

Perceptual learning, motor learning and automaticity

Perceptual learning rules based on reinforcers and attention

Pieter R. Roelfsema^{1,2}, Arjen van Ooyen² and Takeo Watanabe³¹ Department of Vision & Cognition, Netherlands Institute for Neurosciences, an institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), Meibergdreef 47, 1105 BA, Amsterdam, The Netherlands² Department of Integrative Neurophysiology, Centre for Neurogenomics and Cognitive Research, VU University, De Boelelaan 1085, 1081 HV Amsterdam, Amsterdam, The Netherlands³ Department of Psychology, Boston University, 64 Cummington St., Boston, MA 02215, USA

How does the brain learn those visual features that are relevant for behavior? In this article, we focus on two factors that guide plasticity of visual representations. First, reinforcers cause the global release of diffusive neuromodulatory signals that gate plasticity. Second, attentional feedback signals highlight the chain of neurons between sensory and motor cortex responsible for the selected action. We here propose that the attentional feedback signals guide learning by suppressing plasticity of irrelevant features while permitting the learning of relevant ones. By hypothesizing that sensory signals that are too weak to be perceived can escape from this inhibitory feedback, we bring attentional learning theories and theories that emphasized the importance of neuromodulatory signals into a single, unified framework.

Perception improves with training

Visual perception improves with practice. A birdwatcher sees differences between birds that are invisible to the untrained eye. To gain an understanding of perceptual learning one can compare the perception of bird experts to the perception of subjects with other interests (as explained in detail in [1]). Alternatively, one can study perceptual learning in the laboratory, which has produced many important insights. Training improves perception, even in adult observers, provided they are willing to invest some effort in the task. Subjects typically have to train for a few hundred trials per day over a few days before perceptual improvements are noticeable. Under these conditions, subjects' discrimination between basic features improves, for example between subtle variations in the orientation or motion direction of a visual stimulus [2]. Once perceptual learning has occurred, it is persistent and can last for many months [3] or years [4]. The learning effects are often specific so that perceptual improvements in a particular version of a task do not generalize to other versions. Performance improvements are not observed, for example, if the test stimulus has a different orientation [4–6], motion direction [7,8] or contrast [9,10] than the trained stimulus. Moreover, the training effects are often retinotopically specific. After training in one region of the visual field,

the improvement in performance does not transfer to other visual field locations [4,6–9,11,12], although special learning procedures can cause better generalization [13,14].

What are the mechanisms that determine perceptual learning? The improvements in perception could be the result of changes in sensory representations, but they could also be the result of the way that sensory representations are read out by decision-making areas [15–17]. Furthermore, the role of selective attention in learning is unclear. It appears to be important for some forms of learning [10,18–22], but not for others [8]. Similarly, in some cases learning takes place without giving explicit feedback to the subject about the accuracy of the responses [23], whereas in other cases such feedback facilitates learning [24]. The goal of the present review is to combine recent neurophysiological and psychological findings into a coherent theoretical framework for perceptual learning. In the context of this framework, we will discuss attention-gated reinforcement learning (AGREL), a model that posits that selective attention and neuromodulatory systems jointly determine the plasticity of sensory representations [25]. We will proceed by proposing a generalization of this model that provides a new, neurophysiologically plausible demarcation between the conditions where attention is required for learning and the conditions where it is not.

Neuronal correlates of perceptual learning

How does the visual cortex change as a result of perceptual learning? The available evidence implicates early sensory representations but also higher association areas in perceptual learning, although the relative contribution of low-level and high-level mechanisms is under debate [15,16]. With regard to early visual representations, functional imaging studies have revealed increases in neuronal

Glossary**AGREL:** attention-gated reinforcement learning**Feedforward connection:** propagates information from lower to higher levels**Feedback connection:** propagates information from higher to lower levels**Perceptual learning:** improvement of perception through learning**Selective attention:** behavioral selection of one representation over another one**Neuromodulatory systems:** systems that release neuromodulators to code the rewarded outcome of a trial**RF:** receptive field

Corresponding author: Roelfsema, P.R. (p.roelfsema@nin.knaw.nl).

activity at the representation of the location in the visual field that is trained [26], often with particularly strong effects in the primary visual cortex [27–31]. Moreover, neurophysiological studies have demonstrated that neurons in early visual areas change their response properties during perceptual learning [5,32–34]. For example, when monkeys are trained to judge the orientation of a stimulus, neurons in the primary visual cortex (area V1) become sensitive to small variations around the trained orientation. In addition to area V1, increased sensitivity of neurons to category boundaries is also observed in higher visual areas, including area V4 [32,35], the inferotemporal cortex [36], area LIP [37] and the prefrontal cortex [38]. From a functional point of view, the amplified representation of feature values close to a category boundary is useful, because small changes in input should lead to categorically different behavioral responses [39,40]. If the stimuli that need to be classified differ in multiple feature dimensions, the increases in sensitivity caused by training are strongest for the features that distinguish between categories and weaker for features that do not [41,42]. Thus, neurons in many areas of the visual cortex change their tuning in accordance with the arbitrary categories imposed by a task.

A few studies have directly compared plasticity in lower and higher visual areas and found stronger effects in the higher areas [15,36,43], although there are also tasks where the changes in lower areas predominate [27,28]. On the one hand, some tasks require a categorization on the basis of features that are easy to discriminate, and subjects can learn these tasks as new stimulus-response mappings that might not depend on plasticity in the visual cortex. Genuine perceptual learning paradigms, on the other hand, train subjects to perceive small variations in features invisible to the untrained eye, and might therefore engage plasticity in the visual cortex. Ahissar and Hochstein [19,44] demonstrated that learning in easy (or low precision [45]) tasks generalizes across locations and feature values, suggestive of plasticity at high representational levels, whereas training in higher precision tasks is more specific to the trained stimulus implicating lower representational levels.

Theories of perceptual learning therefore have to explain where, when and why plastic changes occur. A particularly challenging question for these theories is how learning effects occur in early sensory areas, remote from the areas where perceptual decisions are made and task performance is monitored. What signal informs the sensory neurons to become tuned to the feature variations that matter? In what follows we consider two important routes for these effects to reach sensory areas: diffuse neuromodulatory systems and feedback connections propagating attentional signals from higher to lower areas.

Global neuromodulatory systems that gate plasticity

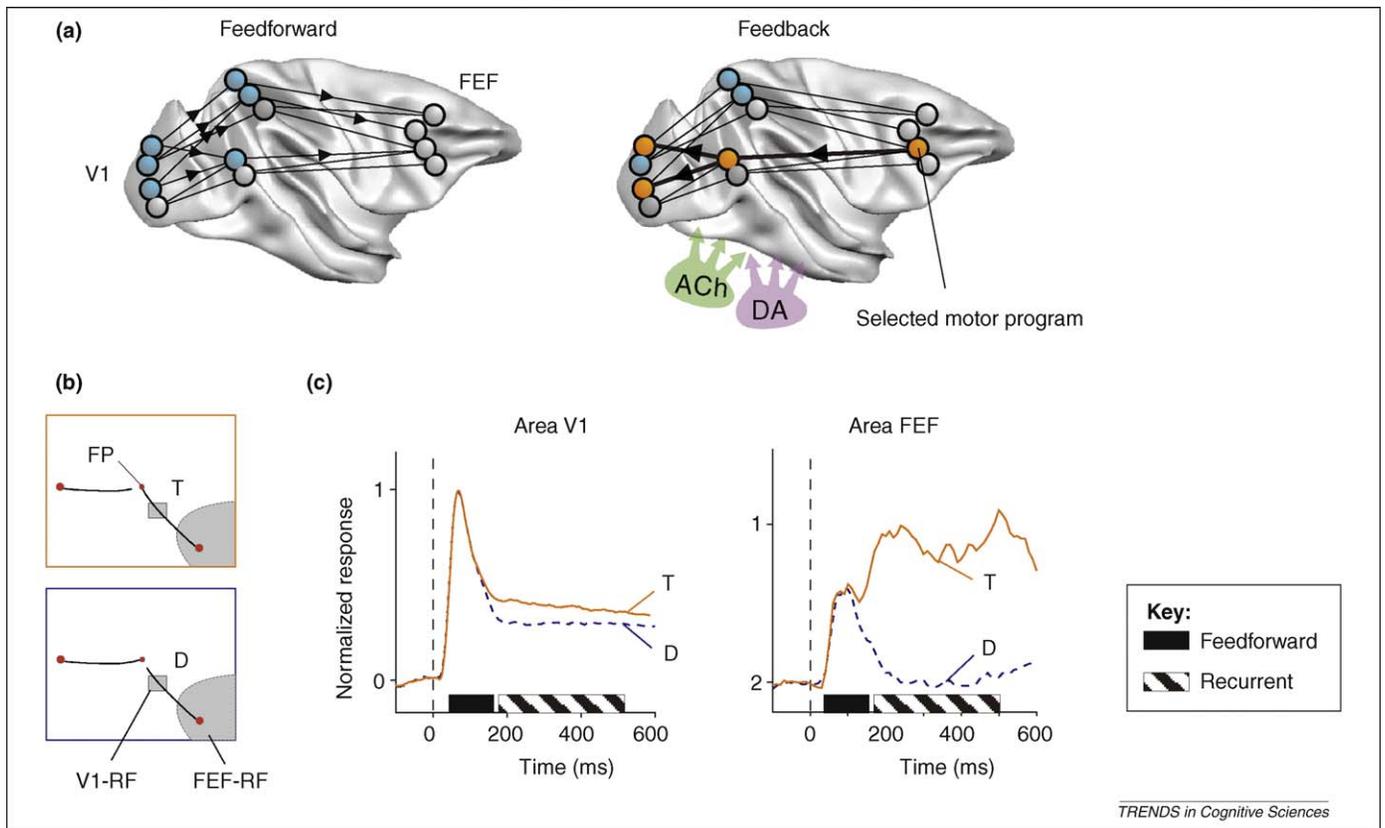
There are a number of neuromodulatory systems that project broadly to most areas of the cerebral cortex and deliver information about the relevance of stimuli and the association between stimuli and rewards. The two neuromodulatory systems most often implicated in neuronal plasticity are dopamine and acetylcholine. The substantia nigra and the ventral tegmental area are dopaminergic

structures in the midbrain that project to the basal ganglia and the cerebral cortex. In an elegant series of studies (reviewed in [46]), Schultz and co-workers demonstrated that dopamine neurons code deviations from reward expectancy. They respond if a reward is given when none was expected and also to stimuli that predict rewards, causing a surge of dopamine in the basal ganglia and cerebral cortex [47]. Because the increase in the dopamine concentration signals that the outcome of a behavioral choice is better than expected, it is beneficial to potentiate active synapses and thereby increase the probability that the same choice will be made again in the future. In slice preparations of the basal ganglia, dopamine has indeed been shown to control synaptic plasticity [48]. Moreover, there is *in vivo* evidence for the control of plasticity by dopamine. If transient dopamine signals are paired with an auditory tone, the representation of this tone is expanded in the auditory cortex [49].

Acetylcholine is another neuromodulator that has been linked to synaptic plasticity; neurons in the basal forebrain project to the cortex to supply acetylcholine. These neurons also respond to rewards [50], although the relation between their activity and reward prediction is not as well understood as for the dopamine neurons. If artificial stimulation of the basal forebrain is paired with an auditory tone, then the representation of this tone in the auditory cortex increases [51,52]. Thus acetylcholine promotes neuronal plasticity *in vivo* and it also influences synaptic plasticity in cortical slice preparations [53]. Other studies have shown that acetylcholine is necessary for plasticity, because a reduction of the cholinergic input reduces cortical plasticity [54] and impairs learning [55–57]. These results, taken together, provide strong support for the idea that learning and plasticity of cortical representations are controlled by neuromodulatory systems that change their activity in relation to rewarding stimuli or stimuli that predict reward.

Role of selective attention in learning

Visual attention provides a second route for signals about behavioral relevance to reach the visual cortex. There is substantial evidence for a role of selective attention (here we will not consider the effects of ‘general attention’ or arousal [58] and do not use the word ‘attention’ for the effects of neuromodulators) in determining what is learned and what not. One powerful approach for studying the role of attention in learning is given by the ‘redundant relevant cues’ method [18,59]. The subjects have to learn to associate stimuli with responses and can use multiple features of a stimulus, for example color and shape, to determine the correct response. The crucial manipulation is that the subjects are cued to direct their attention selectively to one of the features and not to the other. In these situations, they usually learn to use the attended feature and even exhibit an increase in perceptual sensitivity for this feature [18] whereas they do not learn to use the other, redundant feature even though it is presented and rewarded equally often. As a result, the subjects cannot perform the task after the training phase if the attended feature is taken away so that they are forced to use the redundant feature. Thus, in these cases attention to a feature determines which representations undergo plasticity and which do not. Similar effects occur for spatial



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Figure 1. Factors that modulate visual cortical plasticity. (a) Left, a visual stimulus is initially registered by a fast feedforward wave of activity that activates feature selective neurons in the many areas of the visual cortex. Right, neurons in the frontal cortex engage in a competition to select a behavioral response, and the neurons that win the competition feed attentional signals back to the visual cortex. Neuromodulatory systems, including acetylcholine (green) and dopamine (purple), modulate the activity as well as the plasticity of sensory representations. (b) Contour grouping task where monkeys have to trace a target curve (T) that is connected to a fixation point (FP). A red circle at the end of this curve is the target for an eye movement. The animals have to ignore a distractor curve (D). The two stimuli differ so that the RFs of neurons in areas V1 and FEF are either on the target curve (upper panel) or on the distractor curve (lower panel). (c) Neurons in the frontal cortex (area FEF) and the visual cortex (area V1) enhance their response when the target curve falls in their receptive field. Note that this attentional modulation comes at a delay (striped bar), while the initial neuronal responses do not discriminate between the relevant and irrelevant curve (black bar). Modified from Khayat et al. [70].

attention, because perceptual learning is particularly pronounced for stimuli at attended locations [e.g. 22].

How do these feature-based and spatial attentional effects reach the early levels of the visual system? The most likely route is through feedback connections that run from the higher areas back to lower areas of the visual cortex [60,61]. Cortical areas involved in response selection feed back to sensory areas so that objects relevant for behavior are represented more strongly than irrelevant ones. Such a direct relationship between behavioral relevance and visual selection was made very explicit in the 'premotor theory' of attention [62,63]. When a stimulus is selected for a behavioral response, the relevant features automatically receive attention. This theory is supported by experiments on eye movements, as attention is invariably directed to items that are selected as targets for an eye movement [64–66].

Neurophysiological findings provide support for the coupling between movement selection and spatial as well as feature-based attention. During visual search, for example, the representation of the features of the item that is searched as well its spatial location are enhanced in the visual cortex [67] and also in the frontal eye fields (area FEF) [68], and the frontal eye fields can feed back to cause attentional selection in the visual cortex [69]. The same is true in other tasks where visual stimuli compete for selec-

tion. Figure 1 shows data from a study where monkeys were trained to select the circle at the end of a curve that was connected to a fixation point as the target for an eye movement (Figure 1b), while ignoring a distractor curve [70]. Neurons in area FEF responded to the appearance of the stimulus in their receptive field, although their initial response did not discriminate between the target curve and the distractor (Figure 1c, black bar). After a short delay, however, responses evoked by the target curve became much stronger than those evoked by the distractor (striped bar), and this enhanced activity is a neuronal correlate of target selection [71]. A similar selection signal is observed in area V1 (Figure 1c), where responses evoked by the relevant, attended curve are enhanced over the responses evoked by a distractor curve, in a later phase of the response.

These results support the idea that the appearance of a visual stimulus, be it a target or distractor, initially triggers the rapid propagation of activity from lower to higher areas of the visual cortex through feedforward connections (Figure 1a) [72,73]. This phase is followed by an epoch where neurons in the frontal cortex that code different actions engage in a stochastic competition. The cells that code the action that wins the competition have stronger responses than the neurons that lose, and feed back to the representation of the selected object in the visual cortex

[74,75], causing a response enhancement that is a correlate of selective attention [76]. Such a counter-streams model [77] requires reciprocal connections between the visual and frontal cortex, so that actions that are selected in the frontal cortex provide feedback to neurons that gave input for this particular choice (orange neurons in Figure 1a), thus highlighting the circuits in the visual cortex that determine the course of action. Reinforcement learning theories (such as AGREL, see below) hold that actions are selected stochastically, so that the same visual stimulus can give rise to different actions and therefore also different patterns of feedback [25] (see Box 1).

Such a coupling between motor selection in the frontal cortex and attentional effects in the visual cortex during action selection is useful for guiding plasticity because plasticity occurs for connections between neurons that are important for the selected response. This computational idea is supported by psychological studies showing that attention gates learning [18,59,78–80]. Moreover, a

recent pharmacological study that investigated the role of different receptors in feedforward and feedback processing demonstrated that feedback connections have a larger proportion of NMDA-receptors than feedforward connections [81]. This result suggests that the feedback connections might gate perceptual learning [82] by activating NMDA receptors [83]. Another hypothetical route for feedback connections to gate plasticity involves acetylcholine receptors that are involved in selective attention [84] and also play a role in the gating of synaptic plasticity, as was discussed above.

Interactions between attention and diffuse reinforcement learning signals

So far we have reviewed evidence for the gating of plasticity by neuromodulatory systems as well as selective attention. Roelfsema and van Ooyen proposed a framework called ‘attention-gated reinforcement learning’ (AGREL) [25] that holds that the global neuromodulatory signal and

Box 1. Attention-gated reinforcement learning (AGREL)

Attention-gated reinforcement learning (AGREL) is a reinforcement learning model that learns by trial and error. AGREL uses two complementary factors to guide learning: (1) a global neuromodulatory signal that informs all synapses whether the outcome of a trial is better or worse than expected; (2) feedback from the response selection stage restricts plasticity to those synapses that were responsible for the behavioral choice.

On every trial, a pattern is presented to the input layer (left in Figure 1a), activity is propagated by feedforward connections to the intermediate layer and from there to the output layer. Output units engage in a stochastic competition, in which units with stronger input have a higher likelihood to win. During the action selection process, the winning output unit gives an attentional feedback signal to those lower level units that provided the input during the competition and helped it win. This feedback signal enables plasticity for a selected subset of the connections (thick lines on the right side of Figure 1a). After the response, a reward is delivered or not, and the network computes a global error signal that depends on the difference between the amount of reward that was expected and that obtained. If the outcome is better than expected, globally released neuromodulators (green in Figure 1a) cause synapses between active units to

increase in strength. In case of a wrong response, the neuromodulators produce a decrease in synapse strength (red in Figure 1a).

The problem of adjusting the deep weights v_{ij} in the network proceeds according to the following rule:

$$\Delta v_{ij} = \beta \cdot X_i \cdot f(Y_j) \cdot g(\text{reward}) \cdot FB_{sj} \quad [1]$$

Here Δv_{ij} is the change in synaptic strength, β is the learning rate, X_i and Y_j are pre- and postsynaptic activity, and FB_{sj} is the attentional feedback signal from the winning output unit s . Thus, the plasticity depends on the product of pre- and postsynaptic activity and is gated by the reward through the function g and by the attentional feedback FB_{sj} that conveys whether unit Y_j is responsible for selected action s . This feedback signal could operate by enhancing the plasticity of unit j or by blocking plasticity of other units $Y_l, l \neq j$, by providing inhibition directly or indirectly (Figure 1b). Note that these signals are all available locally, at the synapse. The learning rule for the connections w_{jk} to the output layer is even simpler because it does not depend on the attentional feedback signal. On average, AGREL changes the connections in the same way as error-backpropagation, a learning rule that is popular and efficient but usually considered to be biologically implausible [93]. Further details about the AGREL model can be found in [25].

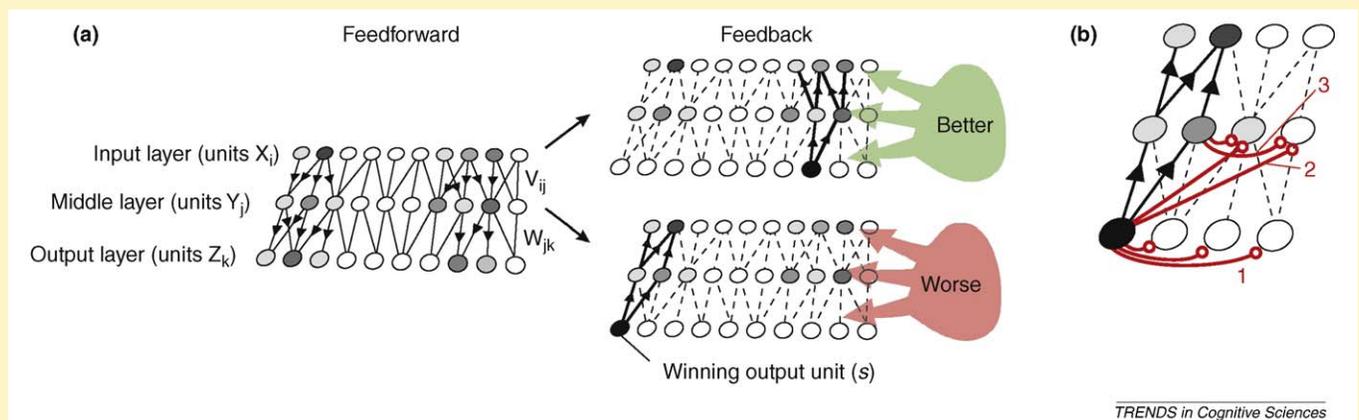


Figure 1. Attention-gated reinforcement learning. **(a) Left**, activity is propagated from lower to higher layers through feedforward connections. The output units engage in a competition to determine the selected action. **Right**, if an action has been selected, the winning output units provide an attentional feedback signal that highlights the lower level units responsible for the selected action (thick connections) enabling their plasticity. The plasticity of other connections is blocked by inhibition (dashed connections). Different actions thereby enable plasticity for different sensory neurons. Neuromodulators indicate whether the rewarded outcome was better (green) or worse (red) than expected. **(b)** Inhibition (red connections) blocks the plasticity of connections that are not involved in the selected action. At the output level, the actions compete through inhibitory interactions (connection type 1). The winning output unit could directly inhibit neurons at lower levels (connection type 2) or indirectly through inhibitory lateral interactions between the lower level units (connection type 3). These inhibitory effects do not occur for stimuli too weak to be consciously perceived.

the attentional feedback signal are complementary and jointly determine plasticity (Box 1). The network receives a reward for a correct choice, whereas it receives nothing if it makes an error. After the action, neuromodulators are released into the network to indicate whether the rewarded outcome is better or worse than expected (Figure 1) [46]. If the network receives more reward than expected, the neuromodulators cause an increase in strength of the connections between active cells, so that this action becomes more probable in the future; the opposite happens for actions with a disappointing outcome. The second signal is the attentional feedback during action selection that ensures the specificity of synaptic changes. Although the neuromodulators are released globally, the synaptic changes occur only for units that received the attentional feedback signal from the response selection stage during action selection. AGREL causes feedforward and feedback connections to become reciprocal, in accordance with the anatomy of the cortico-cortical connections. Consequently, the neurons that give most input to the winning action also receive most feedback. As a result, only sensory neurons involved in the perceptual decision change their tuning, whereas the tuning of other neurons remains the same. The attentional feedback signal thereby acts as a credit assignment signal, highlighting those neurons and synapses that are responsible for the outcome of a trial, thus increasing the efficiency of the learning process substantially [85]. A remarkable result is that under some conditions, the global neuromodulatory signal combined with the attentional feedback signal gives rise to

learning rules that are as powerful as supervised learning schemes, such as error-backpropagation, although the learning scheme operates by trial and error and is plausible from a neurophysiological point of view. Learning rules that combine the two factors, such as AGREL, can reproduce the effects of categorization learning if there is a direct mapping of stimuli onto responses. They steepen the tuning curve of sensory neurons at the boundary between categories and cause a selective representation of 'diagnostic' features that matter for the task. It is still an open question whether these reinforcement learning models can be adapted to explain perceptual learning in tasks that require a comparison between stimuli presented at different times, for example in delayed match-to-sample tasks where subjects have to judge whether two sequentially presented stimuli are the same. These tasks require the comparison between a memory trace of the first stimulus and the perceptual representation of the second stimulus, whereas the existing reinforcement learning models do not have such a working memory.

Perceptual learning without attention

The studies reviewed above demonstrate that attention gates learning, however there are forms of perceptual learning that occur without attention. Watanabe and his colleagues [8] demonstrated that perceptual learning can occur for stimuli too weak to be perceived, if they are paired with the detection of another stimulus. In one of their experiments [86], subjects monitored a rapid serial visual presentation (RSVP) stream for target digits that were

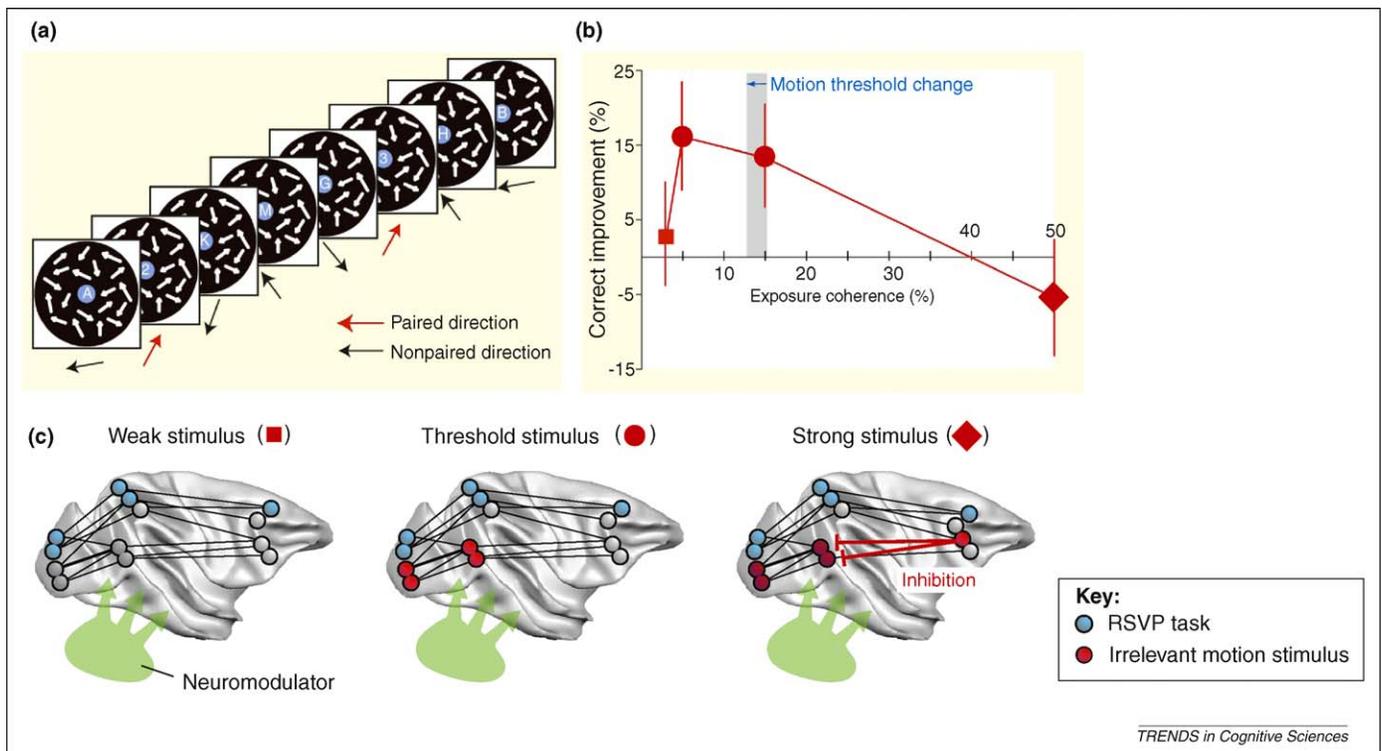


Figure 2. Task-irrelevant perceptual learning. **(a)** Subjects monitor a central RSVP stream to detect target digits that are presented among letter distractors. In the background, motion signals are presented that are irrelevant for the subject's task. **(b)** A separate test determines the motion sensitivity of the subjects. This test reveals that the sensitivity for the motion direction paired with the target digits (red arrows in a) increases. Learning occurs for paired motion stimuli that are at or below the visibility threshold, but not for very weak or strong motion stimuli. **(c)** Blue circles denote neurons involved in the RSVP task. Red circles denote the representation of the irrelevant motion signals. **Left**, weak motion stimuli are not registered well by the visual cortex and are not learned. **Middle**, threshold motion stimuli are represented by motion sensitive neurons and are learned if paired with the neuromodulatory signal. **Right**, strong motion signals might cause interference and therefore receive top-down inhibition from the frontal cortex. These suppressive signals block perceptual learning. Adapted from Tsushima et al. [90].

presented on a background of moving dots (Figure 2a). Unbeknown to the subjects, the target digits were consistently paired with a very weak motion stimulus in one direction and, remarkably, the subjects became better in detecting motion in the paired direction. It is unlikely that they directed their attention to this subthreshold motion stimulus, and yet they learned.

Seitz and Watanabe [87] proposed that neuromodulatory signals can explain these findings if the successful detection of a target letter in the RSVP stream generates an internal reward. In accordance with this view, the pairing of subliminal stimuli only results in learning if they are paired with successfully detected target digits and not if they are paired with targets that are missed [88]. Moreover, it is possible to replace the internal reward by an external one. A recent experiment tested subjects who were deprived of water and food for several hours and then exposed to an orientation that was paired with water as reward, and also to another orientation not paired with water [89]. The subjects became better in discriminating between orientations around the paired orientation. These findings, taken together, indicate that task-irrelevant learning occurs for subliminal, task-irrelevant features if they are paired with external or internal rewards, which presumably cause release of neuromodulatory factors such as dopamine and acetylcholine [87].

Reconciliation of new results and theories

It is evident that the studies reviewed so far agree about the role of neuromodulatory signals but also that they appear to contradict each other regarding the role of selective attention. Some studies demonstrated an important role for attention in learning whereas others demonstrated learning for unattended, irrelevant and even imperceptible stimuli. Theories about the mechanisms for learning can appear to be equally contradictory. Whereas AGREL [25] stresses the importance of attention, the model by Seitz and Watanabe [87] indicates that the coincidence of a visual feature and an internal or external reward is sufficient for learning.

To resolve these apparent contradictions, we propose that the attentional feedback signal that enhances the plasticity of task-relevant features in the visual cortex also causes the inhibition of task-irrelevant features so that their plasticity is switched off. We further propose that stimuli that are too weak to be perceived escape from the inhibitory feedback signal so that they are learned if consistently paired with the neuromodulatory signal. This proposal can explain why studies using stimuli close to or below the threshold for perception observed task-irrelevant perceptual learning whereas studies using suprathreshold stimuli invariably implicate selective attention in learning. A recent study [90] directly compared task-irrelevant learning for a range of stimulus strengths and indeed observed that learning only occurred for motion strengths at or just below the threshold for perception but not for very weak or strong stimuli (Figure 2b). It is easy to understand why very weak motion signals are not learned because they hardly activate the sensory neurons (Figure 2c, left). According to our proposal, the strong motion signals could interfere with the primary letter

detection task and are therefore suppressed by the attentional feedback that also blocks plasticity (Figure 2c, right). Threshold stimuli, however, might stay 'under the radar' of this attentional inhibition mechanism so that they are not suppressed and can be learned if consistently paired with the neuromodulatory signal (Figure 2c, middle).

Recent results of Tsushima, Sasaki and Watanabe [91] provide further support for this view. They measured the interference caused by irrelevant motion stimuli in the letter detection task of Figure 2 and found an unexpected dependence on signal strength. Weak motion stimuli interfered more than suprathreshold motion stimuli, and an fMRI experiment revealed that they caused stronger activation of motion sensitive area MT+. The reason for the enhanced activation of MT+ by threshold stimuli was observed in the dorsolateral prefrontal cortex (DLPFC), a region that generates attentional inhibition signals. The suprathreshold stimulus activated DLPFC, which then suppressed MT+, whereas the threshold stimulus did not (Figure 2c). These psychophysical and fMRI results, taken together, indicate that weak motion signals can indeed escape from the attentional control system so that they can be learned [91].

Concluding remarks

We conclude that there is substantial evidence for an important role for neuromodulatory reward signals and selective attention in the control of perceptual learning. These two factors can act in concert to implement powerful and neurobiologically plausible learning rules in the cortex. The neuromodulatory signals reveal whether the outcome of a trial is better or worse than expected, whereas the attentional feedback signal highlights the chain of neurons between sensory and motor cortex responsible for the selected action.

We here proposed that the attentional feedback signals guide learning by suppressing plasticity of irrelevant features while permitting the learning of relevant ones. By hypothesizing that sensory signals that are too weak to be perceived can escape from this inhibitory feedback, we have brought attentional learning theories, such as AGREL [25], and theories that emphasized the importance of neuromodulatory signals, such as the model of Seitz and Watanabe [87], into a single unified framework.

In most studies on task-irrelevant perceptual learning, attention was focused on the primary RSVP task that was in close proximity to the threshold stimulus to be learned. If task-irrelevant learning and attention-dependent learning are manifestations of the single unifying learning rule, it should even be possible to influence task-irrelevant learning by shifts of selective attention. A recent study [92] manipulated spatial attention by presenting two RSVP streams while instructing subjects to attend only one of them. Task-irrelevant learning occurred for subthreshold stimuli close to the relevant RSVP stream but not for stimuli close to the irrelevant one. In this case the selective attentional signal that gates plasticity has a different origin than the attentional signal in the AGREL model: it could now either come from the instruction to attend one of the RSVP streams or from the response selection stage of the RSVP task. Thus, even the learning

Box 2. Questions for future research

- Which neuromodulatory signals determine learning?
- When are the neuromodulatory signals released?
- How do neuromodulatory signals and selective attention interact with each other?
- Which neurotransmitter receptors convey the reward signals and which ones the effect of attention?
- How do lateral inhibition and top-down inhibition contribute to the gating of plasticity?
- Can the AGREL learning rules be generalized to tasks other than categorization?
- How should perceptual learning in delayed match-to-sample tasks be modeled?
- Can purely bottom-up signals lead to plasticity without attention or reward signals?

of subliminal task-irrelevant stimuli can be brought under attentional control by changing the relevance of nearby suprathreshold stimuli.

In the introduction we asked how sensory neurons could be informed about the relevance of stimuli so that they can sharpen their tuning for features that are important for behavior. The present framework requires two such signals: a global, neuromodulatory signal that signals the rewarded outcome of a trial and an attentional credit assignment signal that restricts plasticity to those sensory neurons that matter in the decision. If acting in concert, these factors can give rise to biologically realistic learning rules that are as powerful as error-backpropagation. Future studies could test the predictions of this new perceptual learning theory, and unravel the mechanisms underlying the interactions between learning, selective attention and reward signaling at the systems level as well as at the cellular and molecular level (Box 2).

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