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Review

Multisensory perceptual learning and sensory substitution

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ABSTRACT

One of the most exciting recent findings in neuroscience has been the capacity for neural plasticity in adult humans and animals. Studies of perceptual learning have provided key insights into the mechanisms of neural plasticity and the changes in functional neuroanatomy that it affords. Key questions in this field of research concern how practice of a task leads to specific or general improvement. Although much of this work has been carried out with a focus on a single sensory modality, primarily visual, there is increasing interest in multisensory perceptual learning. Here we will examine how advances in perceptual learning research both inform and can be informed by the development and advancement of sensory substitution devices for blind persons. To allow 'sight' to occur in the absence of visual input through the eyes, visual information can be transformed by a sensory substitution device into a representation that can be processed as sound or touch, and thus give one the potential to 'see' through the ears or tongue. Investigations of auditory, visual and multisensory perceptual learning can have key benefits for the advancement of sensory substitution, and the study of sensory deprivation and sensory substitution likewise will further the understanding of perceptual learning in general and the reverse hierarchy theory in particular. It also has significant importance for the developing understanding of the brain in metamodal terms, where functional brain areas might be best defined by the computations they carry out rather than by their sensory-specific processing role.

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1. Introduction

The human and non-human animal brain undergoes rapid and extensive change during development. A key area of research for neuroscientists concerns the mechanisms of this plasticity from the molecular to the behavioral levels. Many important studies in the last century established that there can be critical periods during development when neuroplasticity is observed (Hubel and Wiesel, 1970). Since that time, however, there has been mounting evidence that even the adult brain retains significant neural plasticity that accompanies perceptual learning (Gilbert et al., 2001).

Studies of perceptual learning have provided key insights into the mechanisms of neuroplasticity and resulting functional neuroanatomy. The central aim of perceptual learning research is to understand how practice of a task leads to either specific or general improvement. Much research on perceptual learning has been fairly low level and unisensory, focusing for example on how

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practice results in task-specific improvements in performance and neural plasticity at the level of primary sensory cortex. Of great interest, however, is how generalization can be promoted and some of the most striking evidence for high-level perceptual learning and adult neural plasticity has come from studies of sensory deprivation and sensory substitution devices to overcome such deprivation.

To allow a form of functional 'vision' to occur in the absence of visual input through the eyes, visual information can be transformed by a sensory substitution device into a representation that can be processed as sound or touch, and thus give one the potential to 'see' through the ears or tongue (Bach-y-Rita et al., 1969; Meijer, 1992). Investigations of auditory, visual and multisensory perceptual learning can have key benefits for the advancement of sensory substitution, and the study of sensory deprivation and sensory substitution likewise will further the understanding of perceptual learning.

Although there have been numerous studies examining visual, auditory, and multisensory perceptual learning over the past 50 years (Gibson, 1963; Goldstone, 1998), there has not been a synthesis that brings these findings together under the same theoretical structure. Here we bring together advances on the reverse hierarchy theory of perceptual learning (Ahissar and Hochstein, 2004) and the metamodal hypothesis of brain organization (Pascual-Leone and Hamilton, 2001) to provide a behavioral and neural explanation of visual, auditory, and multisensory perceptual learning (Ghazanfar and Schroeder, 2006; Shams and Seitz, 2008). Certainly some aspects are better understood at a behavioral level, and yet other aspects at a neural level, and this synthesis of the reverse hierarchy and metamodal theories will highlight areas where such cross-fertilization of research efforts would be beneficial and specify possible constraints for each theory. We also provide an examination of the reciprocal benefits of sensory deprivation and sensory substitution devices as means to understand the mechanisms and neural basis of perceptual learning. This approach will likely also provide further advances for the development of sensory substitution to aid those with sensory impairments.

2. Visual perceptual learning and the reverse hierarchy theory

Psychophysical studies of visual perceptual learning have established that practicing a task results in improvement that is often restricted to the stimuli used during training (Fiorentini and Berardi, 1980; McKee and Westheimer, 1978). The specificity of improved performance is taken to indicate that neural plasticity manifests at the 'low' level of primary visual cortex because the neurons at that level have receptive field properties for the particular visual features that have been learned. This use of psychophysical findings to constrain the possible neural basis of perceptual learning was termed 'psycho-anatomy' by Julesz (1972).

Training studies have demonstrated the specific improvement of performance for a number of visual features that are often spatial in nature, such as vernier acuity (Beard et al., 1995; Fahle et al., 1995; McKee and Westheimer, 1978; Poggio, 1995; Saarinen and Levi, 1995), orientation and texture (Karni and Sagi, 1991; Vogels and Orban, 1985), motion (Ball and Sekuler, 1982, 1987), and spatial frequency (Fiorentini and Berardi, 1980, 1981). What sort of specificity is normally reported? Learning can be spatially specific such that training in one visual field does not transfer to another (Karni and Sagi, 1991). It can also be feature specific, such that training with one orientation does not transfer to another orientation (Karni and Sagi, 1991). It is important that the underlying mechanisms of such specific perceptual learning have often been described as the retuning of low level sensory areas in the brain. Psychophysical experiments and modeling by Dosher and colleagues have demonstrated that such neural plasticity can, however, be accomplished in other ways such as the reweighting of the visual channels used for a task (Dosher and Lu, 1998; Petrov et al., 2005).

There have been some surprising cases of generalization, however, that seemed to contradict the findings of specific perceptual learning. For example, although a previous report found training benefits restricted to one region of space, and even one eye (Karni and Sagi, 1991), a subsequent study found that a similar texture discrimination task could transfer from one eye to the other (Schoups et al., 1995). The 'reverse hierarchy theory' of visual perceptual learning (Ahissar and Hochstein, 2004) was developed to account for apparently conflicting findings such as this. The reverse hierarchy theory posits that the difficulty and characteristics of a task determine the level of cortical processing at which attentional mechanisms are required (see Fig. 1). An easier task that can be carried out on the basis of more general levels of feature discrimination instead drive processing and attentional resources to higher level cortical association areas, such as the lateral intraparietal area with its larger receptive fields. The harder the task and the more specific the discrimination required, the more it tends to drive processing and attentional resources to lower, primary sensory areas, such as V1 with its smaller receptive fields. The idea is that perceptual learning can occur at all cortical levels of processing: initially higher-level areas would be recruited, however feedback connections to lower-level areas would be employed if necessary. When perceptual learning occurs at higher-level areas, then the training can generalize to other regions of space and to other features (Pavlovskaya and Hochstein, 2011). However, when perceptual learning occurs at lower-level areas, then the training will remain specific to the spatial locations and features used during training. Importantly the use of feedback connections for perceptual learning has gained support from findings in vision (Juan et al., 2004; Zhang et al., 2008), and in audition (Wong et al., 2007).

The role of higher-level cortical areas, rather than just lower-level striate (V1) and extrastriate areas, in perceptual learning, as proposed by reverse hierarchy theory, has been confirmed by other findings in the literature. For example, a novel paradigm that involved double training, where one retinal location was exposed to the relevant task and another to an irrelevant task (Xiao et al., 2008). A transfer of perceptual learning was induced by the irrelevant training at the second location, suggesting that higher order, nonretinotopic brain areas were involved in learning and thus promoted location generalization (Dosher and Lu, 1998; Petrov et al., 2005; Wang et al., 2012; Zhang et al., 2010). Reverse hierarchy theory has provided a framework to characterize both the specific and generalized perceptual learning in vision, and the recruitment of cortical areas along the hierarchy of visual information processing.

3. Auditory perceptual learning

Compared to the abundance of literature on visual perceptual learning, the literature on the specificity and transfer of auditory perceptual learning is scarce, though with Wright and colleagues making many of the seminal contributions to this field in recent years (Wright and Zhang, 2009). As with the vision literature, the first aim in auditory research was to establish whether practice improves performance on auditory tasks. The primary features of interest in the auditory domain are frequency (spectral) information and temporal information, such as the order, interval or duration of stimuli. These features are particular important for speech and music perception in humans. Moreover, temporal cues can be important for spatial localization as well (Jeffress, 1948).

A prototypical paradigm for the study of auditory perceptual learning is a temporal discrimination task (Wright et al., 1997).

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