VISION RESEARCH

An International Journal for Functional Aspects of Vision

ELSEVIER

Benefits of efficient consolidation: Short training enables long-term resistance to perceptual adaptation induced by intensive testing

Nitzan Censor, Dov Sagi *

Department of Neurobiology/Brain Research, Weizmann Institute of Science, Rehovot 76100, Israel

Abstract

Intensive training or testing reduces performance on perceptual and sensorimotor tasks. Here we show, for the visual texture discrimination task, that such adaptation-related performance decrements are practically eliminated following practice with a small number of trials and sleep. Thus, short training produces consolidation of an effective memory within the visual neural network, resistant to the performance decrements that are usually induced by intensive testing. We suggest a link between perceptual adaptation and learning: resistance is achieved by sleep dependent consolidation of distributed changes in network connectivity before saturated due to over-training. This link between memory generation, perceptual adaptation and memory consolidation may have an essential role in the underlying mechanisms of perceptual and motor learning. Therefore, intensive training yielding performance decrements in other modalities, such as the sensorimotor system, may be viewed in the context of the mechanisms suggested here.
© 2008 Elsevier Ltd. All rights reserved.

Keywords: Perceptual learning; Sensory adaptation; Memory consolidation; Sleep; Texture

1. Introduction

The ability to improve our performance in perceptual tasks by effective practice has been widely documented in various studies. However, the underlying neuronal mechanisms of such perceptual learning are constantly being explored and remain largely unknown. Studies using the texture discrimination task (Karni & Sagi, 1991, 1993; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Schwartz, Maquet, & Frith, 2002; Stickgold, James, & Hobson, 2000; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000) have shown that improvements observed hours after termination of practice are specific to retinal location, orientation and in part monocular, suggesting that neuronal changes in early stages of the visual system underlie these performance gains.

However, not only perceptual learning but also perceptual decrements were observed in texture discrimination (Censor, Karni, & Sagi, 2006; Mednick et al., 2002; Mednick, Arman, & Boynton, 2005; Ofen, Moran, & Sagi, 2007). These decremental effects were obtained by over-exposure to the task, either in closely spaced sessions (Mednick et al., 2002, 2005) or within a single prolonged session (Censor et al., 2006; Ofen et al., 2007). Due to specificity of the perceptual decrements to retinal location and other basic properties of the stimulus (Mednick et al., 2002, 2005; Ofen et al., 2007), it was suggested that specific neural networks in early stages of the visual stream become saturated due to repeated activation, whereas general fatigue was ruled out. Threshold increase and performance decrease with repeated stimulation within a session, along with reduced electrophysiological activity (Blakemore & Campbell, 1969) and reduced perceptual gain (Dao, Lu, & Dosher, 2006) is a phenomenon traditionally referred to, within the context of visual perception, as "adaptation". Previous results presented increasing peripheral vernier thresholds due to repeated over-exposure (Ludwig & Skrandies, 2002). Therefore it was suggested that the reduced sensory performance, appearing in parallel with

---

* Corresponding author. Fax: +972 8 934 4131.
E-mail address: Dov.Sagi@Weizmann.ac.il (D. Sagi).

decreased electric-field VEP measurements, is due to adaptation of the neural network to the training stimuli. Reduced performance due to over-training has been shown also in other modalities, such as focal hand dystonia in the sensorimotor system (Hallett, 1998; Rothwell & Huang, 2003).

Recently we have shown (Censor et al., 2006) that both discrimination thresholds and learning depend on the number of trials used during training: intense sessions produce higher discrimination thresholds and reduce between-session learning, pointing to an interaction between reduced sensory processing related to adaptation, and the generation of long-term memory.

Our study here was designed to investigate the effects of perceptual learning on perceptual decrements related to adaptation. The results show a novel correlation between the two processes: effective practice followed by sleep, eliminates perceptual decrements within following sessions, pointing to a common underlying neuronal mechanism.

We used the standard texture stimuli (e.g. Censor et al., 2006; Karni & Sagi, 1991; Stickgold, James, et al., 2000) consisting of a target frame followed by a patterned mask, as shown in Fig. 1. Observers had to decide whether a peripheral array of 3 diagonal bars embedded in a background of horizontal bars was horizontal or vertical. Fixation was enforced by a central letter-discrimination task. The time-interval between the target stimulus and the mask (stimulus-to-mask onset asynchrony, SOA) was gradually decreased by steps of 3 blocks of trials per SOA. Blocks contained 12 trials or 50 trials each, depending on the experimental group.

In the main experiment (experiment 1), one group of subjects practiced the texture discrimination task with 12 trials/block and a second group serving as a control, practiced the task with 50 trials/block (more decremental processes producing higher thresholds, previously shown to reduce between-session learning, see Censor et al., 2006). Both groups returned for additional intense test-sessions with 50 trials/block, a week to 9 months following practice. In experiment 2, no sleep was allowed between the 12

trials/block practice session and the 50 trials/block test-session. A third session of 50 trials/block was performed in the following morning, after a night's sleep. In experiment 3, three additional 12 trials/block sessions were performed immediately following the first 12 trials/block session, to test whether decremental processes within these sessions would affect processes allowing resistance to performance decrements in an intense 50 trials/block session held in the following day. In the third day, a single 12 trials/block session was performed.

2. Methods

2.1. Apparatus

The stimuli were presented on a 19″ Mitsubishi Diamond Pro 930SB color monitor, using a PC with an Intel Pentium processor. The luminance of the stimulus (line textures) was 64 cd/m^2 in an otherwise dark environment.

2.2. Stimuli and task

The standard texture stimuli was used (e.g. Censor et al., 2006; Karni & Sagi, 1991; Stickgold, James, et al., 2000), consisting of a target frame, which appeared for 40 ms. The target was followed by a patterned mask which appeared for 100 ms, as shown in Fig. 1. Observers had to decide whether an array of 3 diagonal bars embedded in a background of horizontal bars (19 × 19, 0.5° × 0.035° each, and spaced 0.72° apart) was horizontal or vertical. Display size was 14° by 13.5° of visual angle, viewed from a distance of 100 cm. The target appeared randomly and equally, either in the lower left or lower right visual quadrant, with its center at 5.3° of visual angle from center of display. Fixation was enforced by a forced-choice letter-discrimination task, between a "T" and an "L", at the center of the display. The time-interval between the target stimulus and the mask (stimulus-to-mask onset asynchrony, SOA) was manipulated. After an initial SOA wherein above 90% correct texture discrimination occurred was determined, the SOA was gradually decreased by SOA-dependent steps of 20–40 ms of 3 blocks of trials per SOA. At the SOA for which below 85% correct responses were given, or in extreme cases of large performance variations between blocks of the same SOA, an additional block was added until stable performance was achieved. Blocks contained 12 trials (~450 trials per session, 30–60 min) or 50 trials (~1600 trials per session, 90–150 min) each, depending on the experimental group. Each psychometric curve obtained was fitted with the Weibull function, with an additional finger error parameter $1 - p$, yielding the function
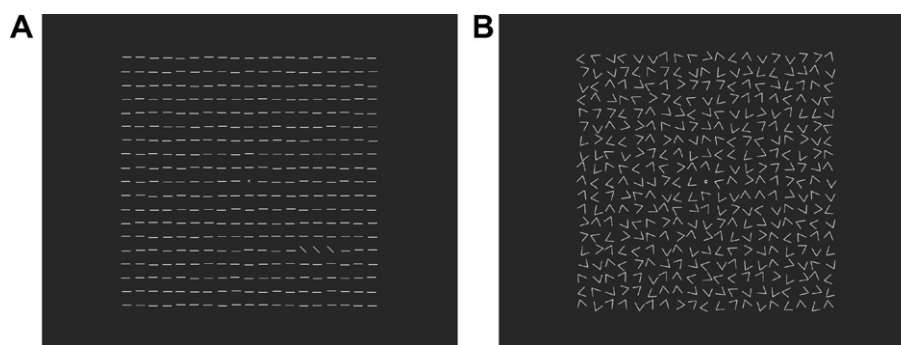
Fig. 1. Trial sequence of the texture discrimination task. Subjects fixate at a circle in the center of the screen and activate the sequence: (A) target consisted of three diagonal bars differing only in orientation from a background of horizontal identical bars, appears at the lower-left or lower-right quadrant of display for 40 ms. Subjects have to discriminate whether the 3 bars were vertical or horizontal. A small rotated letter (T or L) at center of display serves as a fixation target; after a blank inter-stimulus interval (SOA), 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.

$$P(t) = p\left\{1 - \frac{1}{2}\exp\left[-\left(\frac{t}{T}\right)^{\beta}\right]\right\} + \frac{1-p}{2} = \frac{1}{2}\left\{1 + p\left[1 - \exp\left[-\left(\frac{t}{T}\right)^{\beta}\right]i\right]\right\},$$

where T is the threshold for each curve, defined as the SOA for which 81.6% of responses were correct. In each session, the threshold SOA for the left and right targets was averaged. Sessions were terminated when the subject reached an SOA with close to chance level of performance (defined as less than 65% correct responses).

2.3. Subjects

The subjects were 20 paid undergraduate students with normal or corrected-to-normal vision. Due to possible effects of prior experience, all of the experiments were performed by naïve subjects. All subjects started the experiments with no prior experience in the task.

2.4. Experimental procedures

Experiment 1. Twelve subjects participated in the experiment. One group of subjects ($n = 6$) practiced the texture discrimination task with 12 trials/block and a second group ($n = 6$) serving as a control, practiced the task with 50 trials/block. Practice included three sessions: a morning session, followed by an evening session and a third session in the next morning, after a night of sleep. Both groups of subjects returned for three additional consecutive intense test-sessions with 50 trials/block (morning, evening, morning2), a week to 9 months following practice.

Experiment 2. Five subjects participated in the experiment. Three subject performed an initial morning session with 12 trials/block, followed by a 50 trials/block evening session 8–10 h later (no sleep allowed), and a third 50 trials/block session on the following morning, after a night's sleep. Two subjects performed an initial 12 trials/block session, followed by a 50 trials/block session in the next day, after a night's sleep (in these two sessions, targets were randomly presented at the lower-right or upper-left quadrant of display).

Experiment 3. Three subjects participated in the experiment, each tested for three consecutive days. On day 1, subjects performed 4 consecutive sessions of the texture discrimination task, with 12 trials/block each. On day 2, subjects performed a single session with 50 trials/block. On day 3, subjects performed a single session with 12 trials/block.

3. Results

Experiment 1 was designed in order to study whether short training can produce an efficient memory with long-term resistance to performance decrements. Subjects practicing short sessions of 12 trials/block returned for intense test-sessions with 50 trials/block. Subjects practicing sessions of 50 trials/block, performed identical intense 50 trials/block test-sessions, serving as control. Both groups of subjects performed the test-sessions a week to 9 months following initial practice.

The results (Fig. 2) showed significantly (*t*-test: $p < 0.005$) higher thresholds in practice sessions with 50 trials/block as compared to practice sessions with 12 trials/block, as described in our earlier report (Censor et al., 2006), demonstrating that neuronal processes yielding within-session performance decrements accumulate with increasing number of trials.

Most importantly, the present results showed (Fig. 3) that the average threshold for the morning 50 trials/block test-session, was significantly lower for the subjects trained with sessions of 12 trials/block as compared to the threshold of the control group of subjects trained with sessions of
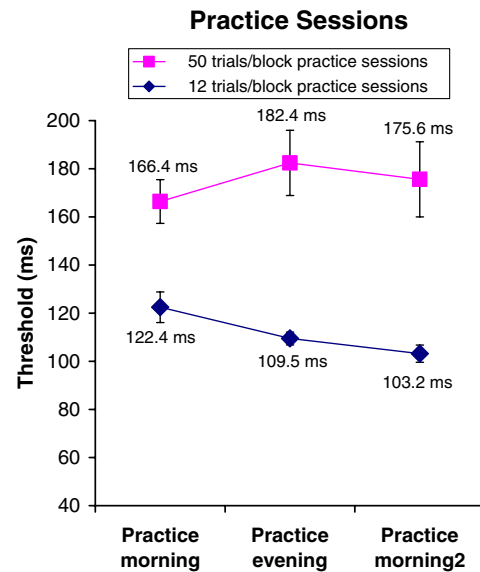

Fig. 2. Experiment 1, subjects ($n = 6$) practicing shorter sessions (12 trials/block) showing significantly lower average thresholds than subjects ($n = 6$) practicing long sessions of 50 trials/block. Error bars represent standard errors.
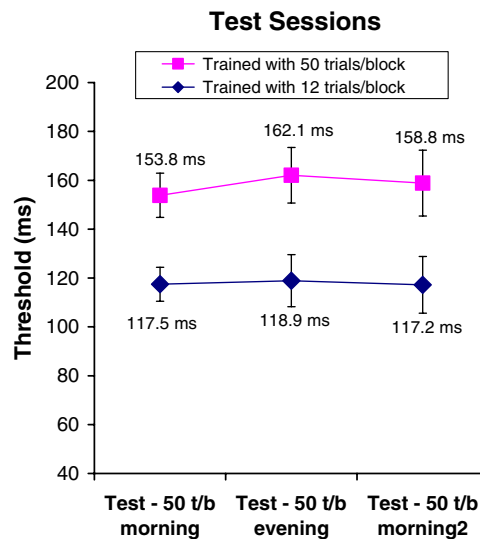

Fig. 3. Experiment 1, thresholds at the 50 trials/block test-sessions: subjects trained with short sessions of 12 trials/block show significantly lower average thresholds than control subjects trained with 50 trials/block. Error bars represent standard errors.

50 trials/block (mean threshold difference 36.4 ms, *t*-test: $p = 0.005$). These pronounced differences between the two groups of subjects were preserved also when all subjects (except one subject that could not return) returned for additional test-sessions in the evening (mean threshold difference 43.2 ms, *t*-test: $p = 0.01$) and in the following morning (mean threshold difference 41.6 ms, *t*-test: $p = 0.02$), after a night of sleep (see Fig. 3).

Furthermore, the results show that the average threshold for the 50 trials/block morning test-sessions of the subjects trained with sessions of 12 trials/block was

significantly lower than the average initial threshold of naïve subjects ($n = 20$, including subjects from our previous studies, Censor et al., 2006) performing 50 trials/block sessions (mean threshold difference 56.7 ms, t-test: $p = 0.00002$). This difference was preserved for the evening test-session (mean threshold difference 55.3 ms, t-test: $p = 0.001$) and the test-session in the following morning (mean threshold difference 57 ms, t-test: $p = 0.002$). On the other hand, the differences between the thresholds in test-sessions of subjects trained with 50 trials/block, and thresholds of naïve subjects performing 50 trials/block sessions were not significant (mean threshold differences between naïves and morning, evening, or following morning test-sessions 20.4, 12.1 and 15.4 ms, respectively, t-test: $p = 0.06$, $p = 0.20$ and $p = 0.18$, respectively).

Individual data for subjects trained with 12 trials/block sessions is shown in Fig. 4a. Pairwise comparisons show that there were no significant differences between all the 12 trials/block training sessions and 50 trials/block test-sessions of these subjects (mean difference 5.5 ms, paired t-test: $p = 0.13$). These results show that performance decrements are eliminated following short practice. On the other hand, for subjects trained with 50 trials/block sessions (Fig 4b), only small differences were observed between their 50 trials/block training sessions and test-sessions (mean difference 16.6 ms, paired t-test: $p = 0.0007$).

In experiment 2, we asked whether resistance to performance decrements could be obtained by short training without following sleep. Therefore, subjects were trained with a short 12 trials/block morning session, but performed the 50 trials/block test-session in the same evening 8–10 h later, with no sleep in between. Subjects performed an additional 50 trials/block session in the following morning, after a night of sleep.

Following the morning 12 trials/block short training session, subjects did not show resistance to performance decrements in the evening 50 trials/block session (Fig. 5), obtaining high thresholds of 192.9, 145.4 and 215.3 ms (subjects LK, AB and DV, respectively). These thresholds were significantly higher than the thresholds of the 12 trials/block morning session: 53.2 ms for subject LK, 27 ms for subject AB and 49 ms for subject DV. The mean threshold difference between the 12 trials/block morning session and the 50 trials/block evening session was 43.1 ms (paired t-test: $p = 0.02$). This difference between the 12 trials/block and 50 trials/block sessions is similar to the average initial threshold differences between naïve subjects ($n = 20$) performing 50 trials/block sessions and subjects ($n = 15$) performing 12 trials/block sessions (mean threshold difference of 46.8 ms, t-test: $p = 0.00003$). Performance in the 50 trials/block session improved overnight, however not significantly (mean threshold improvement 16.8 ms, paired t-test: $p = 0.07$).

To confirm that a single session of 12 trials/block training is sufficient to produce resistance to performance decrements we tested two subjects with a single 12 trials/block session during day 1 followed the next day with a 50 trials/block session. The results showed comparable perfor-
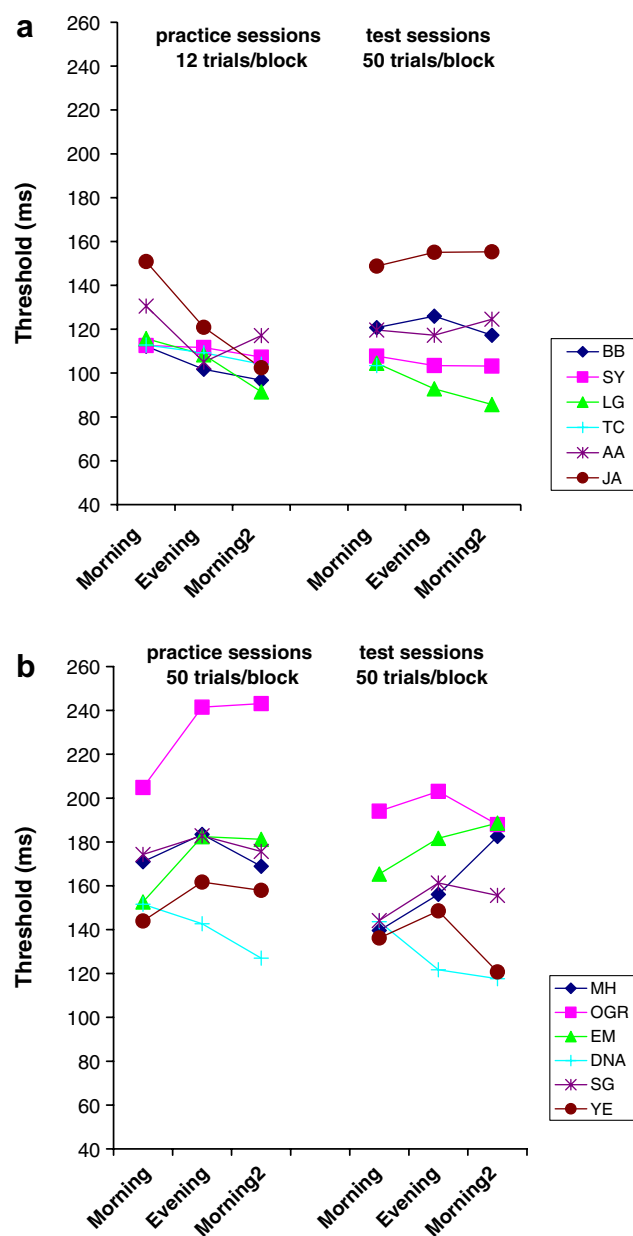

Fig. 4. Experiment 1, individual data: (a) No significant difference between thresholds of 12 trials/block practice sessions and 50 trials/block test-sessions. (b) Small differences between thresholds of 50 trials/block practice sessions and 50 trials/block test-sessions.

mance levels between the 12 trials/block and 50 trials/block sessions (differences for the two observers: 4.8 and 8.7 ms), within the range found in experiment 1 (mean difference 5.5 ms, SD ± 19.1 ms, see Fig. 4a).

These results show that resistance to performance decrements is not achieved within an 8–10 h time interval without sleep following the 12 trials/block training session.

Experiment 3 was designed using conditions shown to allow processes yielding resistance to performance decrements, and then testing whether these processes could be blocked by further training producing decremental adaptation-like processes. In the first phase of the experiment
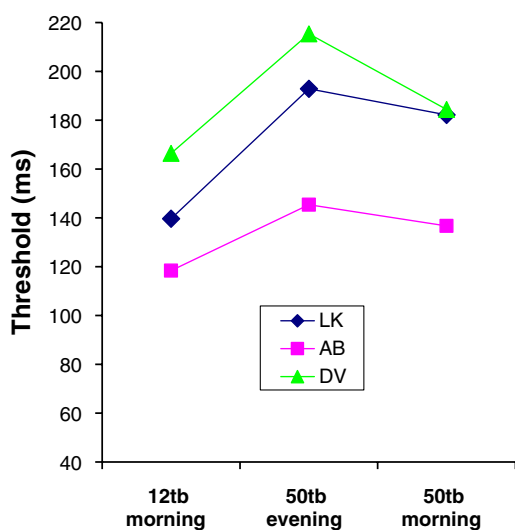
Fig. 5. Experiment 2, subjects ($n = 3$) practicing short morning sessions (12 trials/block) show high thresholds in the 50 trials/block test-session, held 8–10 later with no sleep in between. Thresholds remained high in an additional 50 trials/block test-session performed in the following morning, after a night's sleep.

(DAY1), subjects performed four consecutive short sessions with 12 trials/block each. The results (Fig. 6) showed that all three subjects obtained low thresholds for the initial session, and by the fourth session deteriorated significantly in performance: subject MG deteriorated by 45.9 ms, subject SS by 55 ms and subject NT by 54.5 ms (mean threshold difference between 1st and 4th sessions 51.8 ms, paired t-test: $p = 0.002$). This difference between the 1st and 4th 12 trials/block sessions is similar to the average initial threshold differences of subjects ($n = 20$) performing 50 trials/

block sessions and subjects ($n = 15$) performing 12 trials/block sessions (mean threshold difference of 46.8 ms, t-test: $p = 0.00003$). Since the amount of trials in 4 sessions of 12 trials/block and a single session of 50 trials/block is similar, these results imply that within-session deterioration in performance builds with accumulating number of trials (see also Mednick et al. 2002, 2005, showing within-session deterioration and deterioration in closely spaced sessions). The fact that in four short 12 trials/block sessions SOAs changed dynamically as opposed to a single long 50 trials/block session, rules out the possibility that decremental processes accumulate due to adaptation to a large number of trials with the same SOA.

In the second phase (DAY2), subjects performed a single intense session with 50 trials/block. Thresholds of the 50 trials/block session (see Fig. 6) were significantly higher than the low thresholds obtained at the initial short 12 trials/block session of the previous day (subject MG: 32.6 ms difference, subject SS 37.2 ms difference, subject NT 86.5 ms difference). Furthermore, there were no significant differences between performance in the 50 trials/block intense session and the 4th 12 trials/block session of the previous day (mean difference of 0.3 ms, $p > 0.5$). These results show that the additional 12 trials/block sessions not only caused performance deterioration within the same training day, but also prevented subjects from achieving low thresholds in the intense 50 trials/block session held in the following day.

In the third phase (DAY3), subjects performed a single short session with 12 trials/block. The results (Fig. 6) showed that for all subjects, the threshold was even lower than their initial 12 trials/block threshold obtained at the first session of DAY1 (mean difference 14.7 ms, SE $\pm$ 3.7, paired t-test: $p = 0.03$). These results imply that the intense 50 trials/block held in the previous day, did not produce a sustained effect on the network's ability to improve in the short 12 trials/block session, following sleep.

4. Discussion

The results of experiment 1 show that subjects practicing short sessions did not show the performance decrements in the following sessions, as opposed to control subjects that practiced long sessions. This long-term resistance to perceptual decrements was observed a week to 9 months following initial training.

The results show that the average threshold for the 50 trials/block test-sessions of the subjects trained with sessions of 12 trials/block were significantly lower (55–57 ms) than the average initial threshold of naïve subjects performing 50 trials/block sessions. It should be taken into account that this large effect may be a combination of reduced deterioration with some small general improvement, since it was previously shown (Censor et al., 2006) that subjects trained with short sessions of 12 trials/block, show a small improvement (mean 15.7 ms, SE $\pm$ 3.5) when performing the same session 24 h after initial practice. This
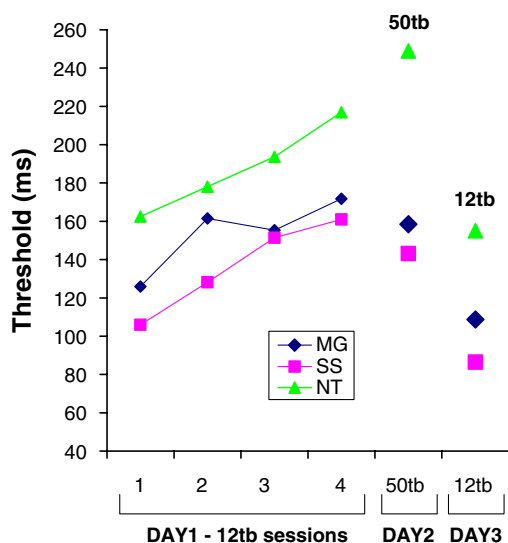

Fig. 6. Experiment 3, subjects ($n = 3$) practicing four consecutive sessions of 12 trials/block show deterioration in performance (DAY1). Furthermore, these additional sessions prevented subjects from achieving low thresholds in the 50 trials/block session in the following day (DAY2). However, the 50 trials/block sessions did not affect performance in the 12 trials/block single session performed in the following day (DAY3).

improvement is consistent with the threshold improvement observed in experiment 3 between the initial 12 trials/block session of DAY1 and the 12 trials/block session of DAY3 (mean 14.7 ms, SE ± 3.7) and may point to a general learning process rather than reduced deterioration, since this learning is unaffected by the intense sessions held in the previous days. Furthermore, in experiment 1 subjects performed the intense 50 trials/block sessions with gradually decreasing SOAs. It is possible that the magnitude of resistance to deterioration depends on the specific order of SOAs presented during the session. Overall, our results showing a dramatic reduction in thresholds during long sessions after practicing short sessions, clearly demonstrate that there are situations where deterioration can be greatly reduced, possibly avoided, thus pointing to a strong link between deterioration and learning.

The results of experiment 2 further show that without sleep following the 12 trials/block training session, resistance to performance decrements is not achieved within an 8–10 h time interval. Our previous study (Censor et al., 2006) and other studies (Mednick, Nakayma, & Stickgold, 2003; Stickgold, Jones, et al., 2000, Stickgold, Whidbee, et al., 2000) have shown that only with between-session sleep, similar time intervals are sufficient for learning processes to occur.

Reduced electrophysiological activity is shown in classical studies referring to adaptation (Blakemore & Campbell, 1969), and more recent studies showing reduced fMRI activity referred to adaptation (Grill-Spector & Malach, 2001) or to habituation due to repeated activation (Karni et al., 1995). Based on anatomical evidence demonstrating a net increase in synaptic density in animals directly stimulated or exposed to enriched environments (Klintsova & Greenough, 1999), together with results in humans showing that brain metabolism and local slow wave activity increases during wakefulness (Braun et al., 1997), other studies have suggested (Huber, Felice Ghilardi, Massimini, & Tononi, 2004; Tononi & Cirelli, 2006) 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. Thus limited resources, saturated at the local network level, may result in performance decrements.

Our results suggest a novel link between perceptual adaptation 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 & 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 decrements, 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; Tononi & Cirelli, 2006) have suggested that during sleep, renormalization downscales the synapses: 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. Downscaling of cortical synapses has been observed in vitro and in vivo (Desai, Cudmore, Nelson, & Turrigiano, 2002; Turrigiano, 1999). Our latest study (Censor et al., 2006) supports this connection between over-exposure and homeostatic processes occurring during sleep by showing that in intermediate practice sessions (26 trials/block) sleep can counteract the effect of over-exposure on learning, yielding significant between-session delayed gains. But moreover, the experiments showed that practicing extremely long sessions (50 trials/block) interferes with learning (Censor et al., 2006). Therefore, the renormalization and modified network-connectivity described above may not be effective following these over-intense sessions, thereby not preventing further saturation as indicated by our current experiment 1, in which practicing long 50 trials/block sessions did not prevent saturation in following 50 trials/block sessions.

Experiment 3 provides a direct link between network-saturation and efficient network connectivity: when additional trials are added to the short 12 trials/block training session, not only does the network saturate causing reduced performance within the session, but also efficient network connectivity seems to be disrupted, not showing reduced saturation in following 50 trials/block sessions. These results show that even when using conditions allowing processes yielding resistance to performance decrements, these processes could be blocked by further training producing adaptation-like processes. Thus, these results rule out the possibility that in 50 trials/block sessions there are no conditions allowing efficient learning and network connectivity simply due to session structure, such as performing a large number of trials at high SOAs.

The results showing similar within-session decremental processes with four sessions of 12 trials/block and a single session of 50 trials/block suggest that these processes, affecting also further resistance to decremental processes, are not SOA-dependent. Thus, these processes do not depend on performing many trials at high SOAs as in the 50 trials/block sessions, since SOAs change dynamically across trials in the consecutive short 12 trials/block sessions.

Experiment 3 further shows that the saturation in the 50 trials/block session did not persist following sleep, allowing low threshold in the following 12 trial/block session. This further supports synapse downscaling and renormalization processes during sleep as described above, and is consistent with previous results (Mednick et al. 2002, 2005), showing that sleep reduces performance deterioration. However, the

low thresholds at these short 12 trials/block sessions do not imply that within-session saturation was reduced compared to the within-session saturation obtained at the 50 trials/block session of the previous day, since in these short sessions there is no saturation in the first place, due to the small number of trials. Furthermore, the improved thresholds between the initial 12 trials/block session of DAY1 and the 12 trials/block session of DAY3, which is consistent with between-session improvements shown previously (Censor et al., 2006), may point to a general learning process rather than reduced saturation, since this learning is unaffected by the intense sessions held in the previous days.

It is important to note that in all of the experiments, subjects started as naïve subjects, with no prior experience in the task. This point may be crucial since our current results show that different training protocols affect future performance. Furthermore, pilot studies to be published elsewhere show that resistance to perceptual decrements is affected if long sessions are performed before the short training sessions.

Previous results (Mednick et al., 2005) have shown that unlike in learning (Karni & Sagi, 1991), perceptual deterioration in texture discrimination transfers to untrained background orientations. These results may support the notion of network saturation due to over-training, with saturation affecting not only neurons tuned for the trained orientations, but also neurons in surrounding orientation-columns of the visual cortex. Furthermore, our results suggest that perceptual decrements due to over-training can be prevented and are affected by consolidation of early network connectivity changes, rather than by general attention-related mechanisms. Perceptual decrements are widely documented in various other aspects, such as contrast adaptation (Blakemore & Campbell, 1969). Although their underlying mechanisms remain largely unknown, they may share some of the processes explained above. 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 as in our current study (Blakemore & Campbell, 1969), pointing to additional or different underlying mechanisms. Other studies (Adorjan, Schwabe, Wenning, & Obermayer, 2002; Barlow, 2001) suggested adaptation to be part of a coding strategy in the visual cortex. These studies used the information theory to hypothesize that neuronal codes are designed to optimize the information a neuronal representation conveys about an input stimulus for any increasing time window beginning with stimulus onset, and apply redundancy reduction to increase future efficiency of the network.

Reduced performance due to intensive training has been shown in other modalities, such as focal hand dystonia in the sensorimotor system. Focal hand dystonia is characterized by co-contraction of muscles and overflow of activity to muscles that are not usually involved in a task (Hallett, 1998). Studies have suggested that dystonia forms such as the musician's cramp and the writer's cramp involve mal-

adaptive plasticity caused by over-training (Rothwell & Huang, 2003) and impairment of homeostatic mechanisms that stabilize excitability levels within a useful dynamic range (Quartarone, Siebner, & Rothwell, 2006). The processes discussed in our current study may have a role in the underlying mechanisms of these sensorimotor performance decrements. Therefore, further studies should test whether effective short training could help reduce these repetition-induced decremental effects, as shown here in the visual system.

What are the exact mechanisms enabling short effective practice to prevent decrements in sensory processing in following intense sessions? Does the modified network function to reduce accumulating noise that usually alters performance? Does it enhance signals which may be reduced due to over-exposure, or does it operate on both? Further behavioral and electrophysiological studies are to be carried out in order to obtain further knowledge regarding the processes enabling these effects of perceptual learning on adaptation-related limited sensory performance, nevertheless, this proposed link may have an essential role in the underlying neuronal mechanisms of perceptual learning.

References

Adorjan, P., Schwabe, L., Wenning, G., & Obermayer, K. (2002). Rapid adaptation to internal states as a coding strategy in visual cortex? *Neuroreport, 13*, 337–342.

Barlow, H. (2001). Redundancy reduction revisited. *Network, 12*, 241–253.

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. *Journal of Physiology, 203*, 237–260.

Braun, A. R., Balkin, T. J., Wesenten, N. J., Carson, R. E., Varga, M., Baldwin, P., et al. (1997). Regional cerebral blood flow throughout the sleep-wake cycle An $H_2(15)O$ PET study. *Brain, 120*, 1173–1197.

Censor, N., Karni, A., & Sagi, D. (2006). A link between perceptual learning, adaptation and sleep. *Vision Research, 46*, 4071–4074.

Dao, D. Y., Lu, Z. L., & Dosher, B. A. (2006). Adaptation to sine-wave gratings selectively reduces the contrast gain of the adapted stimuli. *Journal of 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. *Nature Neuroscience, 5*, 783–789.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica (Amsterdam), 107*, 293–321.

Hallett, M. (1998). Physiology of dystonia. *Advances in Neurology, 78*, 11–18.

Huber, R., Felice Ghilardi, M., Massimini, M., & Tononi, G. (2004). Local sleep and learning. *Nature, 430*, 78–81.

Karni, A., Meyer, G., Jezzard, 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.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America, 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.

Klintsova, A. Y., & Greenough, W. T. (1999). Synaptic plasticity in cortical systems. *Current Opinion in Neurobiology, 9*, 203–208.

Ludwig, I., & Skrandies, W. (2002). Human perceptual learning in the peripheral visual field: Sensory thresholds and neurophysiological correlates. *Biological Psychology, 59*, 187–206.

Mednick, S. C., Arman, A. C., & Boynton, G. M. (2005). The time course and specificity of perceptual deterioration. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 3881–3885.

Mednick, S. C., Nakayama, K., Cantero, J. L., Atienza, M., Levin, A. A., Pathak, N., et al. (2002). The restorative effect of naps on perceptual deterioration. *Nature Neuroscience, 5*, 677–681.

Mednick, S., Nakayma, K., & Stickgold, R. (2003). Sleep-dependent learning: A nap is as good as a night. *Nature Neuroscience, 6*, 697–698.

Ofen, N., Moran, A., & Sagi, D. (2007). Effects of trial repetition in texture discrimination. *Vision Research, 47*, 1094–1102.

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.

Rothwell, J. C., & Huang, Y. Z. (2003). Systems-level studies of movement disorders in dystonia and Parkinson's disease. *Current Opinion in Neurobiology, 13*, 691–695.

Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences of the United States of America, 99*, 17137–17142.

Stickgold, R., James, L., & Hobson, J. A. (2000). Visual discrimination learning requires sleep after training. *Nature Neuroscience, 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. *Journal of Cognitive Neuroscience, 12*, 246–254.

Tononi, G., & Cirelli, C. (2006). Sleep function and synaptic homeostasis. *Sleep Medicine Reviews, 10*, 49–62.

Turrigiano, G. G. (1999). Homeostatic plasticity in neuronal networks: The more things change, the more they stay the same. *Trends Neuroscience, 22*, 221–227.