A common framework for perceptual learning

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In this review, we summarize recent evidence that perceptual learning can occur not only under training conditions but also in situations of unattended and passive sensory stimulation. We suggest that the key to learning is to boost stimulus-related activity that is normally insufficient exceed a learning threshold. We discuss how factors such as attention and reinforcement have crucial, permissive roles in learning. We observe, however, that highly optimized stimulation protocols can also boost responses and promote learning. This helps to reconcile observations of how learning can occur (or fail to occur) in seemingly contradictory circumstances, and argues that different processes that affect learning operate through similar mechanisms that are probably based on, and mediated by, neuromodulatory factors.

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Introduction

Recent behavioral and neuroscience research demonstrates a significant degree of plasticity within the sensory cortices [1,2]. However, the extent of the sensory plasticity and the circumstances in which it occurs in adult animals are matters of great debate [3–6]. The amount of plasticity and the readiness for evoking learning processes is significantly greater during early development than in post-ontogenetic adult systems. For example, during early weeks of life, blocking visual input from one eye results in dramatic restructuring of ocular dominance maps in visual cortex, but after a few months of age such manipulations have minimal effects [7]. Furthermore, training adult subjects for multiple weeks on visual tasks can often fail to produce learning effects [8] and months of training can fail to elicit plasticity in the visual cortex [9]. Differences can be assumed to be due to the presence of additional mechanisms during development that control maturation and growth processes and that are lacking, or differently regulated, in adults (for reviews, see [10,11]).

However, studies of perceptual learning show that, even in adults, perceptual abilities can be sharpened with extensive exposure or training. For example, experts such as radiologists develop with training refined abilities to distinguish subtle patterns of tumors in images that show no pattern to the untrained eye. Behavioral studies show that effects of perceptual learning can be highly specific to the trained stimulus features — for example, to auditory frequency and intensity [12••], to digits used in tactile training [13], or to retinotopic location [14,15], visual orientation [16,17] and direction [15,18]. The lack of generalization is taken as evidence that learning might be mediated by cells in early sensory areas [19]. Recanzone *et al.* [20] were the first to demonstrate that the gain in training-induced performance was correlated with the amount of expansion of the cortical map that represented the trained skin area, providing the first evidence for alterations of low-level cortical processing in perceptual learning. Adult sensory plasticity has now been observed in all sensory systems.

Given that learning occurs in developing and adult systems, an important question in evaluating the aforementioned studies of perceptual learning is how do we know what to learn? In other words, how does a neural system know which information is behaviorally relevant and which is not? There must be some mechanism that gates what is learned (i.e. to control what aspects are allowed and what aspects are restricted).

Numerous studies give answers to this question, but they are typically presented in support of opposing viewpoints. For example, evidence showing that attention has a role in perceptual learning is presented as evidence that passive learning does not occur [21]. Also, paradigms that show evidence of passive learning [22–23], reinforcement processes in learning [24–26] or how stimulation procedures result in learning [27••,28•] are often used as evidence against attentional learning theories. In this article, we review perceptual learning studies from the past two years and discuss the current prevailing views of when sensory plasticity occurs. We attempt to reconcile how these seemingly contrasting views of learning can operate in parallel with each other and through similar actions.

Attentional learning

Perceptual learning has probably been most extensively studied in the visual modality. In such studies, subjects

are typically trained explicitly to distinguish visual features, and learning is assessed by how performance or neuronal activity is modified through training. These studies show that learning of features is determined not only by stimulus presentation but also by the subjects' tasks [14,21,29]. For example, orientation tuning curves of macaque monkey V1 cells are sharpened in relation to the location of oriented stimuli that were discriminated during training, but not in relation to a location where orientated stimuli were merely exposed [17]. Similarly, behavioral and electrophysiological studies of hyperacuity show that encoding of perceptual learning is affected by specific task demands [30,31] and that neuronal tuning curves in V1 change according to which task the animal is performing [32].

Along similar lines, studies of tactile and haptic learning find that extensive training yields improvements in tactile discrimination abilities [20]. These studies also show a lack of cortical reorganization in animals that did not attend the stimuli during a discrimination tasks. Furthermore, electrical source localization following somatosensory evoked potential recordings after finger stimulation reveals different dipole locations for unattended versus attended conditions, suggesting that attention has an important role in modulating the cortical processing of tactile information [33].

Studies of auditory learning show additional evidence of how attention influences learning. For example, in a recent study Polley *et al.* [12••] exposed rats to auditory stimuli that varied in both frequency and intensity. Rats that were trained to discriminate the frequency of these stimuli demonstrated improved performance in frequency discrimination and an expanded representation in the primary auditory cortex (A1) of the 4 kHz frequency used during training, whereas no such frequency-related learning was found in animals trained on an intensity-discrimination task. However, these animals did demonstrate improved intensity discrimination and expanded representation of the trained intensity range in the suprarhinal auditory field, whereas frequency-trained rats showed now such improvements.

Research along these lines has been taken as support for the hypothesis that subjects need to be aware of and focus their attention on a stimulus feature for that feature to be learned. In this framework, focused attention mediates selection and learning of only the information that is deemed to be of importance.

Reinforcement and neuromodulatory systems

However, recent behavioral research has shown that perceptual learning of visual motion can occur as a result of mere exposure to a subliminal stimulus — that is, without external reinforcement, the subject actively attending to a task, or the motion-stimulus being a relevant feature of the particular task [23,24,34]. For example, Seitz and Watanabe [24] peripherally presented four different directions of motion an equal number of times while subjects performed a foveal letter-identification task. Sensitivity for each motion direction was assessed by discrimination tasks that preceded and followed a week of practice with the letter task. Improved performance was found for the motion direction that was temporally paired with the letter-task targets but not for the other motion directions. A similar experiment showed that learning for the paired motion direction fails during the attentional blink of a target, indicating that learning is gated by a reinforcement signal that is triggered by target processing [35••]. A related study [36•] showed that depth perceptions of bistable stimuli can be altered by classically pairing the stimuli with an additional cue.

Although direct evidence for reinforcement in visual perceptual learning is somewhat lacking (however, see [25]), the role of reinforcement has been clearly established in studies of auditory learning. For example, pairing a tone with stimulation of the ventral tegmental area (VTA), which releases dopamine, results in increased representations of the paired tone in A1 [26]. Similarly, pairing a tone with stimulation of the nucleus basalis of the basal forebrain, which releases acetylcholine, results in an increased representation of the paired tone in A1 [37]. If the temporal relationship between the VTA or nucleus basalis stimulation and the tone presentation is reversed, such that the tone follows the stimulation, representations of the tone in A1 are reduced [38,39]. In human subjects, application of an antagonist of muscarinic acetylcholine receptors (scopolamine) blocked the conditioning-specific enhancement of blood oxygen-level-dependent (BOLD) responses in the auditory cortex, implying a role for acetylcholine-mediated modulation of experience-dependent plasticity [40].

These findings suggest that the learning found in behavioral reinforcement paradigms [12••,41] might be regulated through the release of neuromodulators, such as acetylcholine and dopamine, which gate learning, and thus restrict sensory plasticity and protect sensory systems from undesirable plasticity. It is important to note that these same neuromodulators have also been implicated in attentional processes, and thus they might provide a mechanistic basis that is common to attentional and reinforcement learning [4].

Passive learning

A recent coactivation paradigm developed by Dinse and coworkers shows that improvement of tactile performance in humans can be achieved through passive, unattended stimulation on a time-scale of a few hours or less [42,43••,44–48]. Coactivation induces improvements of tactile perceptual performance and results in cortical reorganization. The amount of perceptual gain resulting

from this procedure linearly correlates with the amount of cortical reorganization, and suggests a causal relationship [44,45,47,48]. Coactivation closely follows the principles of Hebbian learning, which states that synchronous neural activity drives neuronal plasticity. The Hebbian nature of coactivation was demonstrated in a control experiment, in which only a small skin area was stimulated (i.e. there was no coactivation) [48]. This protocol caused neither changes of discrimination performance nor changes in cortical activation, implying that 'co'-activation is indeed crucial. Coactivation-induced improvements of tactile acuity were large (15–20%) for short-term passive stimulation, and were not much smaller than gain in performance after a year of practice in musicians (20–25%) [46]. Protocols consisting of low-frequency stimulation (LFS) or high-frequency stimulation (HFS) can also result in perceptual changes, with HFS improving and LFS impairing perception [49,50].

Passive stimulation paradigms have also been shown to cause reorganization of visual cortex. For instance, V1 plasticity can occur in mice owing to mere stimulus exposure [51•]. Other evidence of passive visual learning is found in situations where there are retinal lesions [52] or macular degeneration [53]. However, other studies find limited evidence for V1 reorganization [54••,55] and evidence for stimulus-driven plasticity in primates remains highly controversial (see [5,6] for discussion). In fact, plasticity in primate visual cortex can fail even in cases of intense training [9].

Many reports indicate that prolonged and unattended stimulation is ineffective in driving plastic changes. In studies of auditory learning, pairing of sensory stimulation with electrical stimulation of the nucleus basalis has been shown to result in rapid and selective reorganization of cortical maps [37]. However, control experiments revealed that sensory stimulation alone, without stimulation of the nucleus basalis, was ineffective. These apparent discrepancies with passive learning can be settled in the light of the findings of Dinse *et al.* [48] that simple (i.e. small field) prolonged stimulation had no effect on discrimination abilities, and that more massive 'coactive' stimulation was required for plasticity. To accomplish this, the sensory stimulation must take advantage of neuronal processing principles such as spatial (coactivation) and temporal (high-frequency) summation that work together to drive the neural system more effectively.

Electrical and magnetic stimulation

The idea of unattended, activation-based learning has been taken one step further still by short-cutting the entire sensory pathway, by enforcing synchronized activity in a specific brain region. For example, intracortical microstimulation (ICMS) — local application of high-frequency weak electrical stimulation that resembles known long-term potentiation (LTP) protocols — has been demonstrated to change the sizes of receptive fields and cortical maps in the somatosensory cortex [56]. In area 18 of adult cats, ICMS altered the layout of visual orientation-preference maps over a range of several millimeters [22].

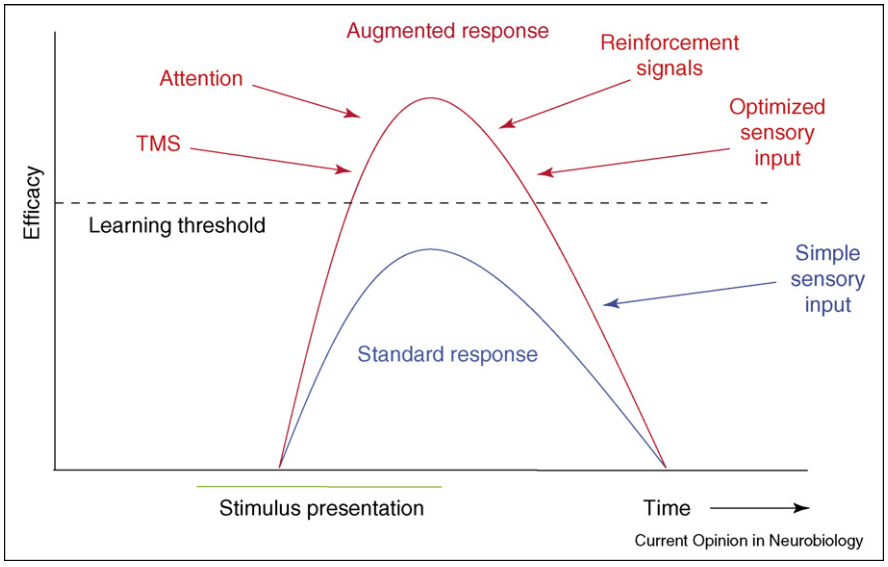
Transcranial magnetic stimulation (TMS) can also induce learning [27••,57•]. Applying 20 min of 5 Hz TMS over an area of primary somatosensory cortex (SI) that represents a finger caused changes that were similar to those observed after coactivation. These changes were paralleled by an expansion of the cortical finger representation in SI and recovered after about 2–3 h [27••]. Application of high-frequency TMS ($\geq$5 Hz) during an ongoing training or stimulation procedure had a further potentiating effect on the training outcome [28•,58]. These TMS findings demonstrate that meaningful improvement of perceptual performance can even be obtained by specific (high-frequency) stimulation of brain areas from outside the skull. Most notably, this intervention does not leave the cortical processing in a disorganized state but, on the contrary, leads to the emergence of a different, yet organized and meaningful, behavior as indicated by the improvement of discrimination performance.

Conclusions

In this review, we have summarized recent findings showing that perceptual learning can occur not only under training conditions but also in situations that lack attention and reinforcement. To explain their effectiveness, we suggest that all these types of learning occur through a similar process — namely, that the key to learning is that sensory stimulation needs to be sufficient to drive the neural system past the point of a learning threshold.

This idea is emphasized in Figure 1, which illustrates that typical sensory inputs by themselves are not sufficient to drive learning. However, well-known plasticity-inducing factors such as attention or reinforcement can affect learning by interacting with stimulus signals to surpass this learning threshold. Furthermore, we argue that optimization of sensory inputs (such as by synchronization or multisensory stimulation [59•]), or magnetic or electrical stimulation, can also boost signals that normally are insufficient to surpass this learning threshold. In particular, specific spatiotemporal stimulation properties such as high-frequency, burst-like stimulation protocols, which induce synaptic plasticity in brain-slice preparations, are also effective in driving perceptual improvements [41,42]. We postulate that this common learning mechanism involves a Hebbian learning process gated by neuromodulatory signals (e.g. acetylcholine and dopamine) that are activated both in attentional and reinforcement paradigms. However, further research will be required to address this hypothesis; particularly in the case of the passive protocols.

Figure 1



Schematic illustration of the processes that gate perceptual learning. The key assumption is that for sensory stimulation to be sufficient, it must drive the neural system past the point of a learning threshold. Whereas simple sensory stimulation is insufficient, factors such as attention or reinforcement have important permissive roles. In addition, sensory inputs or magnetic or electrical stimulation that are optimized to meet further requirements such as synchronization can also boost signals that normally are insufficient to surpass this threshold. In particular, specific spatiotemporal stimulation protocols such as high-frequency burst-like stimulation, which induce synaptic plasticity in brain-slice preparations, are highly effective.

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