen neuronal feature selectivity in V1 and improved perceptual discrimination (Lee et al. 2012).

A number of studies, including training on a contrast discrimination task (Furmanski et al. 2004) and a texture discrimination task (TDT) (Schwartz et al. 2002, Walker et al. 2005, Yotsumoto et al. 2008), have found that VPL is associated with increases in the blood-oxygenation-level-dependent (BOLD) signal in the region of V1 in humans that corresponds to the location of the trained stimulus. It has been found that within the first few weeks of training, performance on TDT increased and the BOLD signal in the trained region of V1 increased (Yotsumoto et al. 2008). However, after the performance increase saturated, brain activation in V1 decreased to the level observed before training, whereas the high performance was retained. In that case, no systematic activity change particularly in the region or hemisphere corresponding to the trained location was observed in any other brain area. This rules out the possibility that top-down influence or feedback from a higher cortical area(s) modulates V1 activation changes (see sidebar Do Response Changes in a Brain Area Shown after Training Always Indicate That Plasticity Has Occurred in This Area?).

Another study found that during non-rapid eye movement (N-REM) sleep following training on the texture discrimination task, a significantly higher BOLD signal was observed in the trained visual quadrant of V1 than in another quadrant (Yotsumoto et al. 2009). It has been found that BOLD signals are better correlated with field potential than action potential and reflect the input of activity to intracortical processing of a given area from another area(s) rather than the area's action potential output (Logothetis et al. 2001). This finding might lead one to think that BOLD signal activation in V1, for example, reflects the input of activity to V1 from a higher area. However, most research that showed V1 changes did not find any systematic activity change in higher areas.

WHAT IS INVOLVED VERSUS WHAT IS CHANGED

In some cases, what is involved during training is confused with what is changed by training (**Figure 4**). During training on a visual task, attention and/or reinforcement processing may be involved in order for subjects to perform the task. For example, if subjects are asked to judge whether two successively presented orientations are the same or different in a task during training, they have to direct attention to the presented orientations. In this case, there is no doubt that focused attention is involved, which indicates that the source mechanism of focused attention is used and areas corresponding to that specific mechanism are activated. However, this does not necessarily indicate that VPL is caused or associated with changes in the attention source mechanism. Likewise, in some cases during training reinforcement, processing may play an important role in forming VPL, but this does not necessarily indicate that reinforcement processing itself is changed in association with VPL.

Thus, it is reasonable to assume that BOLD changes in V1 correspond to those in neural circuits within V1.

How is the early stage changed? It is generally assumed that attention or feedback to V1 during training plays an important role in forming task-relevant VPL. Several studies have found cases in which a task-irrelevant feature that is presented while a subject is performing a task on another feature during training does not lead to learning of the task-irrelevant feature (Ahissar & Hochstein 1993, Schoups et al. 2001, Shiu & Pashler 1992). It has also been found that in some cases perceptual learning of a task on a feature does not transfer to another task on the trained feature (Huang et al. 2007, Westheimer et al. 2001). These findings suggest that attention/feedback signals play an important role in sending signals that are highly specific for the trained feature and/or task, possibly to lower-level stages.

Ahissar & Hochstein (1993) have found that as task difficulty increases, VPL becomes more specific with respect to both orientation and position, and they suggested that as perceptual learning proceeds, the stage/cortical area involved in VPL becomes lower. This so-called reversed hierarchical model has been influential in VPL research and in other fields in visual sciences (Ahissar & Hochstein 1997, Hochstein & Ahissar 2002). For example, discrimination between two relatively distant orientations can be successfully performed in a high visual stage that processes relatively coarse orientation and location signals. However, if fine-grained orientation discrimination is required, a lower visual area that processes finer orientation and location signals needs to be used and learned, and attention is regarded as an important driving factor (Hochstein & Ahissar 2002).

Fahle (2009) has also suggested that for easy tasks, elaboration of top-down influences usually is not required, and learning is restricted to late-stage selection of the appropriate signals on higher cortical levels, which seems easier and faster to achieve. However, to reach the absolute limits of sensory performance, VPL seems to optimize the entire chain of sensory processing (Fahle 2009). These models assume that demands to improve a task ultimately require changes in V1 in which primitive visual features including orientation and spatial frequency are processed highly locally. Furthermore, horizontal connections have also been observed within V1 (Ts'o & Gilbert 1988). Gilbert and his colleagues (Piech et al. 2013) assume that feedback signals driven by a task demand interact with horizontal connections in V1 and change the local gains in V1 that are associated with perceptual learning. Note that although these models assume an important role of attention in task-relevant VPL, they do not assume that the attentional system or higher-level cognitive processing related to attention is changed in association with task-relevant VPL (see sidebar What Is Involved Versus What Is Changed?).

Mid-Stage Model

What is changed? Some studies have suggested that VPL is not associated with changes at the early stage such as V1 but rather with changes at the mid stage. As aforementioned, the mid stage includes V2, V3, V4, and MT (V5). Here we review psychophysical and neurophysiological studies.

In psychophysics, it has been found that some types of VPL depend on perceptual constancy that corresponds to stable representation of certain properties of an object despite variable visual input. Such representation is thought to occur in the mid visual stage (Garrigan & Kellman 2008). Although training on a task of discriminating close motion directions or orientations leads to VPL specific to the trained direction (Ball & Sekuler 1987) or orientation (Ahissar & Hochstein 1993), learning by training in discriminating larger direction or orientation differences transfers to untrained directions (Ahissar & Hochstein 1993, Liu 1999). These results suggest that in some conditions VPL occurs in the mid stage, in which location and feature signals are less specific in comparison with V1. As aforementioned, the reversed hierarchy model (Ahissar & Hochstein 1997, Hochstein & Ahissar 2002) indicates that VPL proceeds from higher to lower stages including V1. Thus, in this model it would be natural to assume that VPL starts with some mid-level stage. However, note that in psychophysics the distinction between the mid and late stages is not highly clear, and results that seem to support the mid-stage changes could also be interpreted as changes in the late stage.

In studies involving V4 of monkeys, tuning properties changed in association with VPL of an orientation discrimination task (Yang & Maunsell 2004). However, no tuning change was observed in V1 (Ghose et al. 2002, Yang & Maunsell 2004). In another monkey study (Chowdhury & DeAngelis 2008), inactivation of MT by injection of the gamma-aminobutyric acid agonist muscimol prior to coarse absolute depth discrimination training was shown to impair performance. However, fine relative depth discrimination training with MT inactivation neither impaired coarse depth discrimination nor led to changes in the disparity tuning of MT neurons. The authors concluded that when MT activation is inhibited, other areas in the ventral visual pathway are recruited and mediate coarse depth discrimination.

It has been found that VPL of discrimination of coherent motion directions is associated with changes in V3A of humans (Shibata et al. 2012a). In this study, behavioral tuning function changes after global motion detection training were compared with decoded tuning function changes for eight visual areas using pattern classification analysis of BOLD signals (Kamitani & Tong 2005). It was found that the behavioral tuning function changes were extremely highly correlated to decoded tuning function changes only in V3A (Shibata et al. 2012a), which is known to be highly responsive to global motion with human subjects (Braddick et al. 2001, Koyama et al. 2005).

How is the mid stage changed? Doshier, Lu, and colleagues have built a reweighting model of perceptual learning that has been highly influential in VPL research (Doshier & Lu 1998; Liu et al. 2010; Lu et al. 2005; Petrov et al. 2005, 2006). The model assumes that VPL occurs because of two independent mechanisms, improved filtering of external noise and removal of internal noise. The investigators assumed that selective reweighting or read-out of connections between V1 and a decision unit (that is, the mid stage) leads to reductions of these two noises (Doshier & Lu 1998). V1 was regarded as a place for stimulus representation in which spatiotemporal filtering occurs. This model assumes no change in the stimulus representation and therefore does not support the model in which task-relevant VPL occurs due to changes in the stimulus representation and therefore V1 (Petrov et al. 2005).

Recently, the model has been modified to include both location-specific and location-independent representations (Doshier et al. 2013) to explain location transfer demonstrated by double training (Wang et al. 2012, Xiao et al. 2008, Zhang et al. 2010a), which is discussed in the late-stage section. Based on their analysis of data indicating that responses of neurons in LIP, but not in MT, were changed in association with VPL of coherent motion (Law & Gold 2008), investigators have suggested that weighting changes occur between MT and LIP (Gold et al. 2008). Although these reweighting models do not assume changes in V1, it has been pointed out that theoretically speaking, VPL can result from weighting changes in the feedforward connections between the thalamus and V1 (Bejjanki et al. 2011).

Late-Stage Model

The role of the late stage, which is defined as all processing higher than mid stage, in task-relevant VPL has been much more emphasized owing to a number of recent physiological and psychophysical studies.

What is changed? As a result of training on a shape identification task, resting state functional connectivity and directed mutual interactions between trained mid-visual areas and frontal-parietal areas involved in the control of spatial attention were modified (Lewis et al. 2009). In addition, in association with VPL of a visual discrimination task, individual differences in performance changes that resulted from the training are related to spontaneous cortical activity between early- and mid-level visual cortices and also between visual cortex and prefrontal association areas. These results suggest that changes associated with task-relevant VPL include changes in connectivity involving an attentional source system (Baldassarre et al. 2012). Another study found that behavioral improvements in an orientation discrimination task occur with activity changes in the anterior cingulate cortex, which suggests that perceptual learning is associated with changes in a high-level cognitive area (Kahnt et al. 2011).

Gold and his colleagues found that perceptual learning of coarse coherent motion direction discrimination was associated with tuning property changes in LIP, an area known to be involved in perceptual decision making (Shadlen & Newsome 2001), but not in MT, an area belonging to the mid stage (Law & Gold 2008). As discussed in the mid-stage model section, the model proposed by this group assumes reweighting in connections between MT and LIP (Gold et al. 2009). However, another possibility that is not mutually exclusive to the reweighting model is that at least VPL of coarse motion direction discrimination is associated with changes in decision factors including a decision criterion, which is reflected in LIP response changes (M.N. Shadlen, personal communication).

In psychophysics, there has been a breakthrough finding with regard to transfer of VPL. Training on a feature (e.g., contrast) at one location and additional training with another feature/task (e.g., orientation) at a second location resulted in a complete transfer of the first learning (e.g., contrast) to the second location (Xiao et al. 2008). On the basis of a series of interesting experiments (Wang et al. 2012, Xiao et al. 2008, Zhang et al. 2010a), Yu and his colleagues have built a model in which task-relevant VPL is associated only with changes in the late stage, which is involved in decision making and the source of attention from which top-down signal is exerted. In this model, location specificity of task-relevant VPL results from long-term inhibition from the cognitive system on all locations in the visual field except the trained location. When training on a second task occurs in a different location than the previously trained location, the connection between the late stage and this location is reactivated, and the inhibition to the location is released. As a result, VPL of the original task is transferred to the location that was trained for the second

task (Xiao et al. 2008). The group led by Sagi also suggests that the transfer of task-relevant VPL results from the abolishment of the link between the early stage and late stage (Harris et al. 2012). However, the models by the Yu group and the Sagi group are fundamentally different. Whereas the Yu group assumes that the link between the early and late stages has been made and kept by the late stage (Xiao et al. 2008), the Sagi group assumes that the location signals from the early stage constrain location specificity of task-relevant VPL (Harris et al. 2012).

Summary of Task-Relevant Visual Perceptual Learning

Task-relevant VPL is roughly classified into the early-stage model, the mid-stage model, and the late-stage model, according to the stage at which processing or mechanisms are changed in association with task-relevant VPL. One possible explanation for such a variety of models is that studies have used highly different experimental conditions with different parameter sets. Despite the variety of methods employed, many investigators overgeneralize their results and draw conclusions as if their specific results can be applied to all types of VPL. However, it is not either certain or even likely that all types of task-relevant VPL are subserved by only one stage. The variance of experimental parameters leaves open the possibility that VPL is subserved by multiple mechanisms.

TASK-IRRELEVANT VISUAL PERCEPTUAL LEARNING

What Is Task-Irrelevant Visual Perceptual Learning?

The previous section focuses on task-relevant VPL, in which performance increase on a task and/or feature occurs as a result of training on the task and/or the feature. In a 2001 study, it was found that a performance increase also occurs as a result of mere exposure to a feature that is irrelevant and subthreshold to a given task during training (Watanabe et al. 2001). In that study, 5% coherent motion was presented in the background while subjects repeatedly performed a rapid serial visual presentation (RSVP) task that required them to report two white letters in a sequence of otherwise black letters. In the pre- and posttests, the performance on the same exposed 5% coherent motion direction was approximately chance level and therefore subthreshold, whereas a significant performance improvement was observed on the same motion direction with 10% coherency, which was suprathreshold.

These results indicate that mere exposure to coherent motion that is task irrelevant and subthreshold induces learning. It is highly unlikely for focused attention to be kept on such a task-irrelevant and subthreshold direction; therefore, it was concluded that VPL of a feature occurs without enduring focused attention being directed to the feature. This new type of VPL was termed task-irrelevant VPL. A number of subsequent studies have reported task-irrelevant VPL (Barbot et al. 2011; Baumann et al. 2008; Beste & Dinse 2013; Beste et al. 2011; Carrasco et al. 2008; Gutnisky et al. 2009; Leclercq et al. 2014; Leclercq & Seitz 2012; Rosenthal & Humphreys 2010; Seitz & Watanabe 2003, 2005; Seitz et al. 2005b; Tsushima et al. 2008; Watanabe et al. 2002; Xu et al. 2012b; Zhang & Kourtzi 2010; Zhang et al. 2010b).

Reinforcement and Task-Irrelevant Visual Perceptual Learning

Further studies found that task-irrelevant VPL, at least in a setting similar to that in the 2001 study by the Watanabe group, does not occur without the involvement of reinforcing factors. Task-irrelevant VPL occurs only when the exposed 5% coherent motion direction is paired with

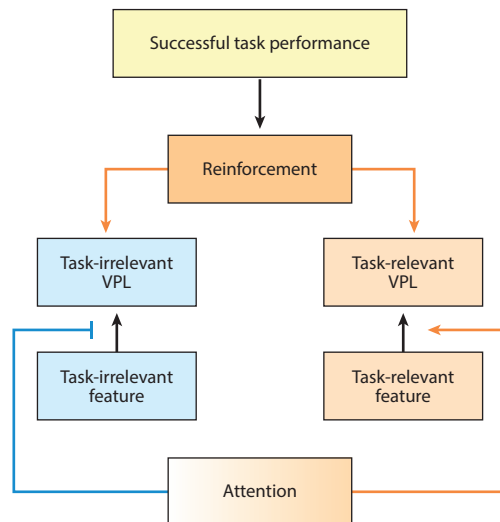


Figure 1

Roles of attention and reinforcement signals in task-relevant and task-irrelevant visual perceptual learning (VPL). The model assumes that VPL results from interactions between spatially diffusive reinforcement signals that are triggered by successful task performance and bottom-up signals from a feature presented during training, irrespective of whether the feature is task relevant or task irrelevant. Attention enhances bottom-up signals from a task-relevant feature, whereas it decreases or suppresses signals from a task-irrelevant feature. Orange arrows represent excitatory stimulation; blue line represents inhibitory stimulation. Task-irrelevant VPL occurs only when task-irrelevant feature signals are so weak that the signals fail to be detected and therefore are not suppressed by an attentional system. However, it is noteworthy that if a task-irrelevant feature is presented in an environment optimal to the feature, task-irrelevant learning can occur if the feature is suprathreshold. Task-relevant VPL and task-irrelevant VPL are location specific due to constraints from the bottom-up signals from a feature presented during training.

a target in an RSVP task (Seitz & Watanabe 2003) and only when subjects make correct detections on targets, which might cause **internal reward or satisfaction** (Seitz et al. 2005a). Furthermore, VPL of the task-irrelevant 5% coherent motion direction occurs when the feature is paired with a reward and does not occur without a reward (Seitz et al. 2009).

On the basis of these findings, Seitz and Watanabe built a unified model in which task-relevant VPL as well as task-irrelevant VPL results from interactions between spatially diffusive reinforcement signals and bottom-up signals from an exposed stimulus feature (role of reinforcement signal in VPL in **Figure 1**). Reinforcement signals arise when subjects are given an external reward or when they have conducted a successful task performance. The bottom-up signals are either from a task-relevant or task-irrelevant feature. In that schema, task-relevant and task-irrelevant VPL share the same underlying principles (Seitz & Watanabe 2005).

Attention and Task-Irrelevant Visual Perceptual Learning

Later findings have suggested that the mechanism or processing that leads to task-irrelevant VPL is not exactly the same as that for task-relevant VPL. Several aspects could reveal differences between mechanisms of the two types of VPL.

First, there are differential effects of cognitive control on the two types. In one study, the coherence (and therefore detectability) of a task-irrelevant motion signal was varied during the performance of a central task (Tsushima et al. 2008). Task-irrelevant VPL occurred only

when the coherent motion signal was below or close to the detection threshold. This result is consistent with a model in which a cognitive control system fails to detect weak or below-threshold task-irrelevant signals and therefore fails to suppress these signals, thus ending up allowing the nonsuppressed signals to exert an influence on information processing to a greater degree than that of originally stronger task-irrelevant signals that can be detected by the attentional system (Tsushima et al. 2006, Tsushima & Watanabe 2009; roles of attention in VPL in **Figure 1**).

At the same time, it is noticeable that in conditions in which task-irrelevant features are above thresholds, task-irrelevant learning occurs. For example, if a suprathreshold task-irrelevant feature is presented spatially distant from a task-relevant feature, learning occurs on the task-irrelevant feature (Watanabe et al. 2002). In a configuration in which the same two suprathreshold features, one task relevant and the other task irrelevant, are presented at different locations, feature-based attention could enhance both features so that task-irrelevant learning may occur (Gutnisky et al. 2009). Exposure to passive low-frequency suprathreshold stimulation of irrelevant orientation improved subsequent performance on the orientation (Beste et al. 2011). Seitz & Dinse (2007) have suggested that task-irrelevant VPL could occur in a condition in which a stimulus environment is optimal to a task-irrelevant feature if the feature is not weak or subthreshold.

Second, task involvement of the trained feature in task-relevant VPL distinguishes its mechanism from task-irrelevant VPL. If task-relevant VPL is at least partially associated with changes in processing of the trained task, the mechanisms of task-relevant VPL should not be the same as the mechanisms of task-irrelevant VPL. As discussed in the previous section, in some cases VPL of one task on a feature does not completely transfer to a different task on the same or similar feature (Huang et al. 2007, Westheimer et al. 2001). This indicates that task-relevant VPL is at least partially associated with changes in the mechanism specific for the trained task, which should not be shared with task-irrelevant VPL.

In another study, double dissociation between task-relevant and task-irrelevant VPL was observed (Beste et al. 2011). First, subjects were asked to conduct a change-detection task on luminance changes; orientation changes were task irrelevant. This task performance was followed by exposure to passive visual high- or low-frequency stimulation of either the relevant luminance or irrelevant orientation feature. High-frequency stimulation using luminance enhanced performance to detect luminance changes, whereas low-frequency stimulation impaired performance. In contrast, low-frequency exposure of orientation as task irrelevant impaired performance, whereas high-frequency orientation stimulation enhanced performance. These results also suggest that task-irrelevant VPL does not share the exact same mechanism as task-relevant VPL.

Patterns of activation similar to the pattern evoked by the presentation of a real and specific target orientation stimulus were induced in V1 and V2 using a new functional magnetic resonance imaging online neurofeedback method (Shibata et al. 2011). These patterns were repeatedly induced without external stimulus presentation and without the subjects' knowledge of what was being induced. As a result, sensitivity only to the target orientation significantly improved. That is, mere repetition of an activity pattern in V1 and V2 corresponding to a feature may be sufficient to induce VPL of that feature. The results also indicate that at least the plasticity with no direct involvement of task training can occur in V1 and V2. This plasticity could manifest as task-irrelevant VPL.

Several studies have compared activations that are related to task-relevant and task-irrelevant learning. One study measured BOLD signals evoked when subjects discriminated the spatial frequency of gratings presented with the same or orthogonal orientation (Baumann et al. 2008). The BOLD signals were significantly higher in V1 and V2 when the gratings had an orthogonal orientation compared to when they had the same orientation. In contrast, the task-irrelevant

stimulus property (orientation) had no significant effect on the prefrontal and intraparietal cortex. The combined results of these studies indicate that it may be plausible to think that task-irrelevant VPL is associated with changes in early stage, whereas task-relevant VPL is associated with changes in higher stages.

Summary of Task-Irrelevant Visual Perceptual Learning

It has been suggested that both task-relevant and task-irrelevant VPL at least partially result from interactions between reinforcement signals and bottom-up signals from the presented feature, irrespective of whether the feature is task relevant or task irrelevant (Seitz & Watanabe 2005). However, different aspects of mechanisms seem to be involved in these two types of VPL. One aspect is the differential effects of attentional control. A task-relevant feature is enhanced by attention, whereas task-irrelevant features may be suppressed if the features are suprathreshold and are detected by the attentional system (Tsushima et al. 2006, 2008; Tsushima & Watanabe 2009). Thus, task-irrelevant VPL of a feature occurs only if the feature is subthreshold or is not salient and therefore cannot be detected by the attentional system, unless a given environment is optimal for task-irrelevant learning. Another aspect is that although task-relevant VPL may be at least partially associated with changes in processing specific for the trained task, task-irrelevant VPL is not (**Figure 1**). Results of recent human imaging studies (Baumann et al. 2008, Shibata et al. 2011, Zhang et al. 2010b) suggest that task-irrelevant VPL is associated with the early or mid stage, whereas changes resulting from training on a task are associated with later stages.

DUAL PLASTICITY MODEL OF VISUAL PERCEPTUAL LEARNING

Background

Although a vast number of results concerning VPL have accumulated, there is no consensus about its mechanism. An unfortunate tendency is for the advocates of one model of task-relevant VPL to deny the evidence of another model and to build a detailed framework that supports only one view of the aforementioned controversies or to draw a conclusion as to what is changed based on the assumption that one model is correct (Jain & Zaidi 2011). In addition, none of the models of task-relevant VPL can satisfactorily explain task-irrelevant VPL. Since it is highly unlikely that the basic mechanisms of task-relevant and task-irrelevant VPL are completely different, it is necessary to build a model that can explain both.

To resolve these issues, we propose a dual plasticity model of VPL that could resolve the issues and account for most of the accumulated data, including those that appear to contradict each other. The dual plasticity model incorporates the controversy as to what stage is associated with task-relevant VPL and the mechanisms of both task-relevant VPL and task-irrelevant VPL. First we describe the dual plasticity model and then discuss the rationalizations for the framework.

Assumptions of the Dual Plasticity Model

Here we propose that there are at least two different types of plasticity, feature-based plasticity and task-based plasticity. These types result from differences in processing during training, include changes in different stages, and occur at different timings (**Figure 2**). Feature-based plasticity is defined as changes in a representation of features. Task-based plasticity is defined as changes in processing related to a trained task.

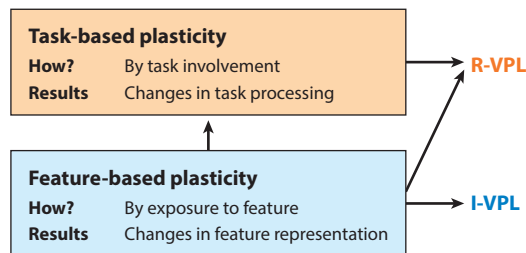


Figure 2

Schematic illustration of the dual plasticity model. In this model, there are two types of plasticity, feature-based plasticity and task-based plasticity. Feature-based plasticity results from the exposure to a feature during training, irrespective of whether the feature is task relevant or task irrelevant. Feature-based plasticity reflects changes in feature representation and constrains visual perceptual learning (VPL) to the trained feature and location. Task-based plasticity arises as a result of involvement of a given task during training. Task-based plasticity reflects changes in task processing and constrains VPL to the trained task. Task-relevant VPL (R-VPL) consists of feature-based plasticity and task-based plasticity. Task-irrelevant VPL (I-VPL) consists of only feature-based plasticity.

How does feature-based plasticity occur? We assume that feature-based plasticity follows our reinforcement model (Seitz & Watanabe 2005). In this model, both task-relevant and task-irrelevant features are learned as a result of interactions between spatially diffusive reinforcement signals and bottom-up signals from a feature exposed during training, irrespective of whether the feature is task-relevant or task-irrelevant. Basic changes in the representation of the exposed feature are constant, irrespective of whether the feature is task relevant or task irrelevant and, if the feature is task relevant, regardless of what kind of task on the feature is trained. However, the overall amplitude of changes, including no change, depends on the rules of cognitive control, as discussed in the early-stage change section. If an exposed task-irrelevant feature is strong, the feature is detected and suppressed by a cognitive control system. If the feature is weak and is not detected by the cognitive control system, the feature is not suppressed, and feature-based plasticity on the feature occurs (Tsushima et al. 2006, 2008). In contrast, a relevant feature is enhanced rather than suppressed by the cognitive control system (**Figure 1**). Whereas Seitz & Watanabe (2005) assumed that the reinforcement mechanism is for the whole model of task-relevant and task-irrelevant VPL, here we propose that this reinforcement mechanism is for feature-based plasticity (**Figure 3**). To explain the whole mechanism of VPL, we now believe that not only feature-based plasticity but also task-based plasticity and its interactions with feature-based plasticity must be assumed.

How does task-based plasticity occur? Task-based plasticity occurs as a result of involvement of a trained task rather than exposure to a feature, as in feature-based plasticity. Thus, training on different tasks (e.g., detection task versus discrimination task) with the same feature (e.g., orientation) can lead to qualitatively different changes in task-based plasticity.

Where do feature-based plasticity and task-based plasticity occur? We assume that feature-based plasticity is a change in a feature representation and occurs in the early or mid stages, depending on the feature on which feature-based plasticity occurs. If a feature is highly primitive or is made as a result of long-range connections in V1 (Gilbert 1994), feature-based plasticity of the feature should occur in V1 that belongs to the early stage. If a feature is more complex and is made of components of more primitive features, feature-based plasticity may occur in the mid stage. For example, orientation starts being processed in V1 in the cortex (Hubel & Wiesel 1968). Thus, the areas in which feature-based plasticity occurs may include V1. Coherent

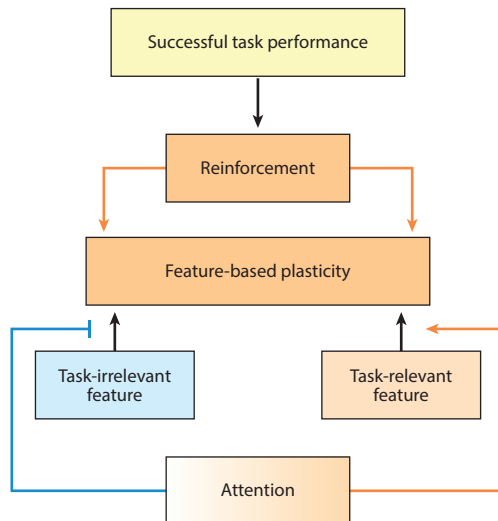


Figure 3

Model of the mechanism of feature-based plasticity. Task-relevant VPL is subserved by this feature-based plasticity mechanism as well as by task-based plasticity that results from performing a given task during training and is also specific for the trained task. Task-irrelevant VPL is subserved only by this feature-based plasticity mechanism. Orange arrows represent excitatory stimulation; blue arrows represent inhibitory stimulation.

motion consists of coherently moving dots and randomly moving dots from one temporal frame to another. V3A/MT in humans (Braddick et al. 2001, Koyama et al. 2005, Rees et al. 2000) or MT in monkeys (Newsome & Pare 1988) responds to a greater degree and/or more selectively to coherent motion than random motion. Thus, feature-based plasticity of coherent motion may occur in areas including V3A/MT in humans and MT in monkeys, which belongs to the mid stage.

Feature-based and task-based plasticity and task-relevant and task-irrelevant VPL. We assume that task-relevant VPL consists of both feature-based plasticity and task-based plasticity, whereas task-irrelevant VPL consists of only feature-based plasticity. Thus, task-relevant and task-irrelevant VPL partially share the same mechanism of feature-based plasticity.

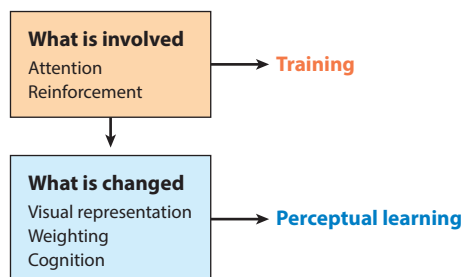


Figure 4

The distinction between what is involved during training on a task and what is changed in association with visual perceptual learning of the task. What is involved is not necessarily the same as what is changed.

Specificity and transfer of feature-based plasticity and task-based plasticity. Feature-based plasticity is specific for an exposed feature and the location in which the feature was presented during training. Task-based plasticity is specific for the trained task. Task-irrelevant VPL is constrained by the specificity from the feature-based plasticity (feature and location). Task-relevant VPL is constrained by the specificity from the feature-based plasticity (feature and location) and also by the specificity from the task-based plasticity. If feature-based specificity is abolished in task-relevant VPL as a result of an experimental manipulation, the feature-based constraints should be eliminated. As a result, VPL of the trained task should be transferred to different locations/features (Harris et al. 2012). If task-based plasticity is eliminated in task-relevant VPL of a feature, VPL of the feature should be transferred to other tasks.

Empirical Studies for the Dual Plasticity Model

The results of several significant studies are in accord with the dual plasticity model. First, during training in one study (Watanabe et al. 2002), an RSVP task was performed at the center of the display while a global motion stimulus, in which local dots moved in random directions within a certain range, was being presented in the background (Watanabe et al. 1989). There are two types of perceived motion in this type of stimulus: the local motion signals of the individual dots and a global motion whose direction corresponds to the spatiotemporal average of local motion signals in the display. The range of local motion directions was varied across different subject groups. As a result, performance increased for all measured motion directions within the range of exposed local motion but not for the global motion. This indicates that VPL occurred for task-irrelevant local motion directions but not for the global motion direction.

In another experiment of the same study, a discrimination task on global motion direction was conducted during training. In this condition, the global motion direction was task relevant. In the earlier phase of training, performance increased within the range of local motion, as in the first experiment in which global motion was task irrelevant. However, in the later phase, performance improved only around the trained directions. From these results it was concluded, “The learning gain for a range of local motion was obtained irrespective of whether the global motion was task-relevant or task-irrelevant. Surprisingly, in a later phase learning gain was obtained only for the task-relevant global motion direction, i.e. only in response to task demand. . . . Based on these findings we propose that task-driven (relevant) learning and task-irrelevant learning of motion may not be processed in the same fashion. Task-irrelevant learning of motion may occur only at a very low-level stage and is processed rather independently of global motion, whether global motion is task-relevant or irrelevant. In contrast, task-driven (relevant) learning may occur in multiple stages” (Watanabe et al. 2002, pp. 4–5).

These results are in accord with the dual plasticity model. That is, the learning gain for a range of local motion is regarded as a manifestation of feature-based plasticity, and the learning gain only for a task-relevant global motion direction is regarded as a manifestation of task-based plasticity.

Second, the Sagi group applied an operation that abolishes orientation adaptation to the orientation trained by the TDT and found that the location specificity observed in VPL of the TDT was eliminated (Harris et al. 2012). This finding is in accord with the dual plasticity model. The results suggest that a type of learning in the early stage constrains the location of VPL to the location of the trained stimulus, whereas another type of learning is related to improvement in task performance (Harris et al. 2012). These proposed two types of learning can correspond to feature-based and task-based plasticity of task-relevant VPL.

Third, learning of a collinearity (regularities in natural contours) occurs by simple exposure without task involvement and is associated with activation by occipitotemporal areas (early and mid

stages), whereas learning to integrate line segments orthogonal to contour paths requires specific training and also is associated with activity enhancement in intraparietal regions that mediate attentional processing (Zhang et al. 2010b). Although this study used different stimuli in different conditions and cannot rule out the possibility that the line segments orthogonal to contour paths themselves are processed in higher stages than are collinear segments, the results suggest that learning due to training with a task is associated with higher stages than is training without a task.

Recently, Shibata and his colleagues (2013) conducted a brain imaging experiment to test the validity of an important aspect of the dual plasticity model. In test stages that were conducted before and after training on detection of coherent motion, BOLD signals were measured in two conditions: a feature-based condition and a task-based condition. In the feature-based condition, a central RSVP task was conducted while the same motion as the trained motion was presented as task irrelevant. In the task-based condition, the same task on the trained motion was conducted. The results showed that V3A, which is known to be highly responsive to coherent motion (Braddick et al. 2001, Koyama et al. 2005), was significantly more activated in the posttest than in the pretest in both the feature-based and task-based conditions. However, multiple areas—including the intraparietal sulcus, which includes the human homologue of monkey LIP—were significantly more activated in the posttest than in the pretest only in the task-based condition. These results are in accord with a key aspect of the dual plasticity model; that is, feature-based plasticity is associated with the changes in representation of a feature, which should be manifested when the feature is presented irrespective of whether the feature is task relevant or task irrelevant. Task-based plasticity is associated with the changes in processing related to the trained task, which should be manifested only while the same task as in training is conducted.

Dual Plasticity Model and Existing Models

How does task-relevant VPL occur? At least two aspects of the dual plasticity model clearly distinguish it from other models of VPL. First, no other model comprehensively explains both task-relevant VPL and task-irrelevant VPL. In the dual plasticity model, task-relevant VPL is associated with both feature-based plasticity and task-based plasticity, whereas task-irrelevant VPL is associated only with feature-based plasticity. Second, to our knowledge all other models assume that task-relevant VPL results from task involvement. These models do not consider the possibility that even task-relevant VPL results from exposure to the trained feature, as in the dual plasticity model.

What is changed? Most models assume that task-relevant VPL is associated with changes at only one of the early, mid, or late stages. Results that support models assuming changes in one stage tend to be ignored by researchers who support models assuming changes in another stage. In contrast, the dual plasticity model assumes that task-relevant VPL is associated with changes in more than one stage, which could comprehensively explain apparently conflicting results.

As discussed above, many early-stage models assume that what is changed is a representation of the trained feature; this assumption is based on experimental results that show high specificity of VPL for the trained location, feature, and eye as well as results indicating that VPL is associated with changes in responses in early visual areas (Adini et al. 2002; Crist et al. 1997; Dill & Fahle 1997; Fahle 2002; Fahle & Edelman 1993; Fahle & Poggio 2002; Gilbert 1994; Harris & Fahle 1995; Karni & Sagi 1991, 1993; Xu et al. 2010, 2012a,b,c; Yang & Maunsell 2004; but see Bejjanki et al. 2011). Double training leads to transfer of one type of task-relevant VPL to another location at which another task is trained or a feature is exposed. It is difficult for these early-stage models to explain transfer of location and features (Wang et al. 2012; Xiao et al. 2008; Zhang et al. 2008,

2010a,b). In addition, it is impossible for the early-stage models alone to explain response changes in higher areas belonging to the late stage (Baldassarre et al. 2012, Kahnt et al. 2011, Law & Gold 2008).

Most mid-stage and late-stage models assume that what is changed is selective reweighting or read-out of connections between different areas (Chowdhury & DeAngelis 2008; Doshier et al. 2004; Doshier & Lu 1998, 1999; Gold et al. 2009; Gu et al. 2012; Kahnt et al. 2011; Lewis et al. 2009; Liu et al. 2010; Petrov et al. 2005; Xiao et al. 2008; Zhang et al. 2008, 2010a,b). However, these models on their own cannot explain the finding that V1 is changed in association with task-relevant VPL or incomplete interocular transfer (transfer of VPL trained with one eye to the other eye) (Karni & Sagi 1991, 1993; Shibata et al. 2012b; Xu et al. 2012b). The dual plasticity model can comprehensively explain changes at the low-, mid- and late stages.

Early-stage model and the dual plasticity model. Most results that have been regarded as evidence for the early-stage model are in accord with the feature-based plasticity of our dual plasticity model, which corresponds to changes in a representation of a feature presented during training. Specificity of the trained feature including its location is in accord with the hypothesis that such specificity is in the changed representation and constrains the performance of VPL (Harris et al. 2012). Tuning curve changes in the early- and mid-stage areas (Hua et al. 2010, Schoups et al. 2001, Yang & Maunsell 2004) may be related to changes in the representation. BOLD signal enhancement in the trained location (Furmanski et al. 2004, Schwartz et al. 2002, Walker et al. 2005, Yotsumoto et al. 2008) is also consistent with the hypothesis that feature-based plasticity occurs in an earlier stage than does task-based plasticity. In addition, an online functional magnetic resonance imaging neurofeedback method repetitively induced the activations only in the subjects' early visual cortex that corresponded to the pattern of activation evoked by the presentation of a real target orientation. As a result, VPL of the orientation occurred. This finding is in accord with some properties of feature-based plasticity, including changes in V1 and no task involvement (Shibata et al. 2011).

Mid- and late-stage models and the dual plasticity model. As discussed above, it is difficult for the late-stage model or the mid-stage model to explain transfer from the trained to untrained locations unless there is an additional stage or processing where no location specificity is assumed (Doshier et al. 2013). In the dual plasticity model, transfer of VPL to a new location could be interpreted as a result of development of a new link between the new location and the task-based plasticity. If the link between feature-based plasticity and task-based plasticity is completely eliminated, task-relevant VPL should have no specificity, as found in Harris et al. (2012).

One of the most influential models that assume changes in the mid stage is the reweighting model (Doshier & Lu 1998; Gold et al. 2008; Liu et al. 2010; Lu et al. 2005; Petrov et al. 2005, 2006). The dual plasticity model does not contradict the reweighting principle. Task-based plasticity could occur as a result of changes in task-driven processing that could result from reweighting between visual areas and cognitive areas.

Summary of the Dual Plasticity Model

The dual plasticity model consists of feature-based plasticity and task-based plasticity. Feature-based plasticity results from changes in a representation of a feature presented during training, irrespective of whether it is task relevant or task irrelevant. Task-based plasticity arises as a result of involvement in a task, irrespective of the trained feature. Task-relevant VPL consists of feature-based plasticity and task-based plasticity. In this case, feature-based plasticity constrains the trained

location of task-relevant VPL. In contrast, task-irrelevant VPL consists only of feature-based plasticity. Thus, task-relevant VPL and task-irrelevant VPL are not completely different; rather, they are commonly subserved by feature-based plasticity.

The dual plasticity model is still a schematic model. Detailed mechanisms of the two types of plasticity and links of these two types have yet to be developed. However, currently most mechanistic models are based on one or two of the three views (early-, mid- and late-stage models) and cannot explain empirical results supporting the other view(s). Moreover, none of the mechanistic models of VPL can explain both task-relevant and task-irrelevant VPL. Thus, it would be fruitful and constructive to build a schematic and comprehensive model as the first step.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Researchers hoped that accumulation of VPL data would lead to the elucidation of general rules of VPL, which would help to establish a general mechanism of visual plasticity at the neuronal level. Given this hope, although a large number of experiments have been conducted, the results have shown a tendency opposite to finding a general rule(s).

One issue is that in conducting their VPL studies, researchers have tended to use different sets of parameters as their stimuli, tasks, etc. This practice has made it very difficult to make direct comparisons between the findings and to identify any general rules of VPL. A variety of results have been obtained under diverse conditions. In some cases, contradicting conclusions were drawn from conflicting results. When a new method and/or stimulus is used and new results of VPL are obtained, in some cases it is difficult to determine whether the new results reveal a hidden important principle/mechanism of VPL or if they identify a trivial variation from an established principle. For future studies, it is recommended that researchers employ one of a few standard methods, as is the convention in experimental physics (S.A. Klein, personal communication).

The second issue, which is related to the first, is that intense efforts have not been made to organize these divergent results to identify potential general rules. In the future, it is recommended that experiments be conducted to test the validity of aspects of a comprehensive model rather than to emphasize one narrow view that explains only a portion of accumulated data.

This review primarily focuses on task-relevant VPL and task-irrelevant VPL of primitive features including motion and orientation. However, some aspects of these types of VPL may generalize to other types of learning and memory. For example, passive characteristics of learning—as in task-irrelevant VPL—have been shown in learning of objects (Hammer et al. 2012; Li & DiCarlo 2008, 2012; Witthoft et al. 2009), categorization learning (Folstein et al. 2010), word learning (Dewald et al. 2011, 2013), speech learning (Vlahou et al. 2012), and general learning (Reed et al. 2011). On the other hand, some aspects of VPL of primitive features may be distinct from other types of memory and learning. Some disparities may be due to the fact that the early stages of processing primitive visual features differ significantly from other types of learning. Future research should include efforts to identify common principles of VPL of primitive features and other types of memory and learning as well as unique aspects of VPL of primitive features.

SUMMARY POINTS

1. Visual perceptual learning (VPL) is classified as either task relevant or task irrelevant. Task-relevant VPL of a feature results from training on a given task on the feature, whereas task-irrelevant VPL of a feature arises as a result of exposure to the feature that is irrelevant to a given task.

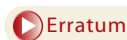
2. Controversy exists over the stage or brain area that is changed in association with task-relevant VPL. The three primary models are the early-, mid-, and late-stage models. Different sets of data tend to be used to support each of these models.
3. Specificity of the trained location and feature was regarded as evidence for the early-stage model. However, it has been recently found that at least in some cases double training results in transfer of VPL to other locations and features. These findings together with results of some imaging and neurophysiological studies suggest that VPL is not associated solely with changes in V1 or the early stage.
4. A reinforcement model of VPL indicates that both task-relevant and task-irrelevant VPL result from interactions of spatially diffusive reinforcement signals and bottom-up signals from a presented feature, irrespective of whether the feature is task relevant or task irrelevant. However, this model alone does not explain transfer of location/feature after double training or differential results from training on different tasks.
5. Attention to a task-relevant feature may enhance signals from the feature and increase the probability of the occurrence of task-relevant learning of the feature. In contrast, if task-irrelevant feature signals are sufficiently strong to be detected by an attentional system, they may be suppressed and cause no task-irrelevant VPL. If task-irrelevant signals are not sufficiently strong to be detected, they may not be suppressed and may cause task-irrelevant VPL. In addition, if a task-irrelevant feature is presented in an environment that optimizes task-irrelevant signals, task-irrelevant VPL may occur if the feature is not weak.
6. A dual plasticity model is proposed here to comprehensively explain apparently contradictory results and task-irrelevant VPL as well as task-relevant VPL. This model comprises feature-based plasticity and task-based plasticity. Feature-based plasticity reflects a change in a representation of a feature presented during training, irrespective of whether the feature is task relevant or task irrelevant. Task-based plasticity reflects a change in processing of the task performed during training. Feature-based plasticity occurs in an earlier stage than task-based plasticity occurs and constrains VPL only to the trained location and feature. Task-based plasticity constrains VPL only to the trained task.
7. One possible explanation for the variety of models of VPL is that different researchers tend to use different sets of parameters as their stimuli, tasks, etc., in conducting their VPL studies. This practice has made it very difficult to directly compare the findings and to detect general rules of VPL. Given the availability of a huge data set, it is an ideal time to start efforts to build a comprehensive framework of VPL.

DISCLOSURE STATEMENT

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LITERATURE CITED

- Adab HZ, Vogels R. 2011. Practicing coarse orientation discrimination improves orientation signals in macaque cortical area v4. *Curr. Biol.* 21:1661–66
- Adini Y, Sagi D, Tsodyks M. 2002. Context-enabled learning in the human visual system. *Nature* 415:790–93
- Ahissar M, Hochstein S. 1993. Attentional control of early perceptual learning. *Proc. Natl. Acad. Sci. USA* 90:5718–22
- Ahissar M, Hochstein S. 1997. Task difficulty and the specificity of perceptual learning. *Nature* 387:401–6
- Andersen GJ. 2012. Aging and vision: changes in function and performance from optics to perception. *Wiley Interdiscip. Rev. Cogn. Sci.* 3:403–10
- Andersen GJ, Ni R, Bower JD, Watanabe T. 2010. Perceptual learning, aging, and improved visual performance in early stages of visual processing. *J. Vis.* 10:4–11
- Ashby FG, Maddox WT. 2011. Human category learning 2.0. *Ann. N. Y. Acad. Sci.* 1224:147–61
- Baldassarre A, Lewis CM, Committeri G, Snyder AZ, Romani GL, Corbetta M. 2012. Individual variability in functional connectivity predicts performance of a perceptual task. *Proc. Natl. Acad. Sci. USA* 109:3516–21
- Ball K, Sekuler R. 1987. Direction-specific improvement in motion discrimination. *Vis. Res.* 27:953–65
- Barbot A, Landy MS, Carrasco M. 2011. Exogenous attention enhances 2nd-order contrast sensitivity. *Vis. Res.* 51:1086–98
- Baumann O, Endestad T, Magnussen S, Greenlee MW. 2008. Delayed discrimination of spatial frequency for gratings of different orientation: behavioral and fMRI evidence for low-level perceptual memory stores in early visual cortex. *Exp. Brain Res.* 188:363–69
- Bejjanki VR, Beck JM, Lu ZL, Pouget A. 2011. Perceptual learning as improved probabilistic inference in early sensory areas. *Nat. Neurosci.* 14:642–48
- Bennett PJ, Sekuler AB, McIntosh AR, Della-Maggiore V. 2001. The effects of aging on visual memory: evidence for functional reorganization of cortical networks. *Acta Psychol. (Amst.)* 107:249–73
- Beste C, Dinse HR. 2013. Learning without training. *Curr. Biol.* 23:R489–99
- Beste C, Wascher E, Gunturkun O, Dinse HR. 2011. Improvement and impairment of visually guided behavior through LTP- and LTD-like exposure-based visual learning. *Curr. Biol.* 21:876–82
- Bi T, Chen J, Zhou T, He Y, Fang F. 2014. Function and structure of human left fusiform cortex are closely associated with perceptual learning of faces. *Curr. Biol.* 24:222–27
- Bouvier SE, Cardinal KS, Engel SA. 2008. Activity in visual area V4 correlates with surface perception. *J. Vis.* 8(28):1–9
- Bower JD, Watanabe T, Andersen GJ. 2013. Perceptual learning and aging: improved performance for low-contrast motion discrimination. *Front. Psychol.* 4:66
- Braddick OJ, O'Brien JM, Wattam-Bell J, Atkinson J, Hartley T, Turner R. 2001. Brain areas sensitive to coherent visual motion. *Perception* 30:61–72
- Carrasco M, Rosenbaum A, Giordano A. 2008. Exogenous attention: less effort, more learning! *J. Vis.* 8:1095a
- Choi H, Watanabe T. 2012. Is perceptual learning associated with changes in a sensory region? *F1000 Biol. Rep.* 4:B4–24
- Chowdhury SA, DeAngelis GC. 2008. Fine discrimination training alters the causal contribution of macaque area MT to depth perception. *Neuron* 60:367–77
- Crist RE, Kapadia MK, Westheimer G, Gilbert CD. 1997. Perceptual learning of spatial localization: specificity for orientation, position, and context. *J. Neurophysiol.* 78:2889–94
- Crist RE, Li W, Gilbert CD. 2001. Learning to see: experience and attention in primary visual cortex. *Nat. Neurosci.* 4:519–25
- de Villers-Sidani E, Merzenich MM. 2011. Lifelong plasticity in the rat auditory cortex: basic mechanisms and role of sensory experience. *Prog. Brain Res.* 191:119–31
- Deloss DJ, Watanabe T, Andersen GJ. 2014. Optimization of perceptual learning: effects of task difficulty and external noise in older adults. *Vis. Res.* 99:37–45
- Dewald AD, Sinnott S, Dumas LA. 2011. Conditions of directed attention inhibit recognition performance for explicitly presented target-aligned irrelevant stimuli. *Acta Psychol. (Amst.)* 138:60–67
- Dewald AD, Sinnott S, Dumas LA. 2013. A window of perception when diverting attention? Enhancing recognition for explicitly presented, unattended, and irrelevant stimuli by target alignment. *J. Exp. Psychol.: Hum. Percept. Perform.* 39:1304–12

- Dill M, Fahle M. 1997. The role of visual field position in pattern-discrimination learning. *Proc. R. Soc. B* 264:1031–36
- Dosher BA, Jeter P, Liu J, Lu ZL. 2013. An integrated reweighting theory of perceptual learning. *Proc. Natl. Acad. Sci. USA* 110:13678–83
- Dosher BA, Liu SH, Blair N, Lu ZL. 2004. The spatial window of the perceptual template and endogenous attention. *Vis. Res.* 44:1257–71
- Dosher BA, Lu ZL. 1998. Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc. Natl. Acad. Sci. USA* 95:13988–93
- Dosher BA, Lu ZL. 1999. Mechanisms of perceptual learning. *Vis. Res.* 39:3197–221
- Eagleman D. 2011. *Incognito: The Secret Lives of the Brain*. New York: Pantheon
- Fahle M. 2002. Perceptual learning: gain without pain? *Nat. Neurosci.* 5:923–24
- Fahle M. 2009. Perceptual learning and sensorimotor flexibility: cortical plasticity under attentional control? *Philos. Trans. R. Soc. B* 364:313–19
- Fahle M, Edelman S. 1993. Long-term learning in vernier acuity: effects of stimulus orientation, range and of feedback. *Vis. Res.* 33:397–412
- Fahle M, Edelman S, Poggio T. 1995. Fast perceptual learning in hyperacuity. *Vis. Res.* 35:3003–13
- Fahle M, Poggio T. 2002. *Perceptual Learning*. Cambridge, MA: MIT Press
- Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* 1:1–47
- Fine I, Jacobs RA. 2002. Comparing perceptual learning tasks: a review. *J. Vis.* 2:190–203
- Fiorentini A, Berardi N. 1980. Perceptual learning specific for orientation and spatial frequency. *Nature* 287:43–44
- Folstein JR, Gauthier I, Palmeri TJ. 2010. Mere exposure alters category learning of novel objects. *Front. Psychol.* 1:40
- Furmanski CS, Schluppeck D, Engel SA. 2004. Learning strengthens the response of primary visual cortex to simple patterns. *Curr. Biol.* 14:573–78
- Garrigan P, Kellman PJ. 2008. Perceptual learning depends on perceptual constancy. *Proc. Natl. Acad. Sci. USA* 105:2248–53
- Ghose GM, Yang T, Maunsell JH. 2002. Physiological correlates of perceptual learning in monkey V1 and V2. *J. Neurophysiol.* 87:1867–88
- Gilbert CD. 1994. Early perceptual learning. *Proc. Natl. Acad. Sci. USA* 91:1195–97
- Gilbert CD, Li W. 2012. Adult visual cortical plasticity. *Neuron* 75:250–64
- Gold JI, Law CT, Connolly P, Bennur S. 2008. The relative influences of priors and sensory evidence on an oculomotor decision variable during perceptual learning. *J. Neurophysiol.* 100:2653–68
- Gold JI, Law CT, Connolly P, Bennur S. 2009. Relationships between the threshold and slope of psychometric and neurometric functions during perceptual learning: implications for neuronal pooling. *J. Neurophysiol.* 103:140–54
- Gold JI, Watanabe T. 2010. Perceptual learning. *Curr. Biol.* 20:R46–48
- Goldstone RL. 1998. Perceptual learning. *Annu. Rev. Psychol.* 49:585–612
- Gu Y, Liu S, Fetsch CR, Yang Y, Fok S, et al. 2012. Perceptual learning reduces interneuronal correlations in macaque visual cortex. *Neuron* 71:750–61
- Gutnisky DA, Hansen BJ, Iliescu BF, Dragoi V. 2009. Attention alters visual plasticity during exposure-based learning. *Curr. Biol.* 19:555–60
- Hammer R, Sloutsky V, Grill-Spector K. 2012. The interplay between feature-saliency and feedback information in visual category learning tasks. In *Proc. 34th annu. meet. Cogn. Sci. Soc.*, ed. N Miyake, D Peebles, RP Cooper, pp. 420–25. Austin, TX: Cogn. Sci. Soc.
- Harris H, Gliksberg M, Sagi D. 2012. Generalized perceptual learning in the absence of sensory adaptation. *Curr. Biol.* 22:1813–17
- Harris JP, Fahle M. 1995. The detection and discrimination of spatial offsets. *Vis. Res.* 35:51–58
- Heekeren HR, Marrett S, Bandettini PA, Ungerleider LG. 2004. A general mechanism for perceptual decision-making in the human brain. *Nature* 431:859–62
- Hensch TK. 2005a. Critical period mechanisms in developing visual cortex. *Curr. Top. Dev. Biol.* 69:215–37

- Hensch TK. 2005b. Critical period plasticity in local cortical circuits. *Nat. Rev. Neurosci.* 6:877–88
- Hochstein S, Ahissar M. 2002. View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron* 36:791–804
- Hua T, Bao P, Huang CB, Wang Z, Xu J, et al. 2010. Perceptual learning improves contrast sensitivity of V1 neurons in cats. *Curr. Biol.* 20:887–94
- Huang X, Lu H, Tjan BS, Zhou Y, Liu Z. 2007. Motion perceptual learning: when only task-relevant information is learned. *J. Vis.* 7(14):1–10
- Hubel DH, Wiesel TN. 1964. Effects of monocular deprivation in kittens. *Naunyn-Schmiedeberg Arch. Pharmacol.* 248:492–97
- Hubel DH, Wiesel TN. 1968. Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* 195:215–43
- Jain A, Zaidi Q. 2011. Discerning nonrigid 3D shapes from motion cues. *Proc. Natl. Acad. Sci. USA* 108:1663–68
- Kahnt T, Grueschow M, Speck O, Haynes JD. 2011. Perceptual learning and decision-making in human medial frontal cortex. *Neuron* 70:549–59
- Kamitani Y, Tong F. 2005. Decoding the visual and subjective contents of the human brain. *Nat. Neurosci.* 8:679–85
- Karmarkar UR, Dan Y. 2006. Experience-dependent plasticity in adult visual cortex. *Neuron* 52:577–85
- Karni A, Sagi D. 1991. Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. *Proc. Natl. Acad. Sci. USA* 88:4966–70
- Karni A, Sagi D. 1993. The time course of learning a visual skill. *Nature* 365:250–52
- Koyama S, Harner A, Watanabe T. 2004. Task-dependent changes of the psychophysical motion-tuning functions in the course of perceptual learning. *Perception* 33:1139–47
- Koyama S, Sasaki Y, Andersen GJ, Tootell RB, Matsuura M, Watanabe T. 2005. Separate processing of different global-motion structures in visual cortex is revealed by fMRI. *Curr. Biol.* 15:2027–32
- Law CT, Gold JI. 2008. Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nat. Neurosci.* 11:505–13
- Leclercq V, Le Dantec CC, Seitz AR. 2014. Encoding of episodic information through fast task-irrelevant perceptual learning. *Vis. Res.* 99:5–11
- Leclercq V, Seitz AR. 2012. The impact of orienting attention in fast task-irrelevant perceptual learning. *Atten. Percept. Psychophys.* 74:648–60
- Lee SH, Kwan AC, Zhang S, Phoumthipphavong V, Flannery JG, et al. 2012. Activation of specific interneurons improves V1 feature selectivity and visual perception. *Nature* 488:379–83
- Levi DM. 2012. Prentice Award Lecture 2011: removing the brakes on plasticity in the amblyopic brain. *Optom. Vis. Sci.* 89:827–38
- Levi DM, Li RW. 2009a. Improving the performance of the amblyopic visual system. *Philos. Trans. R. Soc. B* 364:399–407
- Levi DM, Li RW. 2009b. Perceptual learning as a potential treatment for amblyopia: a mini-review. *Vis. Res.* 49:2535–49
- Lewis CM, Baldassarre A, Committeri G, Romani GL, Corbetta M. 2009. Learning sculpts the spontaneous activity of the resting human brain. *Proc. Natl. Acad. Sci. USA* 106:17558–63
- Li J, Thompson B, Deng D, Chan LY, Yu M, Hess RF. 2013. Dichoptic training enables the adult amblyopic brain to learn. *Curr. Biol.* 23:R308–9
- Li N, DiCarlo JJ. 2008. Unsupervised natural experience rapidly alters invariant object representation in visual cortex. *Science* 321:1502–7
- Li N, DiCarlo JJ. 2012. Neuronal learning of invariant object representation in the ventral visual stream is not dependent on reward. *J. Neurosci.* 32:6611–20
- Liu J, Lu ZL, Doshier BA. 2010. Augmented Hebbian reweighting: interactions between feedback and training accuracy in perceptual learning. *J. Vis.* 10:29
- Liu Z. 1999. Perceptual learning in motion discrimination that generalizes across motion directions. *Proc. Natl. Acad. Sci. USA* 96:14085–87
- Logothetis NK, Pauls J, Augath M, Trinath T, Oeltermann A. 2001. Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412:150–57

- Lu ZL, Chu W, Doshier BA, Lee S. 2005. Independent perceptual learning in monocular and binocular motion systems. *Proc. Natl. Acad. Sci. USA* 102:5624–29
- Lu ZL, Hua T, Huang CB, Zhou Y, Doshier BA. 2011. Visual perceptual learning. *Neurobiol. Learn. Mem.* 95:145–51
- McKee SP, Westheimer G. 1978. Improvement in vernier acuity with practice. *Percept. Psychophys.* 24:258–62
- Morishita H, Hensch TK. 2008. Critical period revisited: impact on vision. *Curr. Opin. Neurobiol.* 18:101–7
- Movshon J, Adelson E, Gizzi M, Newsome W. 1985. The analysis of moving visual patterns. *Pattern Recognit. Mech.* 54:117–51
- Newsome WT, Pare EB. 1988. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neurosci.* 8:2201–11
- Ooi TL, Su YR, Natale DM, He ZJ. 2013. A push-pull treatment for strengthening the “lazy eye” in amblyopia. *Curr. Biol.* 23:R309–10
- Op de Beeck HP, Baker CI. 2010. The neural basis of visual object learning. *Trends Cogn. Sci.* 14:22–30
- Petrov AA, Doshier BA, Lu ZL. 2005. The dynamics of perceptual learning: an incremental reweighting model. *Psychol. Rev.* 112:715–43
- Petrov AA, Doshier BA, Lu ZL. 2006. Perceptual learning without feedback in non-stationary contexts: data and model. *Vis. Res.* 46:3177–97
- Piech V, Li W, Reeke GN, Gilbert CD. 2013. Network model of top-down influences on local gain and contextual interactions in visual cortex. *Proc. Natl. Acad. Sci. USA* 110:E4108–17
- Poggio T, Fahle M, Edelman S. 1992. Fast perceptual learning in visual hyperacuity. *Science* 256:1018–21
- Polat U, Ma-Naim T, Belkin M, Sagi D. 2004. Improving vision in adult amblyopia by perceptual learning. *Proc. Natl. Acad. Sci. USA* 101:6692–97
- Reed A, Riley J, Carraway R, Carrasco A, Perez C, et al. 2011. Cortical map plasticity improves learning but is not necessary for improved performance. *Neuron* 70:121–31
- Rees G, Friston K, Koch C. 2000. A direct quantitative relationship between the functional properties of human and macaque V5. *Nat. Neurosci.* 3:716–23
- Roe AW, Ts'o DY. 1995. Visual topography in primate V2: multiple representation across functional stripes. *J. Neurosci.* 15:3689–715
- Rosenthal O, Humphreys GW. 2010. Perceptual organization without perception. The subliminal learning of global contour. *Psychol. Sci.* 21:1751–58
- Saarienen J, Levi DM. 1995. Perceptual learning in vernier acuity: What is learned? *Vis. Res.* 35:519–27
- Sagi D. 2011. Perceptual learning in vision research. *Vis. Res.* 51:1552–66
- Sagi D, Tanne D. 1994. Perceptual learning: learning to see. *Curr. Opin. Neurobiol.* 4:195–99
- Sasaki S, Watanabe T. 2012. Perceptual learning. In *Visual Neurosciences*, ed. J Werner, L Chalupa, pp. 991–1000. Cambridge, MA: MIT Press
- Sasaki Y, Nanez JE, Watanabe T. 2010. Advances in visual perceptual learning and plasticity. *Nat. Rev. Neurosci.* 11:53–60
- Schoups A, Vogels R, Qian N, Orban G. 2001. Practising orientation identification improves orientation coding in V1 neurons. *Nature* 412:549–53
- Schoups AA, Orban GA. 1996. Interocular transfer in perceptual learning of a pop-out discrimination task. *Proc. Natl. Acad. Sci. USA* 93:7358–62
- Schoups AA, Vogels R, Orban GA. 1995. Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularly. *J. Physiol.* 483(Part 3):797–810
- Schwartz S, Maquet P, Frith C. 2002. Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination. *Proc. Natl. Acad. Sci. USA* 99:17137–42
- Seitz A, Kim D, Watanabe T. 2009. Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron* 61:700–7
- Seitz A, Watanabe T. 2005. A unified model for perceptual learning. *Trends Cogn. Sci.* 9:329–34
- Seitz AR, Dinse HR. 2007. A common framework for perceptual learning. *Curr. Opin. Neurobiol.* 17:148–53
- Seitz AR, Lefebvre C, Watanabe T, Jolicoeur P. 2005a. Requirement for high-level processing in subliminal learning. *Curr. Biol.* 15:R753–55
- Seitz AR, Watanabe T. 2003. Psychophysics: Is subliminal learning really passive? *Nature* 422:36

- Seitz AR, Yamagishi N, Werner B, Goda N, Kawato M, Watanabe T. 2005b. Task-specific disruption of perceptual learning. *Proc. Natl. Acad. Sci. USA* 102:14895–900
- Shadlen MN, Newsome WT. 1996. Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. USA* 93:628–33
- Shadlen MN, Newsome WT. 2001. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J. Neurophysiol.* 86:1916–36
- Shibata K, Chang LH, Kim D, Nanez JE Sr, Kamitani Y, et al. 2012a. Decoding reveals plasticity in V3A as a result of motion perceptual learning. *PLOS ONE* 7:e44003
- Shibata K, Kawato M, Sasaki S, Watanabe T. 2012b. Monocular deprivation boosts long-term visual plasticity. *Curr. Biol.* 22:R291–92
- Shibata K, Sasaki Y, Kawato M, Watanabe T. 2013. Perceptual learning is associated with different types of plasticity. *J. Vis.* 13:604
- Shibata K, Watanabe T. 2012. Preference suppression caused by misattribution of task-irrelevant subliminal motion. *Proc. R. Soc. B* 279:3443–48
- Shibata K, Watanabe T, Sasaki Y, Kawato M. 2011. Perceptual learning incepted by decoded fMRI neuro-feedback without stimulus presentation. *Science* 334:1413–15
- Shiu LP, Pashler H. 1992. Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Percept. Psychophys.* 52:582–88
- Tootell RB, Mendola JD, Hadjikhani NK, Ledden PJ, Liu AK, et al. 1997. Functional analysis of V3A and related areas in human visual cortex. *J. Neurosci.* 17:7060–78
- Ts'o DY, Gilbert CD. 1988. The organization of chromatic and spatial interactions in the primate striate cortex. *J. Neurosci.* 8:1712–27
- Tsushima Y, Sasaki Y, Watanabe T. 2006. Greater disruption due to failure of inhibitory control on an ambiguous distractor. *Science* 314:1786–88
- Tsushima Y, Seitz A, Watanabe T. 2008. Task-irrelevant learning occurs only when the irrelevant feature is weak. *Curr. Biol.* 18:R516–17
- Tsushima Y, Watanabe T. 2009. Roles of attention in perceptual learning from perspectives of psychophysics and animal learning. *Learn. Behav.* 37:126–32
- Vaina LM, Belliveau JW, des Roziers EB, Zeffiro TA. 1998. Neural systems underlying learning and representation of global motion. *Proc. Natl. Acad. Sci. USA* 95:12657–62
- Vlahou EL, Protopapas A, Seitz AR. 2012. Implicit training of nonnative speech stimuli. *J. Exp. Psychol.: Gen.* 141:363–81
- Walker MP, Stickgold R, Alsop D, Gaab N, Schlaug G. 2005. Sleep-dependent motor memory plasticity in the human brain. *Neuroscience* 133:911–17
- Wang R, Zhang JY, Klein SA, Levi DM, Yu C. 2012. Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vis. Res.* 61:33–38
- Watamaniuk SN, Sekuler R, Williams DW. 1989. Direction perception in complex dynamic displays: the integration of direction information. *Vis. Res.* 29:47–59
- Watanabe T, Nanez JE, Sasaki Y. 2001. Perceptual learning without perception. *Nature* 413:844–48
- Watanabe T, Nanez JE Sr, Koyama S, Mukai I, Liederman J, Sasaki Y. 2002. Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. *Nat. Neurosci.* 5:1003–9
- Westheimer G, Crist RE, Gorski L, Gilbert CD. 2001. Configuration specificity in bisection acuity. *Vis. Res.* 41:1133–38
- Witthoft N, Davidenko N, Grill-Spector K. 2009. Exemplar frequency affects unsupervised learning of shapes. In *Proc. 31st annu. meet. Cogn. Sci. Soc.*, ed. N Taatgen, H van Rijn, pp. 3058–63. Austin, TX: Cogn. Sci. Soc.
- Xiao LQ, Zhang JY, Wang R, Klein SA, Levi DM, Yu C. 2008. Complete transfer of perceptual learning across retinal locations enabled by double training. *Curr. Biol.* 18:1922–26
- Xu JP, He ZJ, Ooi TL. 2010. Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. *Curr. Biol.* 20:1864–68
- Xu JP, He ZJ, Ooi TL. 2012a. Further support for the importance of the suppressive signal (pull) during the push-pull perceptual training. *Vis. Res.* 61:60–69

- Xu JP, He ZJ, Ooi TL. 2012b. Perceptual learning to reduce sensory eye dominance beyond the focus of top-down visual attention. *Vis. Res.* 61:39–47
- Xu JP, He ZJ, Ooi TL. 2012c. Push-pull training reduces foveal sensory eye dominance within the early visual channels. *Vis. Res.* 61:48–59
- Yang T, Maunsell JH. 2004. The effect of perceptual learning on neuronal responses in monkey visual area V4. *J. Neurosci.* 24:1617–26
- Yotsumoto Y, Sasaki Y, Chan P, Vasios C, Bonmassar G, et al. 2009. Location-specific cortical activation changes during sleep after training for perceptual learning. *Curr. Biol.* 19:1278–82
- Yotsumoto Y, Watanabe T, Sasaki Y. 2008. Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron* 57:827–33
- Young KG, Li RW, Levi DM, Klein SA, Huang EY. 2004. Interocular transfer in perceptual learning of a vernier task. *Investig. Ophthalmol. Vis. Sci.* 43:63:B824
- Zeki S. 1993. *A Vision of the Brain*. Oxford, UK: Blackwell Sci.
- Zhang J, Kourtzi Z. 2010. Learning-dependent plasticity with and without training in the human brain. *Proc. Natl. Acad. Sci. USA* 107:13503–8
- Zhang JY, Kuai SG, Xiao LQ, Klein SA, Levi DM, Yu C. 2008. Stimulus coding rules for perceptual learning. *PLOS Biol.* 6:e197
- Zhang JY, Zhang GL, Xiao LQ, Klein SA, Levi DM, Yu C. 2010a. Rule-based learning explains visual perceptual learning and its specificity and transfer. *J. Neurosci.* 30:12323–28
- Zhang T, Xiao LQ, Klein SA, Levi DM, Yu C. 2010b. Decoupling location specificity from perceptual learning of orientation discrimination. *Vis. Res.* 50:368–74



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