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Learning in mammalian sensory cortex

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The improvement of perceptual capabilities with training can offer important insight into the physiological basis of learning in the cerebral cortex. The rapid time course and ease with which some perceptual capabilities can improve suggest that learning is an integral part of normal perception. Electrophysiological and neuroimaging studies of sensory systems in the cortex suggest that the changes underlying perceptual learning can occur in a variety of areas and are likely to involve multiple mechanisms. In particular, recent psychological and physiological studies suggest that perceptual learning might often involve the task-specific suppression of signals that interfere with performance.

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Abbreviations

fMRI functional magnetic resonance imaging

Introduction

We live in a world that is constantly changing; we constantly meet new people, navigate through new environments, face new challenges, and acquire new abilities and expertise. Because the cerebral cortex is responsible for high level representations and behaviors, the ability to adopt lasting changes in behaviors and representations according to experience is necessarily manifested in changes in the cortex. Sensory areas are well suited for the study of cortical representations because external stimuli can be carefully controlled and consistently presented. Moreover, a long history of psychological studies [1–3] has demonstrated that perceptual capabilities based on cortical processing can improve with training. Thus, sensory areas of the cortex offer unique opportunities for the exploration of the physiological basis of learning.

An understanding of the neural basis of perceptual learning depends on relating specific changes in sensory physiology to changes in perceptual performance, either directly or by inference. To infer the locus of physiological change, psychological studies of perceptual learning have examined how behavioral improvements are transferred to untrained tasks. If improvements fail to transfer across a particular dimension, the extent of physiological change is said to be limited to neurons with selective responses in that dimension. For example, if training effects fail to transfer across retinotopic locations, then it can be inferred that physiological changes were limited to neurons representing a particular location. If perceptual improvements in a task are strictly confined to the retinotopic locations at which training occurred, it is likely that areas early in the visual processing pathway, in which the mapping of visual space is the most precise and regular, are involved. If there is a dramatic change in functional properties, such as the loss of monocular signals past primary visual cortex, such arguments can further specify the location. The limited transfer of training effects across visual space and orientation observed in early psychophysical studies [4–6] was used as evidence that perceptual learning was occurring in early visual areas such as V1 or V2, in which both visual space and orientation are precisely mapped.

Consistent with these suggestions, the first direct observations of the physiological correlates of perceptual learning also revealed changes in primary sensory areas. Specifically, these studies showed training was associated with both an increase in the number of neurons representing trained parameters and increases in response selectivity [7–11]. Taken together with the psychophysical results regarding transfer of visual improvements after training, these results suggested that primary sensory areas were highly plastic in mature animals and that the representation of specific parameters in these areas could be enhanced by training.

Here, I review recent evidence that suggests the physiological basis of perceptual learning is considerably more complex than originally anticipated. I address recent studies in which perceptual learning is observed without any significant changes in the fundamental receptive field properties of neurons in primary sensory areas, and consider how changes in higher areas might be responsible for observed performance improvements. I also discuss evidence that suggests perceptual learning could arise not from a refinement or amplification of a particular representation but rather from the active suppression of signals that impair task performance.

Location and attention dependence of perceptual learning

Three recent experiments in visual cortex suggest that perceptual learning can take place in the absence of dramatic changes in primary sensory areas. Although all of these experiments revealed changes in primary visual cortex after training, the observed changes were unable to account for specific behavioral improvements. In an experiment related to spatial resolution in which animals were trained to make sensitive bisection judgments, the surround properties of V1 neurons were altered, but primary receptive field properties, such as size and positional scatter, were unaffected [12]. In the other two experiments animals were trained to judge whether or not a grating positioned away from fixation changed in orientation [13,14]. The grating was presented at the same retinotopic location and orientation changes were made around the same orientation throughout training. During the many months of training perceptual abilities were improved and animals were able to detect progressively smaller changes in orientation. However, the experimenters found a reduction in the number of cells that preferred the trained orientation, instead of an expansion as might have been predicted from somatosensory and auditory experiments. In neither experiment was there any evidence that training altered the mapping of visual space.

How is the lack of correlation between physiological changes observed in primary visual cortex and behavioral improvement consistent with the aforementioned transfer studies that implicated early visual areas in perceptual learning? First, in most cases, selectivity for a particular stimulus dimension can be found in a variety of areas. One of the most common failures of transfer with visual learning studies comes with respect to orientation: in many tasks, if training is restricted to stimuli of a particular orientation, performance does not improve for untrained orientations [6,15–19]. This suggests that perceptual improvements are not arising from a generalized enhancement in visual signals but rather from a change in the orientation selective neurons that were activated during training. Because neurons exhibiting orientation selectivity are found in many cortical areas, including V1, V2, V4, and inferotemporal cortex, this transfer failure does not strongly implicate a particular cortical area. Second, transfer results vary considerably among studies [3]. For example, although there have been reports of a task in which perceptual improvements were monocularly specific [6,20], these results have proven difficult to replicate [21]. Similarly, the retinotopic specificity of training effects shows large variations among different studies [22]. Third, it is possible that training can create new selectivities in higher visual areas as a consequence of training. It is a well-established fact that response selectivities in inferotemporal cortex are dependent on training [23,24]. Although it was assumed that plasticity

was limited to shape or view selectivity underlying object recognition, a recent study suggests that even response properties such as receptive field size, which had previously been assumed to be largely immutable, can be modified by training. A survey of studies in inferotemporal cortex showed that measured receptive field sizes are correlated with the size of stimuli used in pre-recording training [25^{*}]. In the most extreme example, receptive field sizes were similar to those commonly observed in areas early visual processing, such as V2. Thus, limited retinotopic transfer of training effects might arise from the creation of small receptive fields in higher visual areas.

Just as perceptual learning can potentially occur on a variety of levels within the cortical hierarchies underlying perception, it can also occur under a variety of training regimens. For example, although selective attention can play an important part in the changes associated with perceptual learning [26] — by concentrating perceptual resources on task relevant signals — it does not appear to be necessary for perceptual learning. In particular, two recent studies call into question whether or not attention is a necessary aspect of learning and point to the possibility that sensory signals can be modified during everyday experiences.

In the first study, subjects are passively stimulated by tactile vibration applied to one fingertip while they carry out a normal regimen of activity [27]. Subjects receiving such stimulation show an improvement in somatosensory acuity that is specific to the stimulated fingertip. In the second set of studies, rapid perceptual learning was demonstrated for distractor stimuli that were not attended to by the individual [28,29]. In these studies, subjects perform a difficult letter identification task, in which the letter is surrounded by a field of random dots. If the random dots contain a weak motion signal in a particular direction, subsequent detection of motion in that direction is improved. The effect remains even when the distractors are only directionally consistent during the presentations of the target letter [30^{*}]. This result shows that stimulus-specific perceptual improvements can occur even for unattended stimuli and without extensive training.

Criteria for establishing the physiological basis of perceptual learning

These results suggest that perceptual improvements can arise from a variety of training regimens and potentially reflect changes in a variety of locations within the cortex. To specify exactly the physiological changes that are responsible for, and not merely correlated with, behavioral improvements there are several criteria that must be satisfied. Although a systematic perusal of these criteria has not been reported for any single perceptual improvement, recent studies indicate that many of these criteria can be addressed with current experimental techniques.

First, physiological changes should reflect the behavioral sensitivities observed after training. For example, the lack of strong orientation specific changes in V1 was not consistent with the orientation specificity of the behavioral improvements observed with training [13,14]. It is also important to confirm the full behavioral implications of the physiological change. For example, if perceptual performance is strongly dependent on the number of neurons representing a particular parameter, as is suggested by the expansion of representations reported in the auditory and somatosensory [11] literature, then perceptual performance should actually worsen for untrained parameters as they are represented by fewer neurons. Analogously, behavioral correlates, such as the worsening of frequency discrimination after tactile acuity increases [31^{••}], should be commensurate with observed physiological changes.

Second, physiological changes should be able to account for intertask variability. In this regard it is important to understand which type of tasks it is difficult to see improvements in, and in which type of tasks the training effects are pronounced. For example, a change in the effects of external noise on V4 neuronal responses [32^{••}] is consistent with the noise dependence of perceptual learning tasks reported in a variety of studies.

Third, physiological changes should be able to account for intersubject variability, which is often considerable. Physiological changes occurring in subjects who show little improvement with training should be different from those observed in well-trained subjects. This criterion is difficult to test in electrophysiological studies because of the large number of subjects necessary to establish such correlations. However, the advent of non-invasive methods to study brain activity, such as evoked potentials, functional magnetic resonance imaging (fMRI) [31^{••}], and magnetoencephalography [33], enables examination of a relatively large number of subjects. Indeed, such experiments conducted on subjects trained in the tactile acuity task have been able to account for a high degree of intersubject performance variability [31^{••}].

Fourth, manipulation of the responsible physiological changes should have behavioral consequences. Blocking the physiological change should prevent learning, whereas enhancement of the physiological change should improve learning [34]. For example, if an increase in the number of neurons representing a particular parameter is responsible for behavior improvement then artificial increases in population activity should be associated with improved behavioral performance. This manipulation was recently done in rat auditory cortex by directed microstimulation. On the one hand, such microstimulation alters the functional map in auditory cortex, yet does not have obvious behavioral consequences [35]. Thus, changes in population activity are not sufficient to explain

behavioral improvements. On the other hand, certain pharmacological manipulations can be sufficient in some circumstances. For example, a recent study showed that experience dependent somatosensory acuity increases can be eliminated or increased with manipulations in the activation of the *N*-methyl-D-aspartate (NMDA) receptor, which has been implicated in activity-dependent synaptic modification [36^{••}].

Fifth, the dynamics of the physiological changes should match the dynamics of behavioral improvements during the training. Because of sampling issues it has been difficult to compare behavioral performance and physiological responses during the course of training. The recent development of chronically implanted electrodes that can record a period of months holds major promise for exploring physiological changes during periods of improving performance. For example, one study using such methods in auditory cortex showed that large response property changes occurred immediately before sudden improvements in behavioral performance [37^{••}].

A suppression-based model of perceptual learning

One complication in addressing these criteria in animal studies is that behavioral improvements are gradual and training often spans many months. For training that extends over such long time periods there is an increased likelihood that learning reflects a sequence of physiological changes, each of which might have different loci and mechanisms. In this respect, training regimens that produce rapid and large behavioral changes are potentially more illustrative because of the increased likelihood that such changes arise from a particular mechanism and cortical locus. One such rapid learning effect, which also illustrates the potential of learning with respect to ignored stimuli, is the direction specific increases in motion sensitivity seen in random dot field distractors [28,29,30[•]]. Although the motion signals themselves are unattended, it should be emphasized that the signals are task-relevant in that their presence hinders task performance. It is therefore possible that perceptual learning in this case reflects an increased capability to suppress sensory signals that interfere with the task. The notion that perceptual learning might involve the selective suppression of signals that impair performance, instead of the enhancement of signals that improve performance, has considerable support in the psychophysical literature. Numerous studies have demonstrated that perceptual learning is particularly strong when stimuli are accompanied by sources of noise [3,38,39]. In extreme examples, perceptual improvements were only observed when noise was presented during training [40,41]. By manipulating the magnitude of this noise, several studies have concluded that perceptual improvements arise from a refinement of a perceptual template [40,42,43,44[•]], in which the influence of inappropriate signals is reduced,

rather than there being any increase in signal strength. A recent study of V4 responses to natural images embedded in noise is particularly relevant in this respect [32^{••}]. Monkeys were trained to recognize a set of images degraded by noise. During the course of training the subjects' ability to recognize these images improved: they were able to recognize progressively more degraded images. Recording the activity of V4 neurons revealed a selective increase in the responses to familiar degraded images, but no difference in the responses to familiar and unfamiliar images that were completely undegraded. This suggests that the effect of perceptual learning was to selectively reduce noise rather than to amplify the signals associated with the trained images.

Such arguments might also apply to signals that interfere with the optimal processing of stimuli but that are not evoked by external noise or associated with internal noise [38]. A neuron's responses are the least sensitive to stimulus variations for stimuli that are very close to its preferred stimulus. For example, imagine a cell tuned for orientation. Very small orientation changes around the optimal orientation do not change the response because the slope of the tuning curve is zero at the peak. However, similar changes in orientation around values defined by the bandwidth of the neuron will produce very different responses. Thus, in an orientation discrimination task the neurons providing the most relevant information for the task are those whose orientation preference is not exactly aligned with the orientations presented in the task [45]. In such a task, therefore, the signals of the highest magnitude do not convey task relevant information. For a decision model in which discrimination is based on the comparison of a sum of neuronal responses [46], these signals actually impair performance. Thus, one way to improve discrimination performance would be to selectively reduce the influence, either permanently or in a task-dependent manner, of the strongest neuronal signals evoked by the task. The studies examining orientation discrimination support this hypothesis: training results in a significant reduction in the number of neurons whose orientation preference corresponds with the trained orientation in area V1 [14]. A selective pooling of only the most sensitive detectors [13] could also produce a change in tuning properties in higher areas such as V4 [47[•]]. An analogous finding has recently been reported in the auditory cortex of monkeys that were trained to recognize modulated tones. In these animals, neurons responded with fewer spikes, but more selectively with respect to frequency, to trained tones than untrained tones [48[•]].

One point of this argument that is particularly appealing is that it connects the rapid and automatic changes in response properties that are associated with stimulus specific adaptation (which operates on the time scale of seconds and has been observed in a variety of sensory systems [49–55]) with the longer lasting changes asso-

ciated with perceptual learning [56]. In both cases sensitivity is increased by the selective suppression of responses with poor discriminative ability [57,58]. A long lasting improvement in discriminative abilities would result from attention or task related signals that extend the duration of changes observed during adaptation. Given evidence that improvements in orientation discrimination are not associated with a permanent suppression of signals, it is likely that these effects are task-specific. In this case, pooling mechanisms might be invoked during task performance that preferentially exclude the least sensitive neuronal signals for the task at hand, but do not permanently disable the potential incorporation of these signals for other tasks. This situation is analogous to that in spatial attention, in which the relative influence of task-irrelevant stimuli on neuronal responses is reduced [59].

Conclusions

Experimental evaluation of the aforementioned criteria for testing this suppression model, or any other model of perceptual learning, depends heavily on the extent of task-relevant neuronal signals. For tasks in which external noise is present, performance-limiting signals might be widely distributed. For such tasks, non-invasive methods that assess population activity, such as fMRI, repeatedly applied during training that occurs over many days could be used to explore the time course of learning. Such non-invasive methods would also prove useful in examining inter-subject variability because of the large number of subjects that could be studied. Finally, because these methods can assess activity throughout the brain, they are also well suited for identifying the particular cortical areas that are most strongly associated with learning. However, in many tasks it is likely that perception is based on more limited populations of neurons. For example, the improvements in direction selectivity of motion noise sensitivity in the aforementioned letter identification task suggest the involvement of only those neurons with a particular directional preference. In such cases, because of the limited spatial resolution of non-invasive methods, electrophysiological methods, especially those that allow recording of the same neuronal populations for long periods of time [37^{••}], are likely to be the most illustrative. Two approaches have proven especially fruitful in relating the activity of neuronal populations to perception. First, the contribution of individual neurons towards percepts is assessed by measuring the covariance between activity and performance on individual trials [60]. Second, the perceptual contribution of particular neuronal populations is assessed by observing the behavioral consequences of localized microstimulation [61,62]. It is likely that major progress in our understanding of perceptual learning is possible by using such techniques to test the criteria for relating physiological changes to learning.

Although the evidence discussed here suggests that primary sensory areas might not be as plastic as previously

thought, clearly the processing of sensory information can significantly and rapidly change according to experience. For example, response properties previously assumed immutable, such as receptive field size, could be subject to behavioral modification, and learning can occur for unattended stimuli. The dynamic nature of perception suggested by such results has profound implications on the interpretation of data from behaving animals because it is possible that even very brief training might be altering representations of interest. In particular, studies that explicitly try to link perceptual performance and neuronal signals require the animal to perform highly challenging tasks that involve months or years of training. Without evidence that the neuronal signals under study are immutable, observations made after such training might reflect changes associated with extensive training rather than fundamental properties of sensory processing. Therefore, the study of perceptual learning is crucial for a complete understanding of the relationships between neuronal activity and perception.

Acknowledgements

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