

EXPLAINING TRAINING INDUCED PERFORMANCE INCREMENTS AND DECREMENTS WITHIN A UNIFIED FRAMEWORK OF PERCEPTUAL LEARNING

NITZAN CENSOR and DOV SAGI*

Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel

Practicing sensory tasks could result in two main perceptual outcomes. The first, and more widely documented, is perceptual learning referring to long-lasting improvement of perceptual thresholds. The second is perceptual deterioration, which is observed when the number of trials is increased within a training session or between closely spaced sessions. Recent results with visual texture discrimination show that these two processes inversely affect each other: decremental effects interfere with further learning, while efficient short practice results in a long-term learning effect in which performance decrements are practically eliminated. Further results show that sleep is necessary to preserve learning effects following short training and facilitates the decay of deterioration that normally results from extensive training. We suggest a theoretical link between perceptual deterioration and learning, assuming a system with saturating connectivity. Training strengthens task related connections, with further training leading to saturation of these connections along with strengthening of less efficient connections corresponding to accumulated noise in the network. Such saturation in network connectivity and reduction of signal-to-noise ratio consequently affects the readout of the network, causing deterioration in discrimination performance. Thus, best learning is achieved with short training sessions. Resistance to saturation is achieved by sleep-dependent consolidation of unsaturated connectivity. The different transfer properties of the performance decrements and increments allow us to identify local and global components of perceptual learning and their interactions. This suggests sleep-dependent consolidation mechanisms that induce modifications in higher brain areas that interact with local early visual networks to enable improvement of perceptual abilities.

Keywords: perceptual learning; perceptual deterioration; adaptation; memory consolidation; texture perception

* Corresponding author; E-mail: Dov.Sagi@Weizmann.ac.il

INTRODUCTION

In this paper, based on recent experimental evidence, we will propose a novel unified framework of perceptual learning, accounting for perceptual increments and decrements induced by training. We will first review perceptual learning of texture discrimination and discuss the role of sleep in the learning process. Then, we will address the problem of perceptual deterioration due to extensive practice. Finally, we will discuss the recent findings showing that learning and deterioration processes affect each other, and propose a unified model accounting for the interactions between these processes and their underlying brain mechanisms.

There is an increasing body of evidence suggesting that early processing stages of human adult sensory systems can undergo long-term neural changes. These proposed modifications are achieved by efficient practice which enables long-lasting improvement in perception, and are referred to as perceptual learning (Fahle, 2004; Zenger and Sagi, 2002). Thus, plasticity in early sensory systems has been suggested to occur not only in early development as was previously believed, but also in adults. This is supported by recent reports showing that damage to the visual system during early development can be repaired, at least in part, in adult age (Polat et al., 2004).

However, other studies have shown that practice does not always result in improved perception. In fact, practice could result in just the opposite; namely, deterioration in performance. Surprisingly, both effects can be obtained with the same experimental paradigm, whereby only the number of trials is manipulated. Studies using the texture discrimination task (Karni and Sagi, 1991) show that intensive “over-practice”, achieved by increasing the number of trials in a given training session, increases the discrimination thresholds (Mednick et al., 2002; Mednick, Arman and Boynton, 2005; Censor, Karni and Sagi, 2006; Ofen, Moran and Sagi, 2007). These effects were specific to basic image features, implicating early stages of the visual stream rather than general fatigue. Accounts of the phenomenon include limited capacity of local networks in the brain (Mednick et al., 2002) and connectivity saturation (Censor and Sagi, 2008) due to strengthening of synapses contributing to noise to a level similar to that of the synapses contributing to signal.

Interestingly, it has been shown that the processes of perceptual learning and perceptual deterioration affect each other, pointing to a common underlying mechanism (Censor, Karni and Sagi, 2006; Censor and Sagi, 2008). Studies show that over-practice causing within-session perceptual deterioration interferes with normally observed between-session learning (Censor, Karni and Sagi, 2006), whereas efficient practice followed by sleep enables long-term resistance to within-session perceptual deterioration (Censor and Sagi, 2008). This resistance was suggested to be achieved by sleep dependent consolidation of unsaturated connectivity (Censor and Sagi, 2008).

Based on this recent experimental evidence, we will present a novel framework suggesting brain mechanisms that could account for the link between the saturation processes involved in perception, and the ability to overcome such saturation by consolidating efficient network connectivity, thus enabling improvements in perceptual abilities. The application of this account to procedural learning in general will be discussed.

PERCEPTUAL LEARNING OF TEXTURE DISCRIMINATION AND THE ROLE OF SLEEP

One of the important tools used to study perceptual learning is the texture discrimination task. The task enables the use of psychophysical methods in order to quantify sensitivity thresholds, thus providing a tool for measuring and observing perceptual learning *per se*. In a typical texture discrimination experiment, observers need to detect a target-figure composed of line segments which differ in orientation from the background (*Fig. 1a*). Since this task is easy, the stimuli are backward masked so that performance is reduced by the presentation of visual noise (*Fig. 1b*). Observers have to decide whether a peripheral array (appearing randomly and equally either in the lower left or lower right quadrant of display) of 3 diagonal bars embedded in a background of horizontal bars was horizontal or vertical. Fixation is enforced by a central letter-discrimination task. The time-interval between the target onset and the mask (SOA: stimulus onset asynchrony) is gradually decreased within the session.

Evidence from psychophysical studies using the texture discrimination task (Karni and Sagi, 1991) shows that improvements in performance observed hours after termination of practice are specific to retinal location, orientation and in part monocular. This suggested that plasticity which induces learning occurs in the primary visual cortex, which includes cells that are monocular as well as retinotopic, and specific to orientation. Moreover, the texture discrimination task demonstrated delayed gains in performance that occur hours after visual experience was terminated, and which are preserved when tested a few years later (Karni and Sagi, 1993). These delayed performance gains were suggested to be part of a consolidation process, involving neuronal changes in early stages of the visual stream. The consolidation process has been studied by various fields and methods. For example, Muller and Pilzecker (1900) proposed a hypothesis regarding consolidation already in 1900, when studies on humans showed a fragile initial state in which new memories could be interrupted by other information, suggesting that the memories consolidate over time to become stable. Consolidation was therefore suggested to be the process in which exposure to an experience becomes hard-wired in the brain, due to synaptic plasticity. Thus, practice through repeated controlled exposure to the task results in protein synthesis, which can involve activation of transcription factors and gene expression that may cause new strengthened synaptic configurations in the cells (Goel et al., 1986; McGaugh, 2000; Dudai, 2002).

Karni et al. (1994) used sleep deprivation methods to show that overnight improvement in texture discrimination is strongly dependent on REM (rapid eye movement) sleep. Further studies performed by Stickgold and colleagues (Stickgold et al., 2000; Stickgold, James and Hobson, 2000) illustrated that after initial training, between-session sleep is required for perceptual improvement to take place. By recording EEG during sleep, Stickgold et al. (2000) also showed that learning was proportional both to SWS (slow wave sleep) in the first quarter of the night, and REM sleep in the last quarter of the night. Similarly, Mednick and colleagues (Mednick, Nakayama and Stickgold, 2003) showed that improvement takes place even after a nap (60–90 minutes) containing both SWS and REM sleep, but not after a shorter nap containing relatively little REM sleep and rich in SWS. However, the latter was found to act against the accumulation of performance deterioration (Mednick et al., 2002). REM sleep alternates across the night with four stages of NREM (non-rapid eye movement) sleep every 90 minutes.

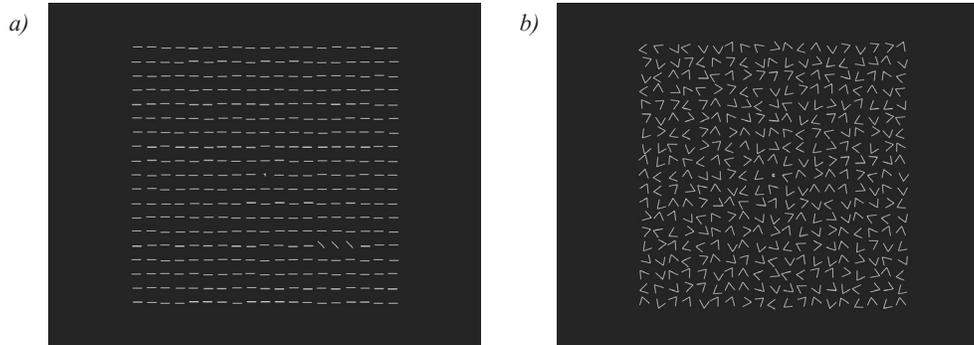


Figure 1. Trial sequence of the texture discrimination task

Subjects fixate on a circle in the center of the screen and activate the sequence: (a) a 40 ms target consisted of 3 diagonal bars at the lower left or lower right quadrant of display, differing only in orientation from a background of horizontal identical bars. Subjects have to discriminate whether the 3 bars were vertical or horizontal, while a small rotated letter (T or L) at center of display serves as a fixation task; after a blank inter-stimulus interval appears (b) a 100 ms mask made of randomly oriented V-shaped micro patterns and at the center, a pattern of superimposed T and L; finally, there is a blank screen until response.

Stages 3 and 4 of NREM sleep, termed SWS, dominate the first half of the night, whereas REM sleep and stage 2 of NREM sleep are more common in the second half of the night. Thus it seems that processes operating during SWS act to reduce perceptual deterioration while processes operating during REM sleep contribute to the long-term preservation of perceptual improvements: brain activity is significantly enhanced in the occipital cortex, thalamic nuclei, amygdala and hippocampus during REM sleep, compared to other stages of sleep (Braun et al., 1997). Marrosu et al. (1995) found that during REM sleep cholinergic systems become more active and acetylcholine activity is dominant in the brain. Acetylcholine initiates a signal transduction cascade which activates transcription factors for genes coding for proteins related to LTP (Graves, Pack and Abel, 2001), and is involved in a cascade of enzymatic events which trigger upregulation of genes related to plasticity (Abel and Lattal, 2001; Walker, 2005). Frey and Morris (1997) have suggested that LTP initiates the creation of a protein-synthesis-independent “synaptic tag” at the potentiated synapse. This process of synaptic tagging was suggested to facilitate the formation of long-term memories through synaptic weight changes caused by repeated stimulation (Govindarajan, Kelleher and Tonegawa, 2006).

PERCEPTUAL DETERIORATION – A PROBLEM OF SATURATION?

Interestingly, while some studies show performance gains following efficient training, other studies have found that extensive practice on the same texture discrimination task can lead to perceptual deterioration. These studies found similar properties for performance deterioration between sessions separated by a few hours (Mednick et al., 2002; Mednick, Arman and

Boynton, 2005) and within a single session (Ofen, Moran and Sagi, 2007), the latter traditionally attributed to visual adaptation.

The transfer of these deterioration effects between eyes pointed to a cortical origin. The underlying mechanisms of these deterioration effects were related to early visual areas due to specificity of the perceptual decrements to retinal location and other basic properties of the stimulus. Therefore it was suggested that the deterioration was not simply due to general fatigue, but rather because specific neural networks in early stages of the visual stream are limited in capacity and become gradually saturated with information through repeated testing. This could decrease the ability of the local neural network to process further information and may lead therefore to perceptual deterioration.

What is the time-scale of these perceptual decrements? Censor and colleagues (Censor, Karni and Sagi, 2006) have shown that increasing the number of trials within the training session increases the discrimination thresholds (*Fig. 2*). In other studies, the authors found that when a second session is performed 2–3 hours after the end of an identical initial session (Censor, 2005; Mednick et al., 2002; Mednick, Arman and Boynton, 2005), discrimination

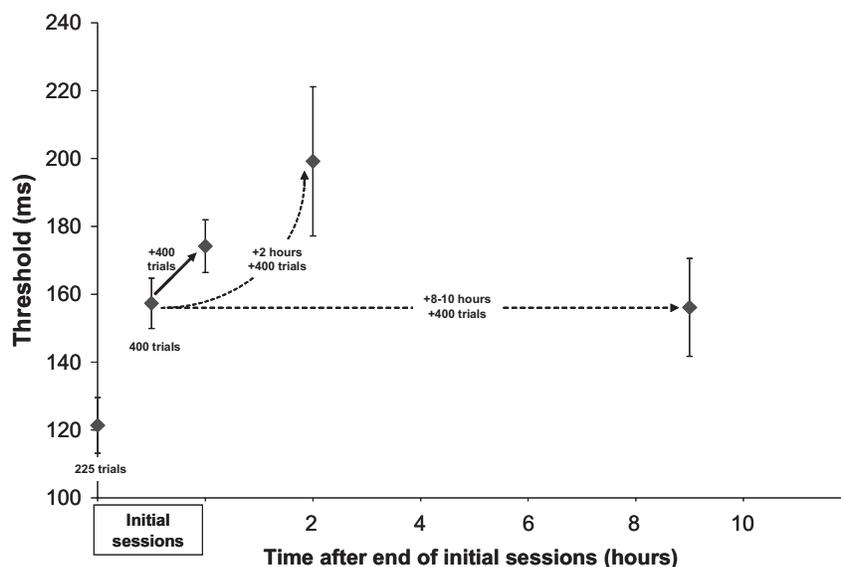


Figure 2. Time-course of perceptual deterioration

Within-session deterioration: Comparison between initial thresholds of participants ($n = 7$) performing sessions with 225 trials per each of the two target locations, participants ($n = 13$) performing sessions with 400 trials and those ($n = 17$) performing sessions with an additional 400 trials (total of 800 trials). More trials per block resulted in a significantly higher initial threshold. Between-session deterioration: When sessions (400 trials per session) are separated 2 hours apart, participants ($n = 6$) show significantly higher thresholds compared to their initial session. When sessions of the same length are separated 8–10 hours apart with no between-session sleep, participants ($n = 7$) show no deterioration compared to their initial session. Error bars represent standard errors. Data from Censor, Karni and Sagi (2006), Censor and Sagi (2008) and Censor (2005).

thresholds increase (*Fig. 2*). However, when the two sessions are separated by 8–10 hours (Censor, Karni and Sagi, 2006), there is no significant threshold increase between the sessions (*Fig. 2*). While perceptual deterioration effects are prevented by short mid-day naps (Mednick et al., 2002), performance seems to return to baseline with an increased interval between training sessions, even without between-session sleep.

Other accounts of perceptual deterioration suggest that over-exposure to the task results in a net increase in synaptic strength, leading to saturation of local neuronal networks and reducing processing efficiency (Huber et al., 2004; Tononi and Cirelli, 2006). Saturation of information or network connectivity may be caused by strengthening of synapses contributing to noise to a level similar to that of the synapses contributing to signal, causing saturation of the network processing the task and deterioration in discrimination performance (Censor and Sagi, 2008). Such accounts are based on anatomical evidence demonstrating a net increase in synaptic density in animals directly stimulated or exposed to enriched environments (Klintsova and Greenough, 1999), as well as findings that brain metabolism and local slow wave activity in humans increase during wakefulness (Braun et al., 1997). Thus limited resources, saturated at the local network level, may result in performance decrements. As stated above, results showing no deterioration when discrimination sessions are separated 8–10 hours apart, suggest that the saturation processes have a limited timescale of effectiveness on perceptual performance, even without subsequent sleep. However, even though these saturation processes do not seem to persist over time, they do seem to have a long-term effect on between-session learning, when no further learning is achieved in saturated conditions (Censor, Karni and Sagi, 2006; Censor and Sagi, 2008).

BUILDING THE LINK – SATURATED CONDITIONS REDUCE FURTHER LEARNING

A first step towards linking perceptual learning and perceptual deterioration processes was established in a recent study using the texture discrimination task (Censor, Karni and Sagi, 2006). In this study, it was found that intensively long practice sessions resulting in over-exposure to the stimuli not only increase the measured thresholds, but also suppress the learning processes. The results indicate that the over-exposure to the stimuli may interfere with consolidation, as even an interval of 24 hours which included a night's sleep was insufficient for developing performance gains after training with 800 trials per target location (*Fig. 3a*). When the number of trials was reduced to 400, learning occurred only after a night of sleep (*Fig. 3b*), while with 225 trials small learning effects seemed to be equally likely with or without sleep (*Fig. 3c*).

Tononi and Cirelli (2006) suggested that plastic processes occurring during wakefulness result in a net increase in synaptic strength in many brain circuits. Due to the net increase in synaptic strength, waking plasticity has a cost in terms of energy requirements, space requirements, and progressively saturates our capacity to learn. EEG experimental results showed a correlation between local SWS homeostasis and learning of a visuomotor task (Huber et al., 2004). Huber and colleagues therefore suggested that SWS helps synaptic consolidation by possibly producing synaptic downscaling and increase in signal-to-noise ratio in specific neu-

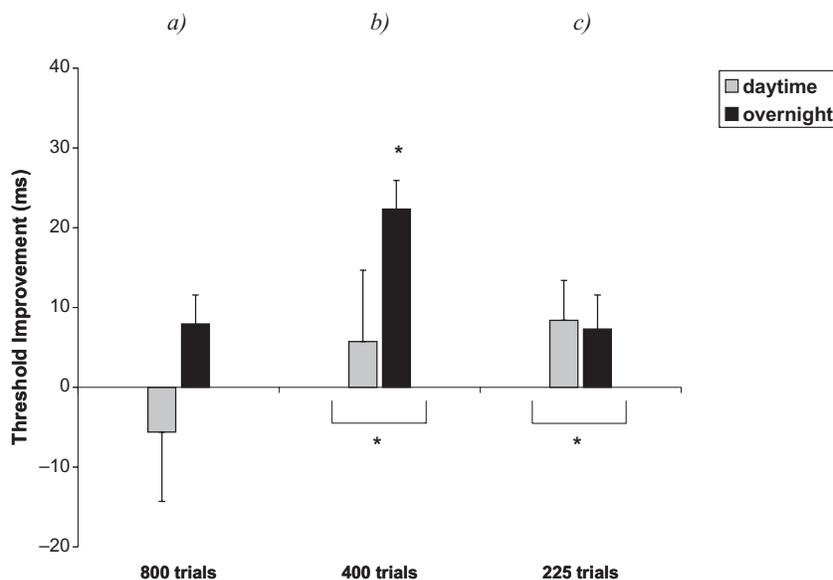


Figure 3. Intensive practice blocks further learning

Group-average threshold improvement for participants during daytime (between the morning and evening sessions) and overnight (between the evening and following morning sessions, including a night of sleep). Asterisks represent significance ($P < .05$) of average improvement. (a) With an intense session (800 trials per target location, $n = 5$), no significant improvement was observed between sessions. (b) When the number of trials was reduced (400 trials, $n = 7$), thresholds were significantly improved only after a night of sleep. (c) When the number of trials was further reduced (225 trials, $n = 7$), threshold was not significantly improved, neither during daytime nor overnight, although a complete 24 h cycle did yield significant improvement. Adapted from Censor, Karni and Sagi (2006).

ral networks. That intermediate practice sessions sleep can counter the effect of over-exposure on learning, yielding significant between-session delayed gains (Fig. 3b), supports this connection between over-exposure and homeostatic processes occurring during sleep. Similarly, the finding that practicing extremely long sessions interferes with learning (Censor, Karni and Sagi, 2006) suggests that the renormalization and modified network-connectivity described above may not be effective following these over-intense sessions, thereby not preventing further saturation and not enabling further learning.

The above results are the first to suggest a link between the memory consolidation stabilizing process and the perceptual deterioration suppressive process. The interaction of these two processes may determine the triggering and effectiveness of memory consolidation processes, with sleep having an important role in counteracting the suppressive effects. Intensive practice may result in saturation of the visual network processing the task. Under these saturated conditions, renormalization during sleep may not leave effective memory traces allowing modification of network connectivity beneficial for learning processes.

CLOSING THE LOOP – USING PERCEPTUAL EXPERIENCE TO AVOID SATURATION

A question remains: if visual networks that gradually saturate with repeated stimulation result in reduced performance, could this deterioration be prevented by efficient practice? Recent results (Censor and Sagi, 2008) show that subjects practicing short sessions with the texture discrimination task do not show the perceptual decrements in following intense sessions. This is in contrast to subjects practicing intense sessions that do show such decrements (*Fig. 4*). This learning effect was not found when training and test were not separated by sleep. Additionally, this learning effect was found to be long-term, and was observed even when training and test sessions were nine months apart.

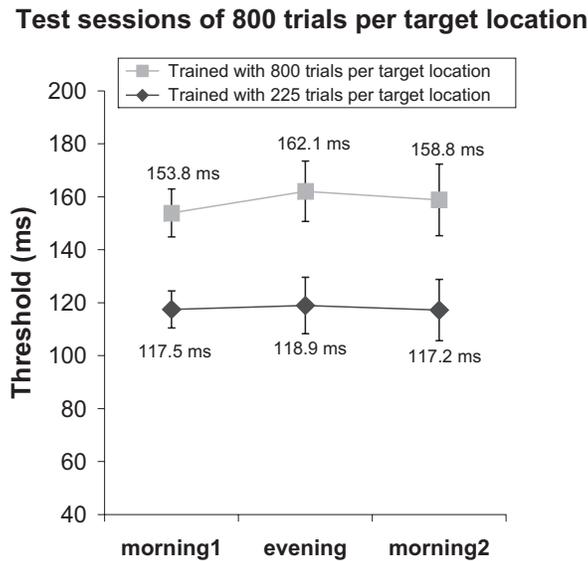


Figure 4. Short training enables resistance to perceptual deterioration

Subjects ($n = 6$) trained with short sessions of 225 trials per target location show significantly lower average thresholds at intense 800 trials test sessions, compared to control subjects ($n = 6$) trained with 800 trials. Error bars represent standard errors. Adapted from Censor and Sagi (2008).

These results expand the newly proposed link between perceptual deterioration and learning processes operating in the visual network: short practice sessions with a stimulus may have a role in consolidating effective network connectivity, serving as a memory trace. The modified network with increased efficiency may prevent saturation by renormalizing connectivity patterns (Huber et al., 2004; Tononi and Cirelli, 2006) or reducing local energy demands by extending network size (Karni et al., 1995). Therefore, the modified network can process longer sessions with lower signal-to-noise ratio and does not show performance dec-

rements, as compared to subjects practicing long sessions, where the saturated network may not efficiently process further information, therefore causing threshold elevation.

Previous studies (Huber et al., 2004; Tონონი and Cirelli, 2006) have suggested that sleep has a role in achieving homeostatic regulation by downscaling and renormalizing synaptic strength (downscaling of cortical synapses has been observed in vitro and in vivo, see Desai et al., 2002 and Turrigiano, 1999). Thus total synaptic weight is reduced while relative differences in synaptic strength achieved by practice are preserved, leaving memory traces. Therefore, connections between strongly correlated neurons (contributing to signal) would survive, while others (contributing to noise) may be eliminated. In this way, increase in signal-to-noise ratio is achieved, allowing the network to process additional information.

RELATIONSHIP TO SENSORY ADAPTATION AND AFTEREFFECTS

Although widely reviewed in the context of texture discrimination tasks, perceptual decrements are also widely documented within the framework of other perceptual tasks, such as contrast adaptation (Blakemore and Campbell, 1969). Traditionally, within the context of visual perception, “adaptation” refers to increased thresholds accompanied by a decrease in performance-levels, electrophysiological activity (Blakemore and Campbell, 1969), and perceptual gain (Dao, Lu and Doshier, 2006) as a function of repeated stimulation within a given session. Although the underlying mechanisms of such adaptation processes remain largely unknown, they may share some of the processes explained above. Blakemore and Campbell (1969) have shown that sensory adaptation affects visual performance by elevating contrast sensitivity thresholds, and is specific to stimuli orientations and spatial frequencies. However, it should be noted that in these studies of contrast adaptation, the subjects were well-trained and experienced in the tasks, yet still did not show resistance to perceptual decrements (Blakemore and Campbell, 1969) as shown in the texture discrimination task (Censor and Sagi, 2008), pointing to additional underlying mechanisms.

An exceptional sensory adaptation is the McCollough effect (McCollough, 1965), an orientation-contingent chromatic aftereffect that is induced by several minutes of adaptation to pairs of gratings differing in orientation and color. It is thought that this aftereffect is due to recalibration of the visual system to changes in environmental parameters (Dodwell and Humphrey, 1990). Unlike typical aftereffects, the “McCollough effect” can last for many hours, even weeks, and is thus believed to reflect plasticity within the visual system (Harris, 1980). Lund and Mackay (1983) found that the strength of the aftereffect is enhanced with increasing sleep periods before induction, suggesting that sleep before induction affects the plasticity of the visual system. While we find that sleep after learning is critical for memory consolidation, it is noted that the accumulated effects resulting in perceptual deterioration, which act against learning (*Fig. 3*), are reduced rather than enhanced by sleep (Censor, Karni and Sagi, 2006; Mednick et al., 2002).

AN ADDITIONAL MECHANISM OF PERCEPTUAL LEARNING?

So far, we have presented an extensive discussion on texture discrimination studies which were the first to suggest a link between perceptual learning and perceptual deterioration, with one affecting the other: best performance is achieved with short training while further training leads to decrements due to connectivity saturation. Resistance to perceptual deterioration is achieved by sleep-dependent consolidation of unsaturated connectivity.

Additional results (Censor and Sagi, 2009) suggest that resistance to performance decrements transfers to untrained locations of the visual field, suggesting involvement of higher brain areas. Studies using the texture discrimination task have shown that improvements after practice are specific to retinal location, suggesting involvement of neuronal changes in early stages of the visual system (Karni and Sagi, 1991, 1993; Schwartz, Maquet and Frith, 2002). Perceptual decrements were also shown to be specific to retinal location (Mednick et al., 2002; Mednick, Arman and Boynton, 2005; Ofen, Moran and Sagi, 2007). Our results (Censor and Sagi, 2009) suggest that higher brain areas are involved in the elimination of perceptual decrements following short practice, possibly by creating an efficient global template or classifier for correct discrimination, able to operate under otherwise noisy conditions. Doshier and Lu (1998) suggested that such a template, amplifying stimulus response relative to noise, underlies learning effects in texture (second-order) tasks (Lu and Doshier, 2004).

These different transfer properties may therefore suggest for the first time an additional mechanism operating in perceptual learning, involving both local and global components in perceptual learning processes. Thus mechanisms that induce modifications of higher brain areas may interact with local early visual networks and enable improvement of perceptual abilities.

LEARNING AND MEMORY: THE EFFICIENT CONNECTIVITY AND SATURATION HYPOTHESIS

Based on the experimental evidence reviewed thus far, we now propose a model to account for perceptual learning in texture discrimination tasks involving saturation conditions: Visual stimulation initiates activation of local neuronal networks, modifying specific synapses processing the stimulus. Practicing the task may modify the synapses involved by changing their synaptic weights as compared to the surrounding synapses. However, intense practice sessions resulting in over-exposure to the stimulus saturate the network. Therefore, the over-exposed network cannot efficiently process further information, resulting in perceptual deterioration. Thus neural networks processing the stimulus become saturated due to repeated activation, with noise increasing with increasing number of trials due to the strengthening of task-irrelevant synapses (i.e. signal to noise decreases, see *Fig. 5*).

Sleep produces downscaling and renormalization, thereby stabilizing the system: connections between strongly correlated neurons specific to the stimulus (i.e. contributing to signal) would survive, while others (contributing to noise) are eliminated. Such notions of memory-related stabilization processes during sleep have also been suggested by Crick and Mitchison (1983), who proposed that REM sleep functions to remove undesirable modes of

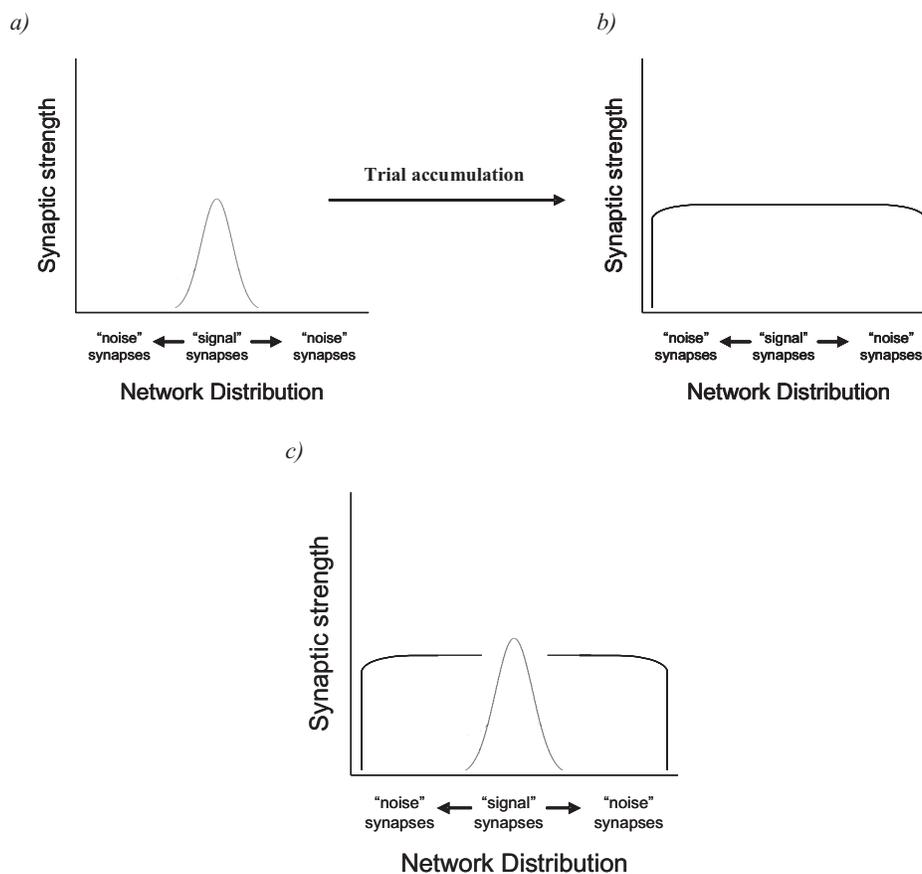


Figure 5. The saturation-learning hypothesis

(a) Short sessions produce a distributed network, composed of synapses contributing to signal and synapses contributing to noise. (b) Largely increasing the amount of trials saturates the network. (c) Consolidation of unsaturated activity creates a template which could be imposed on noisy networks, band-passing the signal and band-stopping the noise, preventing deterioration.

interaction in cortical networks, possibly by reverse learning mechanisms (Hopfield, Feinstein and Palmer, 1983). Such undesirable modes were also termed “frustrated networks” (Bersini, 1998).

As discussed above, and within our suggested framework, following stabilization during sleep (possibly SWS), other stages of sleep (possibly REM sleep) can identify the specific tagged synapses (which are the modified renormalized synapses of the local task-relevant network) and enhance up-regulation of genes related to synaptic plasticity and memory consolidation. The final state of the network following renormalization serves as an input to a “global classifier”, as suggested by our results showing transfer of saturation-resistance to untrained locations (Censor and Sagi, 2009). This classifier uses a general template (Fig. 5a), and im-

poses it on noisy networks (*Fig. 5b*), band-passing the signal and band-stopping the noise (*Fig. 5c*).

The global classifier receives its input from the local domains. This input can originate from any of the local networks. In case of noisy local networks, there is no unique template structure to be passed onto the global domain. Once established, the global template could be imposed on locally saturated networks (*Fig. 5c*). Though saturation does not seem to persist over time, no further learning is achieved in saturated conditions since no unique perceptual template is consolidated.

Additionally, performance gains could occur while generating the optimal classifier. This could account for within-session learning (as in Karni and Sagi, 1993) and for the partial contribution of daytime between-session performance gains to the 24 hours cycle yielding overall significant performance gains (Censor, Karni and Sagi, 2006, see *Fig. 3c*). Thus the current theory can be used to generate a rich variety of experimental situations with fast and slow learning, and local and global effects as documented in the literature (Fahle, 2004).

The classical notion of memory consolidation, whereby the memory of a given experience becomes stable and enduring (Dudai, 2002; McGaugh, 2000), may be related to our framework. Within this notion, after training, the establishment of long-term memory can be blocked by chemical, electrical or behavioral interference (McGaugh, 2000). In the studies presented here, such interference could occur from repeated exposure to the same task. Previous studies have suggested that the time-window for behavioral interference to motor learning lasts up to several hours after training (Brashers-Krug, Shadmehr and Bizzi, 1996; Walker, 2005), whereas the evolution of delayed gains requires sleep (Korman et al., 2007, Walker et al., 2002, 2003). This is in line with the findings presented here which suggest that saturation processes do not persist over time per se, whereas achieving further resistance to perceptual decrements requires sleep after short training.

Models such as the standard model for system consolidation (Dudai, 2004) could further account for the generalization of the learning effects following short training. According to this model, memory traces in different brain areas such as the hippocampus could represent a compressed version of the internal representation. The hippocampal representation later becomes active either in explicit recall, or in implicit processes such as sleep, resulting in incremental adjustment of neocortical connections, probably involving synaptic consolidation. Thus such systems as the hippocampal system can serve as a “teacher” of the neocortical system (Dudai, 2004). Studies have suggested several ways in which the information represented in the hippocampus is able to influence the cerebral cortex by a hierarchy of hippocampo-cortical and cortico-cortical backprojection stages (Rolls, 2000). Further support to such consolidation mechanisms is given by studies showing coordinated memory replay in the visual cortex and the hippocampus during sleep (Ji and Wilson, 2007). Therefore after short training, selective processes occurring during sleep could enhance top-down guidance (“global template”) enabling improved performance in future saturated conditions. Studies showing that between-session motor learning is sleep-dependent for explicit skills (Robertson, Pascual-Leone and Press, 2004) imply that explicitness is needed for generalization of communication between different brain areas.

Reduced performance due to intensive training is also observed in the sensory-motor system. Repetitive hand movements engaged in task performance have been shown to produce

mild to severe motor deficits leading to focal hand dystonia, associated with writer's cramp, typist's cramp and musician's cramp (Nudo, 2003). Such over-training has been suggested to cause maladaptive plasticity (Rothwell and Huang, 2003) and impairment of homeostatic mechanisms that stabilize excitability levels within a useful dynamic range (Quartarone, Siebner and Rothwell, 2006). fMRI studies have correlated focal hand dystonia with altered somatotopic finger representations (Elbert et al., 1998). Processes discussed here could therefore have a role in the underlying mechanisms of such deficits, and potentially be used to reduce these repetition-induced decremental effects.

SUMMARY

In this paper we presented a unified framework of perceptual learning, linking both stabilizing and suppressive brain processes which determine the behavioral response: sleep-dependent consolidation of efficient connectivity enables global learning processes that may involve higher brain areas interacting with local early visual networks to overcome perceptual limitations and improve perceptual abilities. Nevertheless, the interactions between these global mechanisms and the local processes observed in perceptual learning of visual tasks such as texture discrimination should be further explored.

The framework presented here could have important implications on the study of human perception, and the ability of our brain to execute efficient behavioral responses based on the incoming sensory inputs. Furthermore, initiating processes involving brain plasticity which could potentially improve the brain's ability to efficiently process information in limited conditions may have useful applications in treating malfunctions and improving rehabilitation processes.

ACKNOWLEDGEMENTS

This work was supported by the Basic Research Foundation administered by the Israel Academy of Sciences and Humanities and by the Nella and Leon Benoziyo Center for Neurological Diseases at the Weizmann Institute of Science.

REFERENCES

- Abel, T., Lattal, K. M. (2001): Molecular mechanisms of memory acquisition, consolidation and retrieval. *Curr. Opin. Neurobiol.*, 11, 180–187.
- Bersini, H. (1998): The frustrated and compositional nature of chaos in small Hopfield networks. *Neural Netw.*, 11, 1017–1025.
- Blakemore, C., Campbell, F. W. (1969): On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.*, 203, 237–260.
- Brashers-Krug, T., Shadmehr, R., Bizzi, E. (1996): Consolidation in human motor memory. *Nature*, 382, 252–255.
- Braun, A. R., Balkin, T. J., Wesenten, N. J., Carson, R. E., Varga, M., Baldwin, P., Selbie, S., Belenky, G., Herscovitch, P. (1997): Regional cerebral blood flow throughout the sleep-wake cycle. An H₂¹⁵O PET study. *Brain*, 120, 1173–1197.

- Censor, N. (2005): A refined model for consolidation and performance of texture discrimination. *Master of Science Thesis, Weizmann Institute of Science*.
- Censor, N., Sagi, D. (2008): Benefits of efficient consolidation: short training enables long-term resistance to perceptual adaptation induced by intensive testing. *Vision Res.*, *48*, 970–977.
- Censor, N., Sagi, D. (2009): Global resistance to local perceptual adaptation in texture discrimination. *Vision Res.*, in press.
- Censor, N., Karni, A., Sagi, D. (2006): A link between perceptual learning, adaptation and sleep. *Vision Res.*, *46*, 4071–4074.
- Crick, F., Mitchison, G. (1983): The function of dream sleep. *Nature*, *304*, 111–114.
- Dao, D. Y., Lu, Z. L., Doshier, B. A. (2006): Adaptation to sine-wave gratings selectively reduces the contrast gain of the adapted stimuli. *J. Vision*, *6*, 739–759.
- Desai, N. S., Cudmore, R. H., Nelson, S. B., Turrigiano, G. G. (2002): Critical periods for experience-dependent synaptic scaling in visual cortex. *Nat. Neurosci.*, *5*, 783–789.
- Dodwell, P. C., Humphrey, G. K. (1990): A functional theory of the McCollough effect. *Psychol. Rev.*, *97*, 78–89.
- Doshier, B. A., Lu, Z. L. (1998): Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc. Natl. Acad. Sci. USA*, *95*, 13988–13993.
- Dudai, Y. (2002): Molecular bases of long-term memories: a question of persistence. *Curr. Opin. Neurobiol.*, *12*, 211–216.
- Dudai, Y. (2004): The neurobiology of consolidations, or, how stable is the engram? *Annu. Rev. Psychol.*, *55*, 51–86.
- Elbert, T., Candia, V., Altenmuller, E., Rau, H., Sterr, A., Rockstroh, B., Pantev, C., Taub, E. (1998): Alteration of digital representations in somatosensory cortex in focal hand dystonia. *Neuroreport*, *9*, 3571–3575.
- Fahle, M. (2004): Perceptual learning: A case for early selection. *Journal of Vision*, *4*, 879–890.
- Frey, U., Morris, R. G. (1997): Synaptic tagging and long-term potentiation. *Nature*, *385*, 533–536.
- Goelet, P., Castellucci, V. F., Schacher, S., Kandel, E. R. (1986): The long and the short of long-term memory – a molecular framework. *Nature*, *322*, 419–422.
- Govindarajan, A., Kelleher, R. J., Tonegawa, S. (2006): A clustered plasticity model of long-term memory engrams. *Nat. Rev. Neurosci.*, *7*, 575–583.
- Graves, L., Pack, A., Abel, T. (2001): Sleep and memory: a molecular perspective. *Trends Neurosci.*, *24*, 237–243.
- Harris, C. S. (1980): Insight or out of sight? Two examples of perceptual plasticity in the human adult. In Harris, C. S. (ed.), *Visual Coding and Adaptability*. New Jersey: Lawrence Erlbaum Assoc., pp. 95–149.
- Hopfield, J. J., Feinstein, D. I., Palmer, R. G. (1983): ‘Unlearning’ has a stabilizing effect in collective memories. *Nature*, *304*, 158–159.
- Huber, R., Ghilardi, M. F., Massimini, M., Tononi, G. (2004): Local sleep and learning. *Nature*, *430*, 78–81.
- Ji, D., Wilson, M. A. (2007): Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nat. Neurosci.*, *10*, 100–107.
- Karni, A., Sagi, D. (1991): Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proc. Natl. Acad. Sci. USA*, *88*, 4966–4970.
- Karni, A., Sagi, D. (1993): The time course of learning a visual skill. *Nature*, *365*, 250–252.
- Karni, A., Tanne, D., Rubenstein, B. S., Askenasy, J. J. M., Sagi, D. (1994): Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*, *265*, 679–682.
- Karni, A., Meyer, G., Jezard, P., Adams, M. M., Turner, R., Ungerleider, L. G. (1995): Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*, *377*, 155–158.

- Klintonova, A. Y., Greenough, W. T. (1999): Synaptic plasticity in cortical systems. *Curr. Opin. Neurobiol.*, 9, 203–208.
- Korman, M., Doyon, J., Doljanski, J., Carrier, J., Dagan, Y., Karni, A. (2007): Daytime sleep condenses the time course of motor memory consolidation. *Nat. Neurosci.*, 10, 1206–1213.
- Lu, Z. L., Doshier, B. A. (2004): Perceptual learning retunes the perceptual template in foveal orientation identification. *J. Vis.*, 4, 44–56.
- Lund, N. J., Mackay, D. M. (1983): Sleep and the McCollough effect. *Vision Res.*, 23, 903–906.
- Marrosu, F., Portas, C., Mascia, M. S., Casu, M. A., Fa, M., Giagheddu, M., Imperato, A., Gessa, G. L. (1995): Microdialysis measurement of cortical and hippocampal acetylcholine release during sleep-wake cycle in freely moving cats. *Brain Res.*, 671, 329–332.
- McGaugh, J. L. (2000): Memory – a century of consolidation. *Science*, 287, 248–251.
- Mednick, S., Nakayama, K., Stickgold, R. (2003): Sleep-dependent learning: A nap is as good as a night. *Nat. Neurosci.*, 6, 697–698.
- Mednick, S. C., Arman, A. C., Boynton, G. M. (2005): The time course and specificity of perceptual deterioration. *Proc. Natl. Acad. Sci. USA*, 102, 3881–3885.
- Mednick, S. C., Nakayama, K., Cantero, J. L., Atienza, M., Levin, A. A., Pathak, N., Stickgold, R. (2002): The restorative effect of naps on perceptual deterioration. *Nat. Neurosci.*, 5, 677–681.
- Muller, G. Z., Pilzecker, A. (1900): Experimental contributions to the science of memory. *Z. Psychol.*, 1, 1–300.
- Nudo, R. (2003): Retuning the misfiring brain. *Proc. Natl. Acad. Sci. USA*, 100, 7425–7427.
- Ofen, N., Moran, A., Sagi, D. (2007): Effects of trial repetition in texture discrimination. *Vision Res.*, 47, 1094–1102.
- Polat, U., Ma-Naim, T., Belkin, M., Sagi, D. (2004): Improving vision in adult amblyopia by perceptual learning. *Proc. Natl. Acad. Sci. USA*, 101, 6692–6697.
- Quartarone, A., Siebner, H. R., Rothwell, J. C. (2006): Task-specific hand dystonia: Can too much plasticity be bad for you? *Trends Neuroscience*, 29, 192–199.
- Robertson, E. M., Pascual-Leone, A., Press, D. Z. (2004): Awareness modifies the skill-learning benefits of sleep. *Curr. Biol.*, 14, 208–212.
- Rolls, E. T. (2000): Hippocampo-cortical and cortico-cortical backprojections. *Hippocampus*, 10, 380–388.
- Rothwell, J. C., Huang, Y. Z. (2003): Systems-level studies of movement disorders in dystonia and Parkinson's disease. *Curr. Opin. Neurobiol.*, 13, 691–695.
- Schwartz, S., Maquet, P., Frith, C. (2002): Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proc. Natl. Acad. Sci. USA*, 99, 17137–17142.
- Stickgold, R., James, L., Hobson, J. A. (2000): Visual discrimination learning requires sleep after training. *Nature Neurosci.*, 3, 1237–1238.
- Stickgold, R., Whidbee, D., Schirmer, B., Patel, V., Hobson, J. A. (2000): Visual discrimination task improvement: A multi-step process occurring during sleep. *J. Cogn. Neurosci.*, 12, 246–254.
- Tononi, G., Cirelli, C. (2006): Sleep function and synaptic homeostasis. *Sleep Med. Rev.*, 10, 49–62.
- Turrigiano, G. G. (1999): Homeostatic plasticity in neuronal networks: the more things change, the more they stay the same. *Trends Neurosci.*, 22, 221–227.
- Walker, M. P. (2005): A refined model of sleep and the time course of memory formation. *Behav. Brain Sci.*, 28, 51–64; discussion 64–104.
- Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., Stickgold, R. (2002): Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron*, 35, 205–211.
- Walker, M. P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J. A., Stickgold, R. (2003): Sleep and the time course of motor skill learning. *Learn Mem.*, 10, 275–284.
- Zenger, B., Sagi, D. (2002): Plasticity of low level visual networks. In Fahle, M. and Poggio, T. (eds), *Textbook on 'Perceptual Learning'*. Boston: MIT Press, pp. 177–196.