

Perceptual learning

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Perceptual learning, which is the improvement in perceptual performance due to practice, has been studied by psychologists for over a hundred years. Studies over the last two decades have shown that perceptual learning effects in the visual system are highly specific for a variety of properties of the training stimulus, including its location. A similar degree of specificity characterizes the auditory system. In the tactile system, learning effects are task-specific but transfer readily outside the trained location in many tasks. Selective attention may play an important role in shaping the specificity of perceptual learning, but its precise role in relation to other task requirements remains unclear. While the neural basis of these behavioural observations is far from being understood, perceptual learning effects appear to depend on plasticity of neuronal populations within sensory areas of the cerebral cortex.

PERCEPTUAL learning 'refers to an increase in the ability to extract information from the environment, as a result of experience and practice with stimulation coming from it', as E. J. Gibson¹ put it in her classic monograph on the subject. The empirical study of perceptual learning can be traced back to the work of Volkman in the latter half of the nineteenth century¹. One type of perceptual learning, the improvement in perceptual performance that occurs with practice, has been studied intensively in the laboratory and is the focus of the present review. A common example is improvement in the ability to distinguish different wines by taste¹. Along the same lines, the professional tea-taster represents the pinnacle of such achievement, no doubt due to superimposition of the learning process onto his inherent special ability. Gibson¹ also pointed out that various professions demand the acquisition of specific perceptual skills linked to the use of particular instruments. A case in point is the learning of physical methods of diagnosis by medical students. Every medical student remembers those agonizing first days on the wards when their instructors asked them to listen to specific heart sounds and murmurs, using the stethoscope. Initially, these were meaningless sounds which slowly, over days and weeks, crystallized into meaningful sounds. Common experience also tells us that there exist considerable individual differences in the rates of perceptual learning and in the final level of ability attained.

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Gibson^{1,2} made a detailed study of perceptual learning and reviewed the literature extensively. The reader interested in historical perspective is referred to her writings, which provide masterly accounts of the phenomenology of perceptual learning and address theoretical issues that psychologists and neuroscientists are still grappling with today. She conceived of perceptual learning as a process of progressive differentiation whereby the subject learns 'by discovering the dimensions of difference between members of the set of stimuli presented'¹. She considered that while the subject learns to filter out irrelevant variables, differential properties of stimuli are abstracted, emphasizing that perceptual learning, like all of perception, is an adaptive process driven by active exploration of the environment by an organism. Further, she recognized the importance of selective attention to the specific cues afforded by the stimuli used during training¹. When one reads the current literature on perceptual learning, one cannot but be impressed by Gibson's prescience. The present review provides a selective, rather than exhaustive, account of recent developments in the field with particular emphasis on contributions to understanding the neural basis of perceptual learning.

Specificity of perceptual learning in the visual system

Considerable experimental effort has been devoted to the question of the degree of specificity of practice effects for the task used in training and the extent of transfer to other experimental conditions. As we shall see, the results of this kind of psychophysical inquiry in human subjects have yielded substantial insight into the potential locus of the relevant neural mechanisms. No clear consensus emerged from work in the latter half of the nineteenth century and in the early part of the twentieth century². More recent research in the visual system has established that perceptual learning, in a wide variety of tasks, is highly specific for the retinal location and numerous other properties of a visual stimulus, as recently reviewed^{3,4}.

A landmark paper concerning the specificity of perceptual learning is that of Ramachandran and Braddick⁵. The stimuli they used were random-dot stereograms, which had previously been introduced to vision research by Julesz⁶. These stereograms consist of images presented

independently to each eye, the two images being identical except for a lateral shift of part of the pattern between them. Julesz used these stereograms to demonstrate that the binocular disparity between the dichoptically presented images was sufficient for depth perception. It was also known from Julesz' work that the percept of depth in random-dot stereograms requires a finite time period ranging from a few seconds to a few minutes for an inexperienced observer, while occurring much faster on subsequent presentations. Ramachandran and Braddick⁵ found that when the stereograms were made up of oriented line elements, such 'learning' transferred completely to a different pattern with the same element orientation, but failed to transfer to a pattern whose elements were orthogonally oriented. Subsequently, Ramachandran⁷ showed that this kind of perceptual learning was also specific to the retinal location of the stimulus, i.e. the learning effects did not transfer to a stimulus at a different retinal location. Similarly, practice-related improvement in performance is specific for grating orientation and spatial frequency in a task requiring discrimination of grating spatial phase⁸, and for the retinal location and orientation of background elements in a task relying on preattentive texture segregation⁹.

These findings have led to the suggestion that practice effects are mediated by plasticity in particular neuronal pools in primary visual cortex, since it is only here that the neuronal responses show the kinds of specificity that are manifested behaviourally in the experiments summarized above^{3,9}. Karni and Sagi¹⁰ distinguished two phases of perceptual learning in their preattentive, visual texture segregation task: (i) a fast, within-session phase that typically occurred only in the first session for a given subject, and (ii) a slower, between-session phase that reached an asymptote in 5–10 training sessions. They reported that between-session learning (but not within-session learning) was also monocular or eye-specific, i.e. if training was performed through one eye, the learning effects did not transfer to the other eye^{9,10}. This implies that the learning effects are exquisitely specific, depending on a relatively small pool of neurons that are strongly monocular as well as orientation-specific. Such a combination of properties characterizes a sub-group of neurons in primary visual cortex. However, the monocularity of these learning effects is controversial. Another group reported complete inter-ocular transfer of learning in a study¹¹ using the same visual texture segregation task used by Karni and Sagi^{9,10}, and also in a separate study of grating orientation discrimination¹². Recent data from Karni and co-workers¹³ suggest that there may be considerable inter-individual differences in the extent of inter-ocular transfer of learning. This issue must be considered unresolved at the present time.

Monocularity aside, the specificity of perceptual learning appears to be a general principle in the visual system. This has interesting and important implications, for it leads to the design of psychophysical experiments that can offer valuable information about the relevant neural substrate. For instance, training-induced improvement in the ability of humans to discriminate directions of motion differing by 3° is restricted both spatially and directionally, i.e. the improvement does not transfer either to locations distant from the trained one or to directions 45° or more away from the trained direction¹⁴. Since the perception of visual motion is thought to depend on an area of cortex known in the macaque monkey as MT (the middle temporal area, a higher-order visual area), where most neurons are directionally selective¹⁵, these findings suggest that perceptual learning in this case involves the same MT neurons that mediate the perception of visual motion. Direct evidence has now been gathered to support this idea and will be discussed later in this review. Incidentally, these learning effects showed about 75% inter-ocular transfer but no inter-hemispheric transfer¹⁴.

Another example is the study of perceptual learning in visual hyperacuity, which is the ability of the visual system to resolve spatial details with a precision greater than would be expected on the basis of photoreceptor density. Human performance in a hyperacuity task improves rapidly over a few tens of trials, and does not transfer to tasks using stimuli that are oriented orthogonally to or differ in form from those used in training¹⁶. Moreover, a simple neural network can be 'trained' to achieve performance with similar characteristics, consistent with the notion that the learning effects in real brains occur at relatively early stages of processing¹⁶. Interestingly, also, improvement in human performance on a vernier acuity task, a type of hyperacuity task, is accompanied by changes in orientation tuning characteristics of the task¹⁷. In highly practiced observers, the elevation of vernier thresholds induced by a spatial noise mask is maximal when the mask is oriented at a 10° angle to the vernier lines. The function relating vernier threshold to the angle between vernier lines and mask is Gaussian in form, and narrows following training (i.e. the standard deviation of the Gaussian function decreases). Despite wide inter-individual variations in improvement, there is a close correspondence between improvement in vernier acuity and narrowing of the orientation tuning function. This is consistent with practice-induced sharpening in the orientation tuning of the relevant neurons acting as spatial filters—an idea highly reminiscent of Gibson's¹ formulation of perceptual learning. These findings lend support to the notion that certain neuronal properties are not immutable but, rather, are dynamically modifiable throughout life.

Let us consider one more example of the exploration of specificity in the visual system, this time with a somewhat different result. Vidyasagar and Stuart¹⁸ presented subjects with stereo half-images consisting of tilted line elements. Presentation was sequential rather than dichoptic, and they investigated the ability to perceive form based on the apparent motion between the images. Not surprisingly, a period of learning was required for subjects to experience the percept of form in their 'kinematograms', as in the case of dichoptically presented stereograms (see above); however, the form-from-motion percept evolved more slowly than the form-from-disparity percept, suggesting that the former task is more difficult. The novel finding was that learning effects with the kinematograms transferred almost completely to images containing orthogonally oriented line elements and orthogonal directions of motion, although detection of the lines and their motion direction was essential to the form percept. Vidyasagar and Stuart¹⁸ concluded that the neural locus of learning in this case must be at a higher level of the visual processing hierarchy than the level of pattern and motion detectors, i.e. beyond MT.

Role of feedback in perceptual learning

Gibson^{1,2} considered this topic at some length and little definitive knowledge has been added since her writings. She pointed out that feedback about performance was not essential for perceptual learning to occur, although in some instances feedback magnified the learning effect. This is consistent with the idea that perceptual learning effects belong to the class of learning effects that are termed 'non-categorical' or 'unconscious'. That is, they appear to involve recalibrations whose details are not *per se* accessible to consciousness (although this does not imply that the processes themselves cannot be influenced by a conscious process such as attention, see below). Other examples of non-categorical learning include the learning of skills, e.g. motor skills like learning to ride a bicycle or swim. Such kinds of learning are believed to depend on the very neural structures that mediate performance, which is consistent with the body of work on perceptual learning cited above. Of more recent studies of the effect of feedback on perceptual learning, two^{19,20} studies found no effect and a third¹⁴ study found a small effect, but only in the case of a relatively difficult discrimination.

Role of selective attention in perceptual learning

Once again, Gibson¹ recognized the importance of selective attention in the process of perceptual learning.

It has been proposed that the specificity of perceptual learning for retinal location (see above) is actually a consequence of spatially selective attention²¹. O'Toole and Kersten²¹ asked subjects to distinguish between a left-pointing arrow just above the fixation point, a right-pointing arrow just below the fixation point and an upward-pointing arrow occurring with equal probability in either of these two positions. They reasoned that true retinotopic specificity of perceptual learning predicted detection advantages for the left- and right-pointing arrows and none for the upward arrow, while specificity depending on spatially selective attention predicted no interaction between stimulus and position. Since detection of all stimuli was equally good in both practised positions, these workers concluded that spatially selective attention rather than retinal specificity was at work. However, they failed to (i) provide details of the perceptual learning they observed; (ii) establish that perceptual learning in this task was indeed specific to one or other arrow type presented individually; (iii) address the fact that the distinction called for could have depended on a 'cognitive' rather than a 'perceptual' process; and (iv) explore the effect of a wider spacing between their stimuli which were presented so close to fixation that the two locations might well have been treated by the brain as being practically the same. Thus, the notion that location-specificity in perceptual learning depends on spatially selective attention²¹, while attractive, must be considered unproven at the present time.

Attention can be selective not only for regions of space but also for particular aspects of a stimulus at a given location²². When subjects were asked to discriminate line orientation, performance improved with practice, but no improvement in orientation discrimination occurred when they were asked to discriminate the brightness of the same lines²⁰. Similarly, when subjects were shown a rectangular array of line elements and asked in one case to discriminate the orientation of the long axis of the array and in the other case to detect the presence of a uniquely oriented element in the array, learning effects did not transfer between the 'global' and 'local' tasks²³. In both these instances, subjects were presumably attending to different aspects of the identical stimulus in each experimental condition and learning effects were specific to the attended condition. The generality of this phenomenon and the extent to which selective attention is responsible for perceptual learning remain open questions.

Perceptual learning in other sensory systems

Auditory system

The specificity of perceptual learning is by no means peculiar to the visual system. Gibson¹ reviewed a number

of studies showing that improvement in auditory discrimination of pitch is highly specific for the frequency of the tone used. An interesting illustration of the specificity of auditory perceptual learning is that people acquire the ability to distinguish specific sounds in their native language while losing the ability to distinguish certain sounds in other languages. For example, the Hindi sounds 'tha' and 'dha' can be universally distinguished by infants under a year of age²⁴. The ability of adults to discriminate these two syllables, however, is affected by their specific linguistic experience: Hindi speakers or those with early exposure to spoken Hindi can make this distinction, but English speakers lacking exposure to Hindi cannot^{24,25}. The latter group can acquire the ability to make the discrimination, which depends on a voicing contrast, although they apparently cannot learn to make a distinction (Hindi 'ta' versus 'tha') that depends on the precise point of contact made by the tip of the tongue during articulation (a retroflexed palatal contact in the first case and a dental contact in the second)²⁵. Recently, it has been shown in a cross-cultural study of American and Swedish babies, that six-month-old infants can distinguish phonetic prototypes in their native language (which they have heard since birth) but not in a foreign language!²⁶.

The specificity of auditory perceptual learning has been dramatically exploited in the rehabilitation of certain linguistically impaired children^{27,28}. These children are impaired in the auditory processing of language due to an inability to discriminate 'fast formants' in speech, i.e. particular consonant sounds that are composed of relatively high-frequency components. CD-ROM games were developed that put the children through progressive perceptual training routines using non-speech sounds, phonemes and fluent speech. Initially, the particular sounds they had difficulty with were artificially elongated and differentially amplified. The differences between these sounds and normal speech were progressively reduced during training and the children made tremendous gains in their auditory abilities as well as in their linguistic development!

Tactile system

The issue of the specificity of perceptual learning is less clear in the tactile system. Volkman's pioneering studies indicated that the threshold separation for discrimination of two points from one declined with practice and that the effect of practice transferred between hands¹. Further studies of two-point discrimination on the forearm suggested that practice effects transfer outside the trained zone to homologous areas contralaterally^{29,30}, but not to surrounding areas²⁹. It is difficult to evaluate these reports in view of the small numbers of subjects (two

subjects in each of the last two studies cited) and the generally low reliability of the two-point discrimination task^{31,32}. Studies of vibrotactile pattern identification on the fingerpad using the Optacon, a reading aid for the blind, have emphasized the generalizability of tactile learning^{33,34}. Learning effects transfer from one subset of the alphabet to another³³. Craig³⁴ found that training on a letter identification task improved performance on this as well as an untrained task (gap detection). Practised sighted subjects and blind Braille readers with and without specific practice on the Optacon all did equally well. Based on these findings, Craig³⁴ suggested that tactile experience results in a general enhancement of tactile sensitivity. Others³⁵ have emphasized that practice-related improvement in vibratory frequency discrimination in owl monkeys is specific, albeit incompletely, for the trained finger.

Owing to this uncertainty, Andro Zangaladze and I embarked on a study of tactile learning in my laboratory. Texture perception emerges from introspective³⁶ and empirical observations^{37,38} as a prime aspect of the tactile sense. We used gratings, consisting of alternating ridges and grooves, which are simple textures that have been employed in numerous psychophysical and neurophysiological studies of the tactile system³⁹, to study the task- and location-specificity of tactile learning. Our principal finding⁴⁰ was that perceptual learning in the tactile system was quite task-specific, as in other sensory systems, but showed a unique propensity to transfer between fingers of either hand, in contrast to visual learning which is quite location-specific (see above). We found substantial to complete inter-digital and inter-hemispheric transfer of tactile learning in tasks where the finger was actively moved across gratings to discriminate their roughness, as well as in a task where gratings were indented into the immobile fingerpad for subjects to determine their orientation⁴⁰. We have now found a similar extent of transfer of learning effects in a tactile hyperacuity task^{40a}. Our failure to find digit-specificity in tactile learning appeared contradictory to the work on owl monkeys cited above³⁵. However, we analysed the data obtained on vibratory frequency discrimination in owl monkeys and found that, in fact, the results were quite comparable to ours: there was substantial transfer of practice-related improvement between adjacent fingers in this study, despite the authors' emphasis on specificity.

In a recent abstract, it was reported that learning effects in spatial localization of vibratory stimuli on the finger also transfer between hands⁴¹. However, in another recent abstract, inter-manual transfer was not observed for vibratory amplitude discrimination on the palm⁴², consistent with the location-specificity of visual learning. Even more recently, training on discrimination of the duration of the interval between two vibrotactile stimuli

was found to generalize across locations and between hands as well as to shorter intervals, but not to longer intervals or stimulus frequencies other than the trained one⁴³. It is not possible, at present, to reconcile these seemingly disparate findings from various studies. It seems likely, however, that the transfer characteristics of tactile learning are variable depending on stimulus location and task requirements, and reflect the specificity of the neuronal populations involved. Since the study of neural coding in the tactile system is not as advanced as in the visual system, further neurophysiological study will be required for a fuller interpretation of these psychophysical findings.

Neural correlates of perceptual learning

Relatively few studies have directly addressed the neural correlates of perceptual learning. Merzenich and co-workers trained owl monkeys on vibratory frequency discrimination with a particular finger. Subsequent multi-neuron recordings under anesthesia revealed that the cutaneous representation of that finger within the somatotopic map in area 3b (the primary cortical area receiving cutaneous input) was expanded⁴⁴, extending into area 3a (ref. 45) (which normally is dominated by deep inputs); receptive fields on that finger were larger and more numerous in area 3b (ref. 44) and temporal synchrony within the population discharge was higher⁴⁶. The last of these measures correlated best with improved (between-session) psychophysical performance^{35,44-46}. Similarly, training of owl monkeys on auditory frequency discrimination led to improvement that was specific to tone frequency and expansion of the area of primary auditory cortex representing the trained frequency: the extent of expansion correlated with performance improvement⁴⁷. Other measures such as the sharpness of frequency tuning and response latency also changed, but did not correlate with performance changes⁴⁷.

These experiments led to the conclusions that the maps that represent receptor sheets topographically, as well as some functional properties of neurons are modifiable by sensory experience in adulthood and are therefore candidate neural processes mediating perceptual learning. The reliance in these experiments on multi-neuron recordings under anesthesia may have limited the range of neuronal responses observed, so that candidate neural processes are not necessarily restricted to those studied. That neural changes related to perceptual learning occur in primary sensory cortices is consistent with the high degree of specificity of learning effects noted psychophysically. The changes, however, were substantially decreased by engaging the monkey in an auditory discrimination task during tactile training⁴⁴, or vice versa⁴⁷. This indicates the dependence of the neural changes on behavioural relevance of the stimuli, perhaps

signaled by a 'top-down' process such as attentional selection. Thus, processes in higher-order sensory areas may also be involved in perceptual learning³. This is supported by a few studies in behaving macaque monkeys, demonstrating changes in neuronal responses in higher-order visual areas with repeated presentation of particular stimuli in the same session^{15,48,49}.

In one of the last-cited studies¹⁵, changes were reported in area MT that consisted of short-term improvements in neuronal sensitivity to directional discrimination, paralleling within-session perceptual learning manifested as psychophysical improvement in discriminating motion direction. In this report, the investigators also described an interesting experiment to probe the neural locus of perceptual learning. They took advantage of the relatively large receptive fields of MT neurons, selecting two non-overlapping sub-regions of the receptive field with qualitatively similar directional properties. Training was restricted to one sub-region. They found that the improvement in neuronal sensitivity extended to the untrained sub-region, consistent with the notion that perceptual learning in this case involved MT neurons. It is worth noting, as these authors did, that an alternative possibility cannot be ruled out: the relevant neuronal plasticity may have involved more complex multi-neuron networks.

Analogous dynamic modifiability of neuronal response properties has also been demonstrated in studies that have not directly addressed perceptual learning. Prolonged contact of one or two fingertips of owl monkeys with a rotating grooved wheel results in unusually small receptive fields on the stimulated cutaneous zones, whose representations in somatosensory cortex are expanded⁵⁰. Intracortical microstimulation in somatosensory cortex of rats and New World monkeys induces rapid expansion of the cortical area with receptive fields corresponding to the site of stimulation⁵¹. In humans, studies using somatosensory evoked potentials and transcranial magnetic stimulation suggest that the hand representation in somatosensory cortex is expanded in Braille readers relative to controls⁵². Also, magnetoencephalographic recordings of somatosensory cortical activity evoked by tactile stimuli to the fingers indicate that the representation of the left hand is enlarged in musicians who play stringed instruments⁵³.

What mechanisms mediate these diverse neural changes? One idea that has attracted considerable interest is that Hebbian (or similar) changes in the strength of synaptic connections are involved^{54,55}. In other words, correlated activity of pre- and post-synaptic neurons is thought to strengthen the synaptic connection between them, while uncorrelated activity leads to synaptic weakening. (Essentially similar mechanisms have been proposed to be the basis of memory, although obviously the neural locus is different in this case.) In support of

this is the finding, in auditory cortex of behaving monkeys, that the functional connection (evaluated by the cross-correlogram) between neurons was strengthened when activity in one neuron, induced by an auditory stimulus, was paired with activity in another neuron during a behaviourally relevant task⁵⁶. In similar vein is the mutability of neuronal selectivity for orientation, ocular dominance and binocular orientation disparity induced by iontophoretic stimulation or inhibition of single neurons in cat striate cortex^{57,58}. A recent psychophysical demonstration that training increases the extent of local spatial interactions in vision, specifically along the axis of stimulus orientation or orthogonal to it, also suggests a Hebbian process cascading along particular connections⁵⁹, such as orientation-specific long-range cortico-cortical connections³. Thalamocortical excitatory synaptic actions mediated by NMDA receptors in layer IV may be involved in the progressive strengthening of preferred responses, while suppression of non-preferred responses may depend on lateral inhibitory interactions in the upper layers, mediated by GABA receptors^{60,61}. Neuromodulatory mechanisms are probably superimposed on these cortical processes⁵⁵. One piece of evidence for this is the finding that between-session learning of a visual texture segregation task, which requires a few hours of consolidation before it becomes manifest, fails to persist overnight if subjects are deprived of rapid-eye-movement (REM) sleep⁶². This last observation is particularly exciting because REM sleep is the period during sleep when dreams occur, and it has long been conjectured that dreams are important in consolidation of memories. In the present context, it points to cholinergic influences on the relevant neural plasticity, since the cholinergic system is implicated in the generation of REM sleep.

Conclusions

Clearly, much more work needs to be done before we can understand the neural basis of perceptual learning. However, as we approach the close of the twentieth century, we are well poised to ask the right questions and to further unravel the mysteries of the brain in the especially intriguing field of perceptual learning that lies at the confluence of sensory physiology and cognitive neuroscience.

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MEETINGS/SYMPOSIA/SEMINARS

International Conference on Environment and Bioethics

Date: 14-16 January 1999

Place: Chennai

Areas of focus: Health ethics and environment; Biodiversity and environment; Philosophy of environmental ethics; Bioethics and bioresources; Bioethics and education.

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National Symposium on Tropical Meteorology (TROPMET-99)

Date: 16-19 February 1999

Place: Chennai

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Frontiers in Catalysis in the 21st Century

Date: 19-20 January 1999

Place: Dehradun

The symposium will focus on the role of catalysis in energy efficiency, environmentally compatible processing and efficient conversion of unconventional/conventional fossil fuel resources.

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