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Global resistance to local perceptual adaptation in texture discrimination

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ABSTRACT

Intensive training or testing reduces performance on perceptual tasks. These effects are specific to basic image features, implicating early stages of the visual stream rather than general fatigue. Recent results show that such adaptation-like performance decrements are practically eliminated following practice with a small number of trials and sleep. This long-term learning effect suggests a link between perceptual deterioration and learning at the neuronal connectivity level: 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. Resistance to such deterioration is achieved by sleep-dependent consolidation of unsaturated connectivity resulting from short training. Here we show that such training-induced resistance to perceptual decrements generalizes across retinal locations, while suppressive effects due to extensive training were shown to be local. Furthermore, we show that these local suppressive effects are long-term, implying consolidation of these effects into what we term as an "adaptational state" in local visual networks. These experiments, revealing the different transfer properties of performance decrements and increments, allow us to identify local and global components of perceptual learning and their interactions, suggesting mechanisms that induce modifications of higher brain areas which interact with local early visual networks and enable improvement of perceptual abilities.

1. Introduction

Intensive training or over-stimulation reduces performance on perceptual (Hull, 1951) and sensorimotor tasks (Rothwell & Huang, 2003). In texture discrimination, decremental effects were obtained by over-exposure to the task, either in closely spaced sessions (Mednick, Arman, & Boynton, 2005; Mednick et al., 2002) or by increasing the number of trials within a single prolonged session (Censor, Karni, & Sagi, 2006; Censor & Sagi, 2008; Ofen, Moran, & Sagi, 2007). 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 (Mednick et al., 2002, 2005; Ofen et al., 2007). Therefore it was suggested that the deterioration was not 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 (Mednick et al., 2002). Such saturation of information or network connectivity may be caused by strength-ening 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 & Sagi, 2008). Furthermore, it was shown that over-practice causing within-session perceptual deterioration also interferes with normally observed between-session learning (Censor et al., 2006), pointing to a common underlying mechanism of perceptual learning and perceptual deterioration.

Moreover, it has recently been shown that efficient short practice followed by sleep enables long-term resistance to within-session perceptual deterioration, by practically eliminating perceptual decrements within following sessions. This resistance was suggested to be achieved by sleep-dependent consolidation of unsaturated network connectivity (Censor & Sagi, 2008), resulting from short training in which there is higher signal-to-noise ratio. These results therefore suggested a novel reciprocal relationship between perceptual deterioration and learning, pointing to common underlying neuronal mechanisms (Censor & Sagi, 2009).

Our study here was aimed to identify local and global components of perceptual learning involving resistance to performance decrements and their interactions. Studies using the texture discrimination task have shown that learning was specific to retinal location, orientation and in part monocular, suggesting that neuro-

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nal changes in early stages of the visual system underlie the performance gains (Karni & Sagi, 1991). As mentioned earlier, studies showing perceptual deterioration also pointed to involvement of early visual areas, 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). However, most interestingly, the results here show that training-induced resistance to perceptual decrements generalizes to untrained retinal locations. Additional results suggest mechanisms that induce modifications of higher brain areas which interact with local early visual networks and enable improvement of perceptual abilities.

We used the standard texture stimuli (e.g. Censor et al., 2006; Karni & Sagi, 1991; Stickgold, James, & Hobson, 2000) consisting of a target frame followed by patterned masks, as shown in Fig. 1. Observers had to decide whether a peripheral array of three 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 three blocks of trials performed at each SOA. Blocks contained 12 trials (short session) or 50 trials (intense session) each.

In the main experiment (Experiment 1), subjects practiced the texture discrimination task with 12 trials/block and returned for additional intense test-sessions with 50 trials/block at both trained and untrained locations. In Experiment 2, an additional intense 50 trials/block session (more decremental processes producing higher thresholds, previously shown to reduce between-session learning, see Censor et al., 2006) was performed prior to the short 12 trials/block session at the same target locations, to test the effects on the final 50 trials/block test-sessions. In Experiment 3, the intense 50 trials/block session was performed prior to the 12 trials/block session but at different target locations.

2. Methods

2.1. Apparatus

The stimuli were presented on a 19 in. Mitsubishi Diamond Pro 930SB color monitor, using a PC with an Intel Pentium processor. Monitor refresh rate was 100 Hz. The mean luminance of the stimulus (line textures) was 63–65 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 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 three 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 upper-left or lower-right visual quadrant, with its center at 5.3° of visual angle from center of display. When different target-locations were tested, the target appeared either in the lower-left or upper-right visual quadrant. 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. Each session started at an SOA of 340 ms. The SOA was gradually decreased by steps of 20–40 ms. Three blocks of trials were performed at each SOA. Blocks contained 12 trials (~450 trials per session, 20–40 min) or 50 trials (~1600 trials per session, 90–150 min) each, depending on the experimental group. 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. Each psychometric curve obtained was fitted with the Weibull function, with an additional finger error parameter $1 - p$, yielding the function

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

where T is the threshold for each curve, defined as the SOA for which 81.6% of responses were correct when $p = 1$. In each session, the threshold SOA for the two 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, the lowest SOA reached was 50 ms).

2.3. Subjects

The subjects were 17 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.
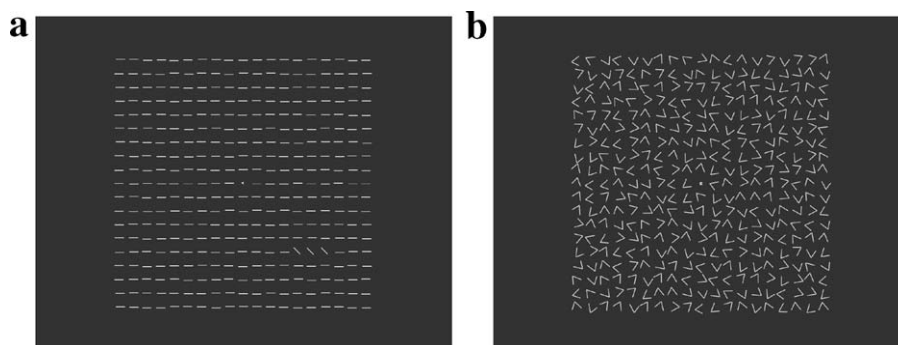

Fig. 1. Trial sequence of the texture discrimination task. Subjects fixate at a circle in the center of the screen and activate the sequence: (a) target consisted of three diagonal bars differing only in orientation from a background of horizontal identical bars, appears at the upper-left or lower-right quadrant of display for 40 ms (when different target-locations were tested, the target appeared either in the lower-left or upper-right visual quadrant). Subjects have to discriminate whether the three 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.

2.4. Experimental procedures

In all of the following experiments, each subject performed each session at a separate day (no more than a single session was performed per day), after a night's sleep of at least 6 h. All sessions were performed at morning-noon times.

Experiment 1: Eight subjects participated in the experiment. On day 1 subjects practiced the texture discrimination task with 12 trials/block, with targets appearing at upper-left or lower-right quadrant of display. Subjects returned on days two and three for intense test-sessions with 50 trials/block at trained (targets appearing at upper-left or lower-right quadrant of display) and un-trained (targets appearing at lower-left or upper-right quadrant of display) locations (as stated above, for each subject, each training day contained only one session).

Experiment 2: Five subjects participated in the experiment. The experimental sequence was similar to that of Experiment 1, with one addition: at least one day prior to the 12 trials/block practice session, subjects also performed an initial intense session of 50 trials/block prior at the same target locations (also, two out of the five subjects performed an additional 50 trials/block session at different locations, with targets appearing at lower-left or upper-right quadrant of display, at least one day prior to the 12 trials/block practice session).

Experiment 3: Four subjects participated in the experiment. The experimental sequence was similar to that of Experiment 1, with one addition: at least one day prior to the 12 trials/block practice session, subjects also performed an initial intense session of 50 trials/block prior at different target locations (compared to the target locations of the 12 trials/block session).

3. Results

Experiment 1 was designed in order to study whether training-induced resistance to perceptual decrements generalizes to un-trained retinal locations. Subjects practicing short sessions of 12 trials/block returned for intense test-sessions with 50 trials/block at both trained and untrained target locations.

Previous results have shown that increasing the number of trials within the session produces higher discrimination thresholds, demonstrating that neuronal processes yielding within-session performance decrements accumulate with increasing number of trials (Censor & Sagi, 2008; Censor et al., 2006). The results of Experiment 1 (Fig. 2) showed that the average threshold for the intense test-sessions with 50 trials/block was not significantly higher than the average threshold for the preceding short 12 trials/block sessions. Individual data are shown in Fig. 3. Pairwise comparisons show that there were no significant differences between the thresholds of the 12 trials/block training sessions and the 50 trials/block test-sessions at the trained locations (mean threshold difference 5.3 ms, S.E. ±6.0 ms, paired *t* test: *p* = 0.20). These results show that performance decrements are eliminated following short practice, and are consistent with previous reports (Censor & Sagi, 2008).

Most importantly, the present results showed that these performance decrements are eliminated also at the untrained retinal locations (Fig. 2). Individual data are shown in Fig. 3. Pairwise comparisons show that there were no significant differences between the thresholds of the 12 trials/block training sessions and the 50 trials/block test-sessions at the untrained locations (mean threshold difference 6.3 ms, S.E. ±6.7 ms, paired *t* test: *p* = 0.19). The only subject (OR) that did deteriorate in the 50 trials/block session at the untrained locations, deteriorated also in the 50 trials/block session at the trained locations thus not showing the resistance effect at all. The robust resistance effect was shown by all other seven
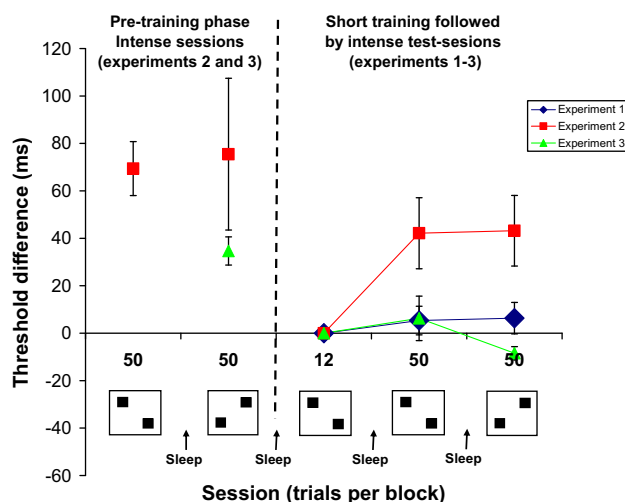

Fig. 2. Experiment 1 (◆): Subjects (*n* = 8) practicing short sessions (12 trials/block) did not deteriorate in the following intense test-sessions (50 trials/block) both at the trained locations (targets at upper-left or lower-right quadrant) and the untrained locations (targets at lower-left or upper-right quadrant). Threshold difference is measured relative to the 12 trials/block session. Experiment 2 (■): Subjects (*n* = 5) performing an intense session prior to the short session deteriorated in the final intense test-sessions at all locations. Experiment 3 (▲): Subjects (*n* = 4) performing the intense session prior to the short session at different target locations, did not deteriorate in the final intense test-sessions at all locations. Error bars represent standard errors.
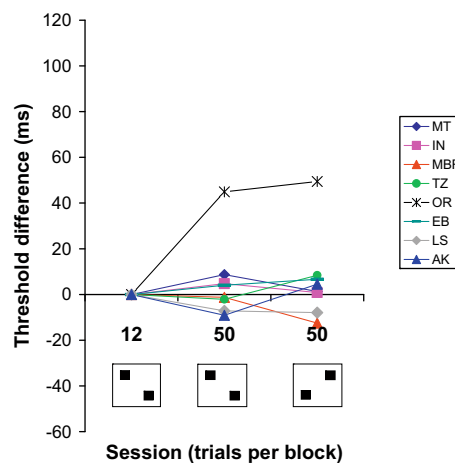

Fig. 3. Experiment 1, individual data (subjects' initials in legend). Following short practice, performance decrements are eliminated, with no significant threshold differences between the 12 trials/block training sessions and the 50 trials/block test-sessions at the trained locations and at the untrained locations. For each subject, threshold difference is measured relative to the 12 trials/block session. Subject OR, the only one showing deterioration in the 50 trials/block test-session at the untrained locations, deteriorated also in the trained locations, thus not showing the effect at all (see text).

subjects in this experiment and all six subjects in our previous report when comparing their initial 12 trials/block practice and 50 trials/block test-sessions (Censor & Sagi, 2008).

In Experiment 2, we asked whether resistance to performance decrements could be obtained by short training, when an initial intense session of 50 trials/block is performed at least one day prior to the 12 trials/block short session, at the same target locations. Therefore, the experimental sequence was similar to that of Experiment 1, with one addition: at least one day prior to the 12 trials/block practice session, subjects also performed an initial intense session of 50 trials/block at the same target locations (also, two

of the subjects performed an additional 50 trials/block session at the untrained locations, at least one day prior to the 12 trials/block practice session).

The results of Experiment 2 (Fig. 2) showed that as opposed to Experiment 1, the average threshold for the intense test-sessions with 50 trials/block was significantly higher than the average threshold for the short 12 trials/block sessions. Individual data are shown in Fig. 4. Pairwise comparisons show that there were significant differences between the thresholds of the 12 trials/block training sessions and the following 50 trials/block test-sessions performed at the same, trained locations (mean threshold difference 42.2 ms, S.E. ±15.0 ms, paired *t* test: *p* = 0.02) and the other locations not trained in the 12 trials/block sessions (mean difference 43.2 ms, S.E. ±14.9 ms, paired *t* test: *p* = 0.02).

These results show that performance decrements are not eliminated following short practice, when an initial intense training session is performed prior to the short training session, at the same target retinal locations. This is the first indication to consolidation of suppressive effects due to intensive training (what we later term as consolidation of an "adaptational state"), resulting in long-term destructive effects.

In Experiment 3 we tested whether the suppressive effects of an initial intense session on the resistance to performance decrements are local or global. Therefore, this time the initial 50 trials/block intense session was performed prior to the short 12 trials/block session at different target retinal locations.

The results of Experiment 3 (Fig. 2) showed that as opposed to Experiment 2, the average threshold for the intense test-sessions with 50 trials/block was not significantly higher than the average threshold for the short 12 trials/block sessions. Individual data are shown in Fig. 5. Pairwise comparisons show that there were no significant differences between the thresholds of the 12 trials/block training sessions and the 50 trials/block test-sessions performed at the same, trained locations (mean threshold difference 6.3 ms, S.E. ±9.4 ms, paired *t* test: *p* = 0.28). Furthermore, in the intense 50 trials/block test-sessions at the other locations (those not trained in the 12 trials/block short sessions) not only was there no deterioration in performance compared to the short 12 trials/block session, but there was even a slight improvement (mean threshold difference −8.4 ms, S.E. 2.8 ms, paired *t* test: *p* = 0.03). The only
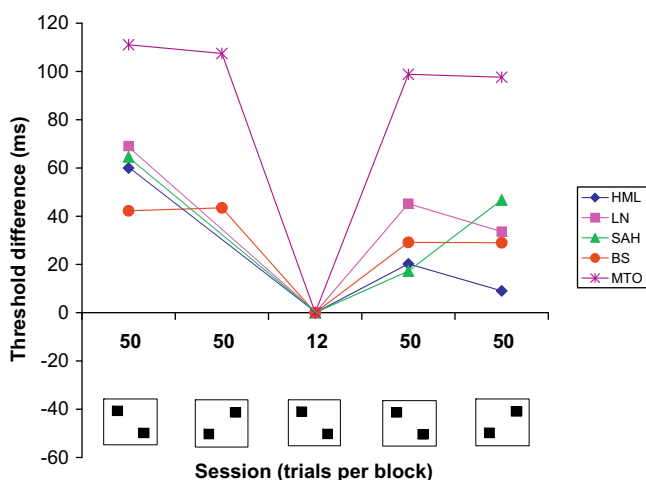
Fig. 5. Experiment 3, individual data (subjects' initials in legend). When an intense session is performed prior to the short training session at different target locations, performance decrements are eliminated, with no significant differences between the thresholds of the 12 trials/block training sessions and the following 50 trials/block test-sessions performed at the same, trained locations (furthermore, in the intense 50 trials/block test-sessions performed at the locations not trained in the 12 trials/block short sessions there was even a slight improvement in thresholds). For each subject, threshold difference is measured relative to the 12 trials/block session. Subject LM that did deteriorate in the 50 trials/block session at the locations trained in the 12 trials/block session, showed no deterioration in the 50 trials/block session at the other locations and did not alter the overall effect.

subject (LM) that did deteriorate in the 50 trials/block session at the locations trained previously with 12 trials/block, showed no deterioration in the 50 trials/block session at the untrained locations and did not alter the overall effect.

These results show that performance decrements are eliminated following short practice, when an initial intense training session is performed prior to the short training session, at different target retinal locations. This implies that the consolidation of the suppressive effects ("adaptational state") suggested by Experiment 2 involves local neural networks processing the task.

4. Discussion

The results of Experiment 1 show that subjects practicing a short session did not show the performance decrements in the following intense session performed with the trained target locations. These results are consistent with our previous results (Censor & Sagi, 2008), showing that short training enables resistance to perceptual deterioration. But moreover, the results of the current experiment showed that performance decrements were eliminated also at the untrained target locations, with low thresholds obtained in the 50 trials/block intense session performed with target locations different from the practiced locations. These results show that the process of resistance to performance decrements is not specific to retinal location, whereas studies using the texture discrimination task have shown that improvements after practice are specific to retinal location and suggested involvement of neuronal changes in early stages of the visual system (Karni & Sagi, 1991; Schwartz, Maquet, & Frith, 2002). Perceptual decrements were also shown to be specific to retinal location and other basic properties of the stimulus (Mednick et al., 2002, 2005; Ofen et al., 2007). Our results 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. Dosher and Lu (1998) suggested that such a template, amplifying stimulus response relative to noise, underlies learning effects in

Fig. 4. Experiment 2, individual data (subjects' initials in legend). When an intense session is performed prior to the short training session at the same target locations, performance decrements are not eliminated, with significant threshold differences between the 12 trials/block training sessions and the following 50 trials/block test-sessions at all locations. For each subject, threshold difference is measured relative to the 12 trials/block session.
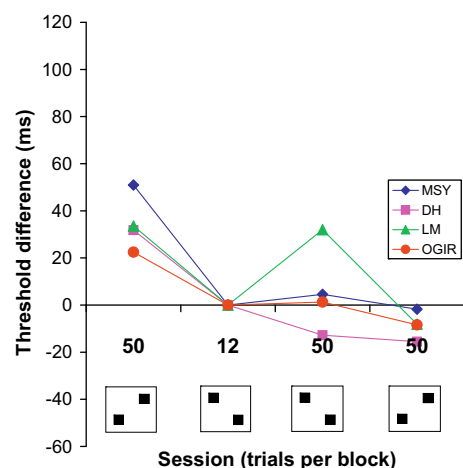
texture (second-order) tasks (Lu & Dosher, 2004). These different transfer properties may therefore suggest for the first time an additional mechanism operating in perceptual learning, involving both local and global components in perceptual learning processes. Thus mechanisms that induce modifications of higher brain areas may interact with local early visual networks and enable improvement of perceptual abilities.

The results of Experiment 2 show that performance decrements were not eliminated when an intense session was performed prior to the short practice session. These results suggest that the intense 50 trials/block session performed before the short practice, resulted in consolidation of what we term as an "adaptational state" preserving the noisy structure of the saturated network, thus not allowing the network to efficiently modulate and prevent further performance decrements. These results extend our previous studies (Censor & Sagi, 2008; Censor et al., 2006), showing that intense practice sessions interfere with further learning, in demonstrating long-term effects of intense training. While the previous results could be explained by absence of learning due to interference within a practice session, the current finding showing no resistance to interference due to short practice performed after extensive practice implies that the "adaptational state" is consolidated and preserved over days. Furthermore, the results of Experiment 3 show that when initial training with an intense 50 trials/block session is performed at target retinal locations different from the following short 12 trials/block training session, it does not interfere with further resistance to performance decrements (both at the locations trained with 12 trials/block sessions and the untrained locations). These results therefore suggest that the consolidation processes involved in interference of an adaptational state with resistance to further performance decrements are local, and that such interference could be impaired by non-noisy inputs to higher brain areas originating from different local neural networks trained with short sessions. Thus these inputs could create an efficient global template able to operate in otherwise noisy conditions.

We have previously suggested that extensive practice results in strengthening of noise synapses along with the synapses contributing to signal, therefore saturating network connectivity and interfering with further learning (Censor & Sagi, 2008). On the other hand, short practice may have a role in consolidating effective network connectivity by synaptic downscaling and renormalization of connectivity patterns during sleep (Huber, Felice Ghilardi, Massimini, & Tononi, 2004; Tononi & Cirelli, 2006), enabling processing of longer sessions with lower signal-to-noise ratio thus preventing performance decrements (Censor & Sagi, 2008). Following our current results we suggest the following account (see also Censor & Sagi, 2009): practicing a visual task activates local neural networks, modifying specific synapses processing the stimulus by increasing their synaptic weights compared to the surrounding synapses (Fig. 6a). However, repeated practice saturates the network, with noise increasing with increasing number of trials due to strengthening of task-irrelevant synapses (i.e., signal-to-noise decreases, see Fig. 6b). Therefore, the over-exposed network cannot efficiently process further information, resulting in perceptual deterioration. The notion that saturation processes involve local networks processing the stimulus is supported by results showing that perceptual decrements are specific to retinal location and other basic properties of the stimulus (Mednick et al., 2002, 2005;
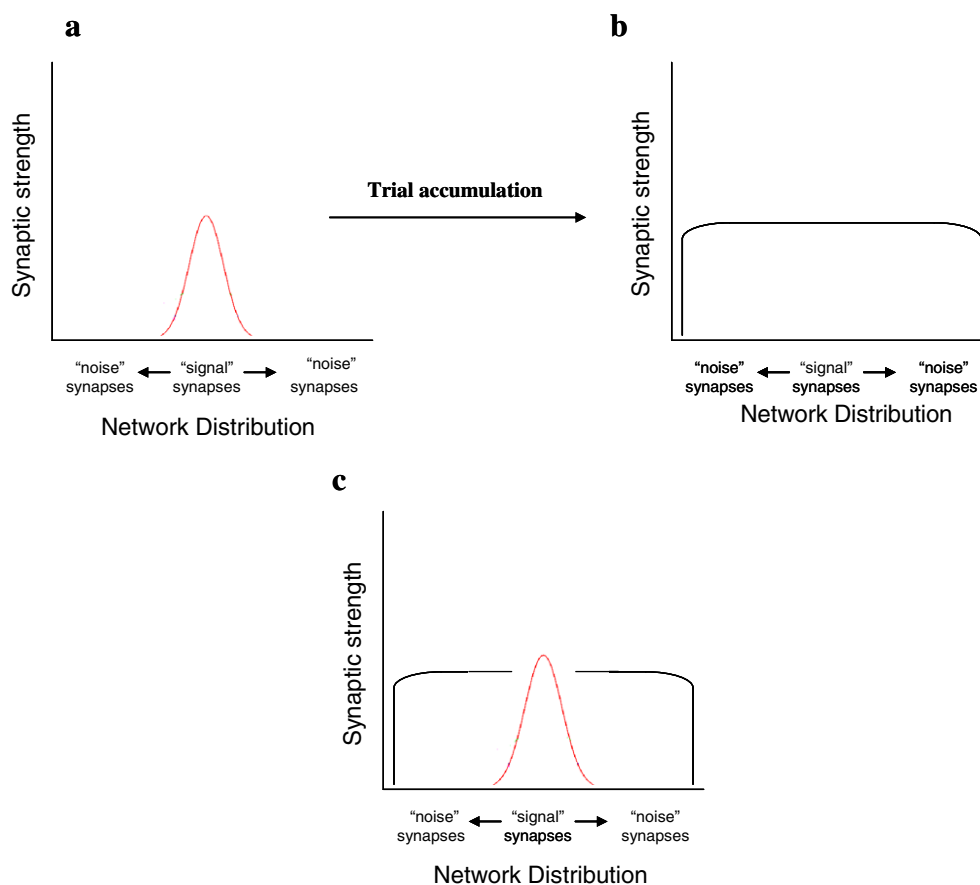
Fig. 6. (a) Short sessions produce a distributed network, composed of synapses contributing to signal and synapses contributing to noise. (b) Largely increasing the amount of trials saturates the network. (c) Consolidation of unsaturated activity creates a template which could be imposed on noisy networks, band-passing the signal and band-stopping the noise, preventing deterioration (Censor & Sagi, 2009).
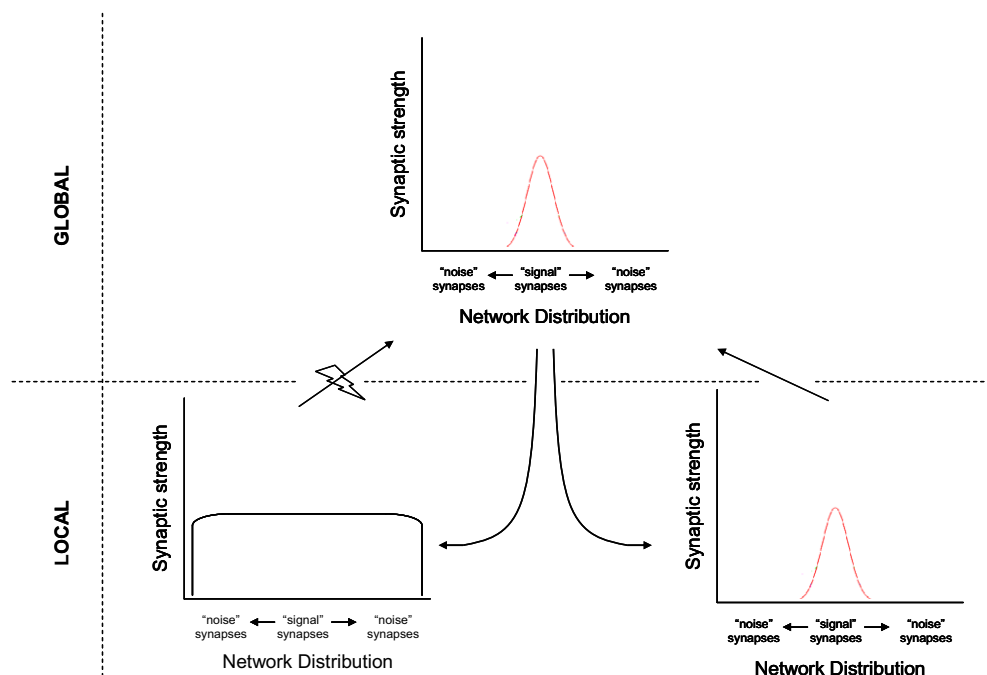
Fig. 7. The global classifier can receive its input from any of the local domains: In case of noisy local networks, there is no unique template structure to be passed on to the global domain. However, inputs originating unsaturated local networks could reproduce an efficient global classifier. Once established the global template can be imposed on local noisy networks and prevent further perceptual decrements.

Ofen et al., 2007). The final-state of the local network consolidates, thereby affecting future performance. 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. The final state of the local network serves as an input to a global classifier. This classifier uses a general template and imposes it on noisy networks, band-passing the signal and band-stopping the noise (Fig. 6c). On the other hand (Fig. 6b), increasing the number of trials preserves the noisy structure of the local network (e.g. by consolidation of noise-synapses), affecting future sessions: if noise re-increases in these future sessions, it will follow the structure of the noisy network, and performance will drop again (Censor & Sagi, 2008; Censor et al., 2006).

As suggested in Fig. 7, the global classifier related to higher brain areas, can receive its input from any of the local domains. In case of noisy local networks, there is no unique template structure to be passed on to the global domain. Furthermore, consolidation processes involving such noisy local networks may affect the ability of these networks to create efficient classifiers following short training sessions, thus perceptual decrements are not prevented as shown in Experiment 2. However, since the global classifier can receive its input from any of the local domains, inputs originating unsaturated local networks could reproduce an efficient global classifier. Once established, the global template can be imposed on local noisy networks and prevent further perceptual decrements as shown in Experiment 3.

The generalization of the learning effects following short training are in agreement with models such as the standard model for system consolidation (Dudai, 2004). According to this model, memory traces in different brain areas such as the hippocampus could represent a compressed version of the internal representation, which becomes active either in explicit recall, or in implicit processes such as sleep (Ji & Wilson, 2007), resulting in adjustment of neocortical connections, possibly involving synaptic consolidation. Thus systems as the hippocampal sys-

tem 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). Following short training, similar processes occurring during sleep could enhance top-down guidance ("global template") enabling improved performance in future saturated conditions. Previous studies showing sleep-dependent explicit motor learning have suggested that explicitness is needed for generalization of communication between different brain areas (Robertson, Pascual-Leone, & Press, 2004).

Our results suggest that processes involving modifications of higher brain areas could interact with local early sensory networks to overcome perceptual limitations and improve perceptual abilities. Such processes may have important applications in treating malfunctions in the sensorimotor system involving maladaptive plasticity caused by overtraining, such as focal hand dystonia (Hallett, 1998; Rothwell & Huang, 2003). Overall, such interactions as those suggested here between higher brain areas and local sensory networks may have an important role in the underlying neuronal mechanisms of perceptual learning.

Acknowledgements

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