



A unified model for perceptual learning

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Perceptual learning in adult humans and animals refers to improvements in sensory abilities after training. These improvements had been thought to occur only when attention is focused on the stimuli to be learned (task-relevant learning) but recent studies demonstrate performance improvements outside the focus of attention (task-irrelevant learning). Here, we propose a unified model that explains both task-relevant and task-irrelevant learning. The model suggests that long-term sensitivity enhancements to task-relevant or irrelevant stimuli occur as a result of timely interactions between diffused signals triggered by task performance and signals produced by stimulus presentation. The proposed mechanism uses multiple attentional and reinforcement systems that rely on different underlying neuromodulators. Our model provides insights into how neural modulators, attentional and reinforcement learning systems are related.

Introduction

A central issue in neuroscience is how the adult brain selectively adapts to important environmental changes. Although the brain needs to adapt to new environments, its architecture must protect itself from modification from the continual bombardment of undesirable information. How the brain solves this so-called ‘stability–plasticity dilemma’ [1,2] in its sensory areas is largely unresolved. The goal of the present review is to clarify the mechanisms that guide plasticity in our sensory system.

Studies of perceptual learning [3–8] show that even in adults perceptual abilities can be sharpened with repeated exposure or training. For example, with training, experts such as radiologists develop refined abilities to distinguish subtle patterns of tumors in images that show no pattern to the untrained eye [9]. In attempts to better understand such perceptual learning, laboratory studies have demonstrated that detection or discrimination thresholds can be reduced and usually show a high degree of specificity with respect to the trained feature (Box 1). These specificity effects have been regarded as a manifestation of plasticity in sensory cortical processes.

An important question in evaluating 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? Given that plasticity can occur in adult sensory systems, there must be some mechanism that gives constraints to gate what is

learned (i.e. to control what aspects are allowed and what aspects are restricted).

A prevailing hypothesis was that focused attention must be directed to a feature for that feature to be learned [8,10–13]. In this framework, attention works to select and learn only the information deemed to be of importance. That is, plasticity is restricted by attention. However, recent evidence from studies of ‘task-irrelevant’ learning [14–16] show that perceptual learning can occur in the absence of focused attention to the learned feature.

How does task-irrelevant learning occur? One possibility is that task-relevant learning and task-irrelevant learning are formed by separate mechanisms. However, we will propose a more plausible model in which the same mechanism produces both task-relevant and task-irrelevant learning. Namely, when signals that are triggered and diffused as a result of a task performance (reinforcement signals) and signals that are produced by presentation of a task-relevant or task-irrelevant feature

Box 1. Rigidity of sensory plasticity

Plasticity in the early sensory systems has traditionally been thought to occur only during early development and then to be hard-wired in adults. This view has been substantiated by studies of critical period development in which gross plasticity of early sensory areas only occurs for a brief period after birth. This data was used to support the hypothesis that the low-level sensory stages need to consistently process primitive sensory features; such as in vision orientation, spatial frequency, and local motion.

Studies of visual plasticity have psychophysically demonstrated that detection or discrimination thresholds can be reduced and usually show a high degree of specificity with respect to the trained visual stimuli. These specificity effects have been regarded as a manifestation of plasticity in sensory cortical processes including very low-level stages of processing. For instance, results showing that learning is specific to the eye of training imply that the learning must take place in V1, because past this point in the visual hierarchy very few cells have monocular receptive fields [36]. Likewise, results showing specificity of learning to retinotopic location [6] or primitive stimulus features (such as orientation [6,37] or direction [15,38]) are thought to involve cells in early visual areas that have small receptive fields and respond to primitive stimulus features, although this line of evidence does not rule out the role of higher-level visual or decision areas in perceptual learning [3,39].

Low-level sensory plasticity involving perceptual learning has been confirmed by studies of electrophysiology in animals and functional imaging in humans. In the case of vision, single-unit recording studies have shown activity changes of cells in early visual cortex of monkeys [8,40,41] and MR signal changes in V1 of humans [42,43] and the human MT homologue [44], in correlation with perceptual learning. Learning of features in other modalities such as audition [45], somatosensation [16] and motor functions [46,47] also implicates neural changes in the primary cortical areas of these modalities.

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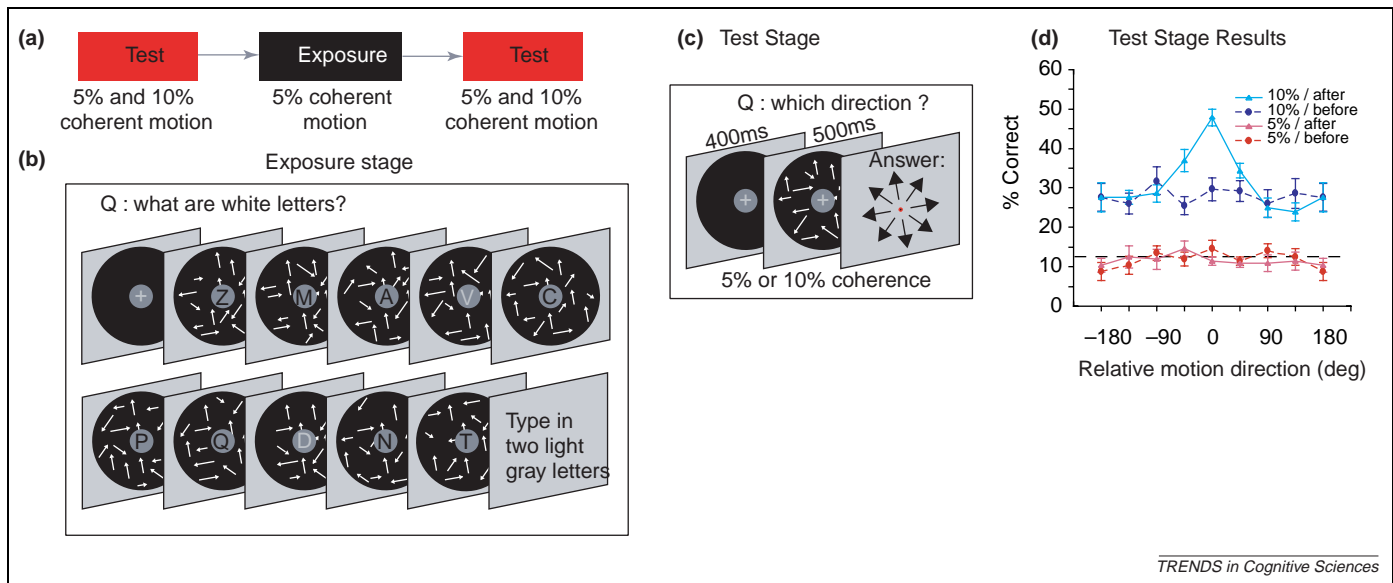


Figure 1. (a) Outline of experiment showing learning of subthreshold coherent motion signals. Two test stages were conducted; one preceding and one following the exposure stage. (b) Procedure of test stages. In each trial, a display was presented that contained either 5% (subthreshold) or 10% (suprathreshold) coherent motion moving in one of eight directions. After 500 ms this motion display was replaced with eight arrows. Subjects selected with a mouse the arrow that best matched the coherent motion direction. (c) Procedure of exposure stage. Subjects reported the two white target letters that occurred in a sequence of black distractor letters. In a peripheral annulus a 5% coherent motion display was presented whose direction was consistent throughout the exposure stage for each subject. (d) Mean performance of test stages. Performance at 5% coherent motion was at the chance level before and after exposure, indicating that 5% coherent motion stayed subliminal throughout the exposure. However, significant improvement was found at and around the exposed direction for 10% coherent motion after the exposure. This same improvement was found in separate tests of coherent motion detection and motion discrimination.

(stimulus signals) temporally coincide, a long-term sensitivity enhancement to the stimulus occurs. That is, plasticity is restricted by the temporal timing of the two signals, irrespective of whether a presented stimulus is task-relevant or not. This view is supported by a recent theory of attention in which there are attentional subsystems that are mediated by different neural modulators [17,18]. Within this framework of attention we can reconcile theories of attention-based task-relevant learning with studies of task-irrelevant learning. Our model thus provides a unified explanation of both task-relevant and task-irrelevant learning.

The role of attention in perceptual learning

It has been suggested that perceptual learning cannot occur without persistent and intensive attention to the feature to be learned [13]. Profound learning effects are present only for the task-relevant features but are typically absent or very limited for the task-irrelevant and unattended features. [19]. For instance, no or little transfer of learning effects was found between two tasks that involved judgments on different stimulus attributes (either orientation of local elements or global shape) of the same stimuli [13]. It was also reported that the ability of subjects to discriminate the orientation of a line did not improve when the brightness rather than orientation of the line was attended [10].

Additionally, a recent single-unit recording study in monkeys found neuronal plasticity manifested as a change in the orientation tuning curves of V1 cells with receptive fields overlapping the spatial location of the training task. No plasticity was found for cells with receptive fields overlapping the location of task-irrelevant stimuli

presented at a different location from those relevant to the task [8].

Task-irrelevant perceptual learning

However, recently, a new type of perceptual learning was discovered in which sensory plasticity occurs in the absence of attention [15]. A series of experiments was conducted in which subjects were repeatedly exposed to a weak background motion signal that was below their perceptual thresholds (Figure 1a). The subthreshold background motion was also irrelevant to a central task that engaged the subject's attention. Despite being below the threshold of visibility and being irrelevant to the central task, the repetitive exposure improved performance specifically for the direction of the exposed motion when that direction was subsequently tested (Figure 1b). A follow-up study demonstrated that this task-irrelevant learning was highly specific to local motion of the exposed stimuli, as opposed to the global motion, and that the learning was retained for months after training [20]. It has also been found that perceptual learning forms as a result of mere presentation of tactile stimuli [16]. These findings indicate that focused-attention is not *necessary* for perceptual learning and, therefore, does not completely restrict plasticity.

Similar findings have been made in studies showing implicit learning of background features in visual tasks. Research of contextual cuing has demonstrated that the configuration of distractors in visual search tasks is implicitly learned and aids in later searches [5]. In addition, the configuration of flanking background elements has been shown to influence learning [21,22].

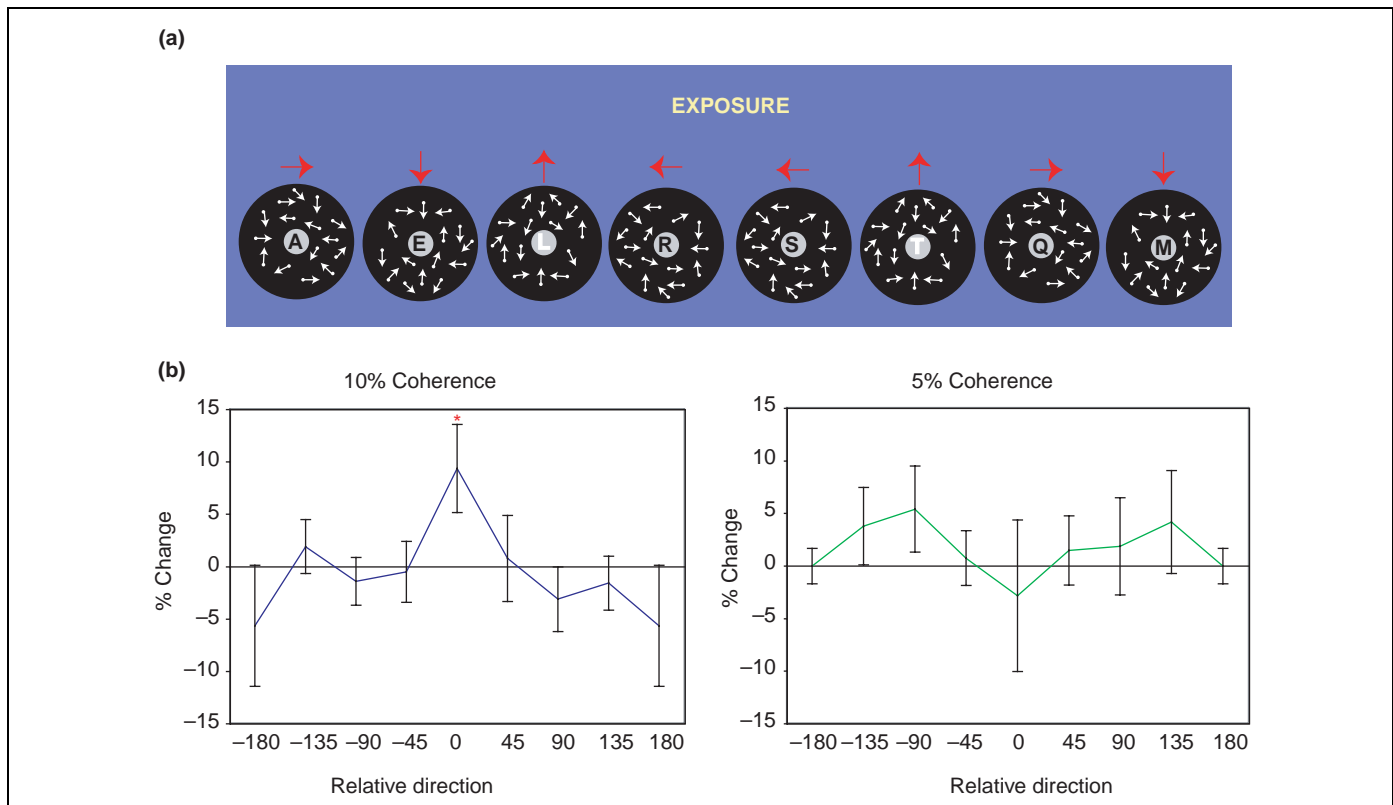


Figure 2. (a) Procedure of the exposure stage in Seitz and Watanabe [14]. A 5% coherent motion direction (shown as up in the figure) was temporally paired with the target-letters (shown as white); three other directions were paired with distractor letters (shown as black). (b) Results show a change in performance between the pretest and post-test. A significant improvement was found for the direction temporally paired with the targets when assayed at 10% motion coherence. No significant changes were found for 5% coherent motion.

Task-performance and task-irrelevant learning

Does task-irrelevant learning occur simply as a result of exposure to a stimulus? The answer might be negative. Recently, Seitz and Watanabe [14] found that a sensitivity enhancement occurred as the result of temporal pairing between the presentation of a subliminal, task-irrelevant, motion stimulus and a task-target. In this experiment, four different directions of subliminal motion were presented an equal number of times during the exposure stage, but a single direction of interest was consistently paired (temporally preceded and then overlapped) with the task targets (Figure 2a). If learning occurs purely as a result of exposure to a feature, learning should occur equally for all four presented directions of motion. However, learning was found only for the motion direction that was temporally-paired with the task targets, not for the other motion directions (Figure 2b).

Presentation of a task-target and a task-irrelevant feature

How can we reconcile the results of studies that found no learning outside the focus of attention with the results of studies showing task-irrelevant learning? The solution relies on recognizing that the studies failing to find task-irrelevant learning lacked a consistent relationship between the task-irrelevant features and the target presentation. For example, in Ahissar and Hochstein [13], two different orientations (vertical/horizontal) of the global texture array (the task-irrelevant features) were paired with the target display and the blank display with

equal probability. In Shiu and Pashler [10], each of two line orientations (the task-irrelevant feature) could be paired with each of two degrees of line brightness (the task-relevant features). Task-irrelevant learning was not observed in these studies. By contrast, in Watanabe *et al.* [15,20], when a target was presented, the same directional coherent motion was present. In Seitz and Watanabe [14], a unique motion direction was consistently paired with a target whereas three other directions were paired with distractors. Task-irrelevant learning was observed in these studies. These results suggest that a necessary condition of task-irrelevant learning is for the task-irrelevant feature to uniquely coincide with the target presentation.

Towards a unified model of task-relevant and task-irrelevant learning

We propose a model for task-irrelevant learning that can also explain task-relevant learning (Figure 3). Perceptual learning occurs through the coincidence of diffusive signals driven by a task activity (reinforcement signals) and signals induced by the presentation of a stimulus (stimulus-driven signals). On the one hand, if a task target and a task-irrelevant feature are presented with an appropriate temporal relationship such that stimulus-driven signals (in this case task-irrelevant signals) and task-driven signals temporally coincide, then task-irrelevant learning occurs. On the other hand, because the task target itself causes both reinforcement signals and stimulus-driven signals, these two signals always temporally coincide and result in task-relevant learning.

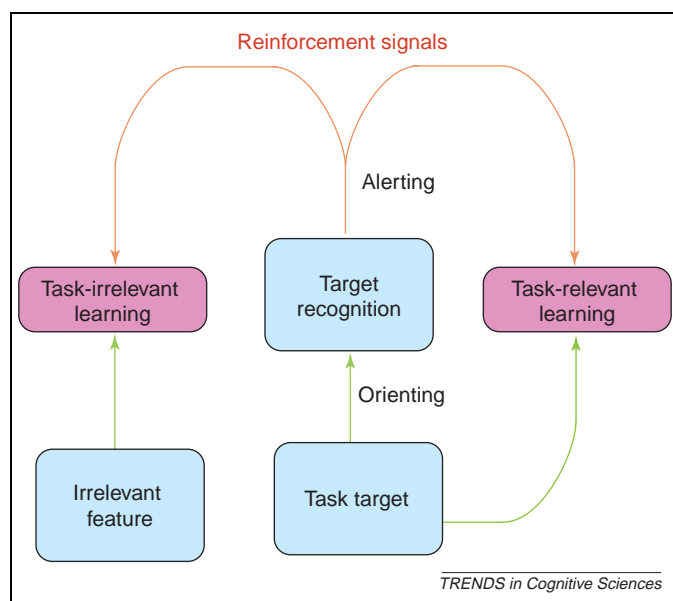


Figure 3. A unified model of task-relevant and task-irrelevant learning. Focused attention (by the orienting system) on a task-relevant stimulus and successful task performance including recognition of a task-target lead to diffusive reinforcement signals. When task-irrelevant signals and the reinforcement signals interact at an appropriate timing, task-irrelevant learning occurs. Task-relevant learning also occurs as a result of timely interactions between the reinforcement signals and signals driven by a task-relevant feature. Thus, the same basic mechanism works for both task-relevant and task-irrelevant learning.

This model is not unlike models invoked to explain reinforcement learning and conditioning (Box 2). We believe that the mechanisms that underlie conditioning are likely to be related to those of perceptual learning. For instance, research has shown that in human learning internal motivation is regarded as an important reinforcer and that successful performance of a task works as an internal reward [23,24]. Future research will be required to better determine the relationships between conditioning and perceptual learning.

Rethinking the role of attention

Does task-irrelevant learning demonstrate that no 'attention' is necessary for perceptual learning? The answer to this question depends on one's definition of attention. For instance, on the one hand, ideas of focused attention in which attention is oriented only to specific stimulus features, at the expense of others, are inconsistent with the learning of unattended features. On the other hand, ideas of non-specific attention in which the subject has an increased alertness during key points of the task do not preclude learning of task-irrelevant features.

Recently, Posner and colleagues [17,18], in an attempt to operationalize attention, have pointed out that there are three different attentional subsystems and that each has different effects on stimulus processing. They argue that alerting, orienting and executive function are triply dissociable attentional subsystems and that the very confusing term 'attention' should be thrown out in their stead. The alerting system controls a non-specific arousal state; the orienting system directs resources to a specific spatial cue or feature; the executive control system is involved in solving a task involving conflict.

Box 2. Conditioning, reinforcement and perceptual learning

A classic solution to the stability–plasticity dilemma can be found in the conditioning mechanisms described by Pavlov [48]. In the **classical conditioning** paradigm, learning is established after repetitive paired presentations of a conditioned stimulus (**CS**, for instance a bell) and an unconditioned stimulus (**US**, for instance some food). Responses that are initially elicited by the US are called unconditioned responses (**UR**, in this case salivation). As result of consistent pairing of the CS and the US, a response similar to the UR will occur following the presentation of the CS alone. This is called a conditioned response (**CR**).

In the framework of conditioning, learning occurs through the consistent temporal pairing of a conditioned stimulus (CS) with an unconditioned stimulus (US). Conditioning occurs most strongly when the CS is presented before the US such that the presentation of the CS predicts the following presentation of the US (**forward conditioning**). Conditioning can also occur when they are presented simultaneously (**simultaneous conditioning**) or even in reverse sequence (**backward conditioning**) but these can be very weak or even inhibitory [49].

Task-irrelevant learning is similar to conditioning in that they both rely on a temporal relationship between stimuli and reinforcers. It has been previously suggested that conditioning and focused attention work together, playing different roles to effectively adapt to the environment whilst at the same time protecting the perceptual architecture from instability [14]. Based on prior knowledge, focused attention is directed to, and leads to learning of, important information in the environment. By contrast, through a process similar to conditioning, the sensory system learns important aspects of the environment, even in the absence of attention, in a rather automatic way through consistent temporal relations between stimuli of known relevance and those that do not necessarily have previous behavioral relevance.

It is important to note that perceptual learning does not necessarily reveal what has been the typical focus of studies of conditioning. Whereas studies of conditioning typically measure behavioral changes of the subject when CS is presented to establish how the relationship between the CS, US and associated responses are changed after repetitive paired presentations of CS and US, perceptual learning reveals sensitivity changes for the critical features of the CS [50]. Future research will be required to further understand the commonalities and differences between the mechanisms of perceptual learning and those of conditioning.

The orienting and executive control systems might be more selective to regions of space (spatial attention), individual features (feature-based attention) or objects (object-based attention) regarded to be task-relevant items. During alerting, a phasic but non-specific signal increases general processing based on the time during which important stimuli are thought to be present.

This framework fits quite well with our unified model (as shown in Figure 3). When a subject is performing a task, the orienting attention subsystem directs attentional resources to the location of the task target. This orienting signal aids in target detection. The alerting attention subsystem is activated by a temporal cue, such as the occurrence of the task target, and serves as a temporal signal that enhances processing of a large extent of the scene, including the task-irrelevant features.

Related neural mechanisms

What are the underlying neural mechanisms in the perceptual learning process? A considerable amount of behavioral and neurophysiological data show that the learning is formed as a result of diffusely released

modulatory neurotransmitters, which have been shown to result in sensory plasticity [19,25]. For instance, pairing a tone with stimulation of the ventral tegmental area (VTA), which releases dopamine [19], results in increased representations of the paired tone in the primary auditory cortex (A1) [26]. Similarly, pairing a tone with stimulation of the nucleus basalis (NB) of the basal forebrain, which releases acetylcholine, results in an increased representation of the paired tone in A1 [27]. Likewise, norepinephrine (NE), which is released from the locus coeruleus, has been shown to be involved in learning both at the behavioral [25,28] and neuronal level [29]. These findings suggest that perceptual learning might be regulated through the release of neuromodulators, such as acetylcholine, norepinephrine, and dopamine, which gate learning and thus restrict sensory plasticity and protect sensory systems from undesirable plasticity.

Most interestingly, these same neuromodulatory systems have been suggested to underlie attention [18]. The orienting system, with which attention is directed to a task-irrelevant location/feature, has been associated with the parietal lobe [30] and is thought to be mediated by the acetylcholine system [31]. On the other hand, the alerting system, which might be highly related to diffusive reinforcement signals, has been associated with the frontal and parietal regions of the right hemisphere and is thought to be mediated by the cortically diffusive norepinephrine system [32–34].

Concluding remarks

In this article, we reconcile conflicting theories of task-relevant and task-irrelevant learning. Based on Seitz and Watanabe [14], we hypothesize that task-irrelevant learning occurs as a result of timely interaction between reinforcement signals resulting from attentional processing of the task target and stimulus signals resulting from the task-irrelevant stimulus. Interestingly, not only task-irrelevant learning but also task-relevant learning can be explained within this framework and therefore this model is regarded as a unified model of task-relevant and task-irrelevant perceptual learning.

Perceptual learning studies showing task-irrelevant learning imply that the concept of specific attention cannot completely account for perceptual learning. Likewise, that this learning is restricted to irrelevant stimuli that temporally coincide with task-relevant events

suggests that a featurally non-specific, but temporally precise, learning signal is involved. Posner's research [22] dissociating the alerting, orienting and executive attentional subsystems provides a conceptual structure of how different types of attention are important during task performance and that the mechanisms of learning might mostly overlap those of attention.

Interestingly, the attentional framework proposed by Posner [17] suggests a very similar explanation of task-irrelevant learning to that of recent reinforcement models. The signal associated with Posner's alerting attentional system was most consistent with the reinforcement signal proposed by Seitz and Watanabe [14]. Likewise, a model of reinforcement learning by Dayan and Yu [35] showing the role of unexpected uncertainty (i.e. cued by an unpredicted features) in learning, implies that learning signals might be activated by the random occurrences of the task targets during the RSVP sequence in the experiment of the Seitz and Watanabe. Most interesting is that both the attention model and reinforcement theories have independently come to the hypothesis that the release of norepinephrine is the underpinning signal for these systems.

Clearly we have insufficient evidence to conclude that a particular neuromodulator is in fact responsible for perceptual learning. It is much more likely that each of the systems discussed in this review, as well as many others systems known to be involved in learning, interact in a complicated manner to produce learning. However, it is highly plausible that stability and plasticity are controlled by a well-regulated system that can signal the time when learning should occur and/or features that should be learned. With these ideas in mind, future neural and behavioral studies can begin to dissociate the different contributions of these distinct attentional/learning systems to plasticity in the sensory systems.

Acknowledgements

We thank Fabio Idrobo and Roger Tootell for their comments and Nozomi Ito for her technical assistance. The present study is supported by NSF (SBS-CN), NSF (CELEST), NIH (NEI), and Human Frontier Science Foundation.

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Box 3. Questions for future research

- What are the individual roles of the different neuromodulatory systems in perceptual learning?
- What are the commonalities and differences between perceptual learning and conditioning?
- In order for reinforcement signals to be triggered, how deep does a target need to be processed?
- For both task-relevant and task-irrelevant features to be learned, do they have to be presented in different spatial regions?
- Does the proposed model also apply to other sensory modalities and/or to motor learning?
- If so, does task-irrelevant learning require learned features to be of the same sensory modality as the task-relevant stimuli, or does crossmodal learning also occur?

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