The time course and specificity of perceptual deterioration

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Repeated within-day testing on a texture discrimination task leads to retinotopically specific decreases in performance. Although perceptual learning has been shown to be highly specific to the retinotopic location and characteristics of the trained stimulus, the specificity of perceptual deterioration has not been studied. We investigated the similarities between learning and deterioration by examining whether deterioration transfers to new distractor or target orientations or to the untrained eye. Participants performed a texture discrimination task in three one-hour sessions. We tested the specificity of deterioration in the final session by switching either the orientation of the background or the target elements by 90°. We found that performance deteriorated steadily both within and across the first two sessions and was specific to the target but not the distractor orientation. In a separate experiment, we found that deterioration transferred to the untrained eye. Changes in performance were independent of reported sleepiness and awareness of stimulus changes, arguing against the possibility that perceptual deterioration is due to general fatigue. Rather, we hypothesize that perceptual deterioration may be caused by changes in the ability for attention to selectively enhance the responses of relatively low-level orientation-selective sensory neurons, possibly within the primary visual cortex. Further, the differences in specificity profiles between learning and deterioration suggest separate underlying mechanisms that occur within the same cortical area.

primary visual cortex | learning | vision | psychophysics | attention

It is said that practice makes perfect, but what happens with too much practice? Everyday experience suggests that intense training in a short period leads to a deterioration in performance, much like how muscles fatigue from lifting weights. In typical perception research, such overtraining is usually avoided rather than studied. This study, however, deliberately investigated how performance deteriorates throughout the day with repeated testing on a perceptual task.

Deterioration of performance with practice has been noted in prior studies. In the 1940s, Hull (1) reported increased reaction time with prolonged testing on simple repetitive tasks, such as letter cancellation, detecting differences in simple shapes, or adding three digits. This so-called "reactive inhibition" was defined as a tendency toward increased response times as a function of the number of repetitions and the intertrial interval. Hull proposed a multimodal fatigue factor that was driven by a natural and constantly increasing inclination to switch from the present task to another. Where reactive inhibition was a general principle, the present study examines deterioration as a specific mechanism of the visual system.

Although perceptual deterioration has received little scientific attention, there is a growing body of research on a related dynamical property of the visual system: perceptual learning. The perceptual learning literature provides a natural framework for studying perceptual deterioration because both learning and deterioration involve the effects of repeated testing on a task across sessions. Studies of perceptual learning show that for most tasks, learning does not transfer across stimulus properties such as retinotopic position (2), orientation (2, 3), spatial frequency (4), motion direction and speed (5, 6) and, in some cases, even eye of origin (7) (for an excellent review, see ref. 8). This stimulus specificity suggests that perceptual learning may be mediated by neuronal plasticity in early, retinotopically organized visual areas. Stimulus specificities in perceptual learning, however, might also be influenced by neurons at higher stages of visual processing that become selective for properties such as orientation and spatial position as a consequence of training (9).

Mednick and colleagues (10, 11) found perceptual deterioration by using the same texture discrimination task developed to study learning (7). They reported that performance deteriorated significantly with each hour-long training session throughout the day. Importantly, this deterioration effect was retinotopically specific; when the target stimulus was shifted to the opposite visual hemifield for the final test session, performance returned to that of the first session. Such spatial specificity shows that perceptual deterioration is not simply due to general fatigue or boredom and further suggests that the effect can be attributed to plasticity of neurons in early visual cortex.

Given the initial similarities between learning and deterioration, we sought to determine whether, like learning, deterioration shows further specificity to the properties of the trained stimulus. In this study, we report that perceptual deterioration is binocular and specific to the target orientation, but not the background orientation. This pattern of effects is different from that of learning and suggests that deterioration does not necessarily share common neural mechanisms with learning.

Furthermore, prior studies using this task have only presented changes in thresholds across hour-long sessions rather than examining the buildup of deterioration within a session. This study investigates the development of deterioration both within and across sessions. We found that after a brief learning period within the first session, performance steadily decreases with continued exposure. This result shows that deterioration builds with the amount of exposure to the task across the day and not with the amount of time between training sessions (10).

Methods

All experiments used the general procedure outlined in this section. Deviations from this procedure are described in each section.

Participants and Procedures. A total of 30 participants gave informed consent to participate in the study, which was approved by the internal review boards of both the University of California at San Diego and The Salk Institute for Biological Studies. All participants, ages 18–30 years, had normal or corrected-to-normal vision and no history of neurological, mental, or physical illness. Participants were restricted from caffeine the day of the study, restricted from alcohol the evening before test day, and were asked to get at least seven hours of sleep the night before

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Abbreviation: ISI, interstimulus interval.

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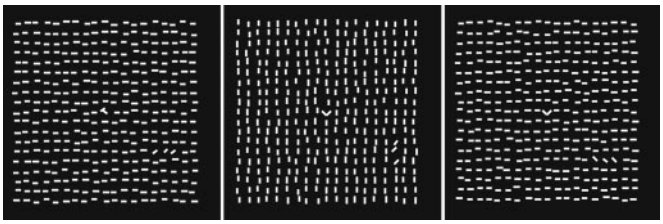

Fig. 1. Example stimuli. Shown are the horizontal background with right-leaning horizontal array (*Left*), vertical background with right-leaning vertical array (*Center*), and horizontal background with left-leaning horizontal array (*Right*). A background and target element orientation combination was randomly assigned to each subject for the first and second testing session. This combination became the control combination for the third testing session, which tested for changes in background and target orientation.

the study. Each participant was tested on the texture discrimination task three times in one day: at 10 a.m., 2 p.m., and 6 p.m. Each session lasted 60–75 min. Participants were tested in a dimly lit, quiet room. The participants' heads were stabilized by using a chin rest, and they maintained a distance of 57.5 cm from the computer screen. The stimuli were programmed in MATLAB by using PSYCHTOOLBOX (12) and presented by using a Macintosh (Apple) Powerbook G3 laptop and a Sony computer monitor.

Texture Discrimination Task. Participants performed a texture discrimination task similar to that developed by Karni and Sagi (7). Participants were asked to discriminate two targets per trial: a central letter ("T" or "L") and a peripheral line array (vertical or horizontal orientation) in one of the lower quadrants at 2.5–5.9° eccentricity from the center of the screen. The peripheral array consisted of three diagonal bars that were either positioned in a horizontal array or a vertical array against a background of uniformly oriented bars (vertical or horizontal), which created a texture difference between the target and background (see Fig. 1).

An experimental trial consisted of the following sequence: central fixation cross, target screen for 32 ms, blank screen for a duration between 50 and 600 ms [the interstimulus interval (ISI)], and mask for 16 ms followed by the response time interval before the next trial. Subjects reported both the letter at central fixation (T or L) and the orientation of the peripheral, three-element array (horizontal or vertical) by making two key presses. A full day's experiment is illustrated in Fig. 2.

Each block consisted of 50 trials, each with the same ISI and lasting ≈2 min. A threshold was determined from the performance across eight blocks, with a progressively shorter ISI, starting with 600 msec and ending with 50 msec. The specific sequence of ISIs across an entire session was (600, 500, 400, 300, 250, 200, 150, 100, 500, 400, 300, 250, 200, 150, 100, 50, 500, 400, 300, 250, 200, 150, 100, 50). A psychometric function of percent correct for each block was fit with a Weibull function to determine the ISI at which performance was 80% accurate. A threshold was obtained in ≈20 min.

Participants controlled block onset and were instructed to take as many breaks as they needed between blocks. Once participants pressed the space bar, a block would begin and trial onset was controlled by the program. Initial training, which occurred at the beginning of the initial test session, consisted of 15 trials of an easy version of the task (ISI of 1,000–1,500 msec), and 50 trials of the easiest block of the actual task (ISI of 600 msec). This training ensured that participants understood the task and were discriminating the peripheral target between 90% and 100% correct on the easiest version of the task.

Before each testing session, participants rated their sleepiness

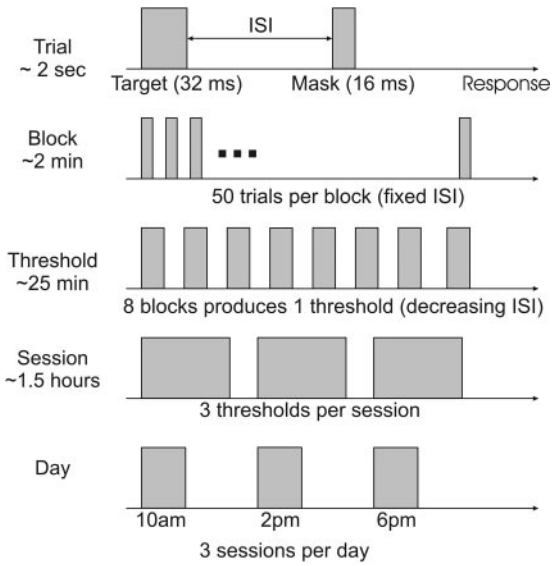

Fig. 2. Experimental design. Each trial consisted of a brief target followed by a mask after an ISI. Blocks consisted of 50 trials with the same ISI. A threshold was obtained over eight blocks, with decreasing ISIs across blocks. A session consisted of three threshold measurements, and a day of testing contained three sessions, starting at 10 a.m., 2 p.m., and 6 p.m.

on the seven-point Stanford sleepiness scale. At the completion of the study, performance ratings and awareness of stimulus changes were assessed.

Experiment 1. The first experiment examined the time course and the feature specificity of deterioration in a within-subjects design. The time course of deterioration within and across sessions was investigated by plotting the six thresholds obtained across the first two sessions (10 a.m.: 1a, 1b, 1c; and 2 p.m.: 2a, 2b, 2c). Feature specificity was examined in the third session by testing all participants in three conditions: (*i*) a change in the target orientation by 90°, (*ii*) a change in the background orientation by 90°, or (*iii*) nothing was changed (control) from the previous two sessions. Deterioration was determined to be specific to a particular stimulus feature if changes to the stimulus in the third session significantly improved performance compared with the control.

We controlled for possible confounds caused by differences in visual processing of vertical versus horizontal lines and rightward versus leftward diagonals in the target and background stimuli by counterbalancing the presentation of the background and target orientations. The counterbalance procedure used was as follows: for sessions one and two, participants were randomized to one of four background/target orientation conditions: horizontal/right-leaning, horizontal/left-leaning, vertical/right-leaning, and vertical/left-leaning (see Fig. 1 for example stimuli). In the third session, we tested for transfer of deterioration from a trained to an untrained target or background orientation. Thresholds were measured for three conditions: a control condition (no change of stimulus conditions from sessions one and two), a background orientation change condition (only the background orientation switched), and a target orientation change condition (only the target orientation switched). The order in which the three conditions (i.e., control, background, or target change) was presented in session three were counterbalanced across participants.

Experiment 2. Eye specificity was examined in a separate study with six naïve participants. For sessions one and two, participants

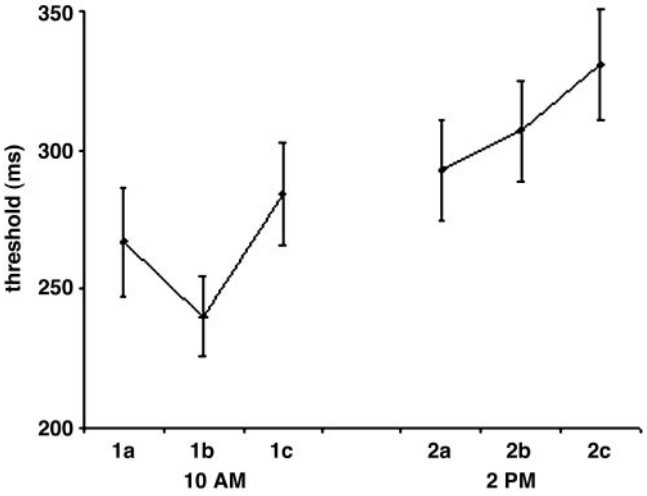

Fig. 3. The time course of perceptual deterioration is spread across six thresholds in two sessions at 10 a.m. and 2 p.m.

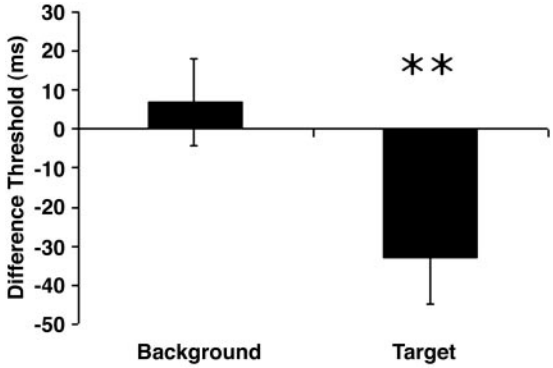

Fig. 4. Test of specificity of deterioration for stimulus features. Differences scores for background orientation change (left bar) and target orientation change (right bar) show significant improvement (specificity) with target orientation change but not background orientation change. **, $P < 0.01$.

were tested on the texture discrimination task with one eye patched. In session three, transfer of deterioration was examined by switching the patch to the opposite eye. If a performance decrement transferred to the untrained eye, it is assumed that deterioration occurred at a level in cortical processing at least as early as binocular cells in primary visual cortex. The trained eye was counterbalanced across participants.

Results

Experiment 1: Time Course of Deterioration. Three thresholds for the peripheral target discrimination task were obtained in each testing session. An overall session threshold was obtained by averaging the three thresholds within each session. The general effect of repeated testing, examined with a paired *t* test on the session averages, demonstrated a significant decrease in performance from the first (270 ms) to the second (313 ms) session ($P = 0.008$). Next, we examined the difference between individual thresholds within and across the first and second sessions. A repeated measures multivariate ANOVA showed a significant difference between the six thresholds ($P = 0.002$). Fig. 3 shows the mean thresholds (plus standard error) across sessions one and two. With the exception of the second threshold from the first session (threshold 1b), performance appears to steadily decrease in a linear fashion. We analyzed the slope of the deterioration by using a planned linear contrast analysis with predicted contrast weights −0.5, −0.33, −0.67, 0.67, 0.33, 0.5, which was significant ($P < 0.001$). A post hoc analysis of the differences between the individual tests within each session was performed by using Tukey's honestly significant different test. Significant differences were not found after adjusting for multiple comparisons.

The performance deterioration was not matched in subjective sleepiness rated on the Stanford sleepiness scale, which showed no significant change in sleepiness across the three sessions in a repeated measures ANOVA ($P = 0.5$).

Threshold 1b, however, does not follow the overall pattern of increasing deterioration. We suspect that this nonsignificant improvement in performance from 1a to 1b represents task learning across the first eight blocks (paired *t* test, $P = 0.11$).

Experiment 1: Specificity of Stimulus Characteristics. The feature specificity of deterioration was examined by testing transfer of deterioration to new target and background orientations in the third test session. We first tested whether the order of presentation of the three conditions affected individual thresholds and found no order effect. Thresholds for each condition were equivalent when tested in the first, second, or third eight-block interval (ANOVA, $P = 0.9$, $P = 0.9$, $P = 0.78$; background, target, and control, respectively). Thresholds for the third session were thus collapsed across subjects for each condition to examine the effect of background and target orientation.

For the sake of comparing the effect of switching the two stimulus characteristics, difference scores for the background and target condition were calculated by subtracting thresholds from the first two conditions (background and target orientation switch) from the control threshold. A significant difference was found between switching background versus target orientation in the third session (paired *t* test, $P = 0.01$; mean and standard error shown in Fig. 4). Absolute thresholds for each condition (slight variation in means between absolute thresholds and difference score due to missing control data from one subject for which a different score could not be calculated): control, 293 ± 17 ms; background, 295 ± 19 ms; target, 257 ± 15 ms. Changing the background orientation did not significantly affect performance (paired *t* test of absolute thresholds of control versus background, $P = 0.29$), whereas performance significantly improved when the target was changed by 90° (paired *t* test of absolute thresholds of control versus target, $P = 0.008$). Further, target switch thresholds were not significantly different from performance at the first testing session (paired *t* test between target switch condition and the session one mean (270 ± 16 ms, $P = 0.70$). Thus, deterioration generalized to new background orientations but not to new target orientations.

Participants completed an exit questionnaire that included asking whether the participant noticed any changes to the stimuli in the third test session. All participants were aware that there was a change in the background, and the majority correctly described the change. No participants noted the orientation change of the target itself, and only one participant reflected that the stimulus "seemed bigger or brighter." Thus, the significant recovery from deterioration with the target switch did not engage awareness, whereas the majority of participants noted the background change.

Experiment 2: Specificity of Eye of Origin. Transfer of deterioration between the trained and untrained eye was examined by testing participants with a patch over one eye for the first two test sessions and then switching the patch to the opposite eye for the third test session. Consistent with experiment 1, deterioration was found between session one and two in the trained

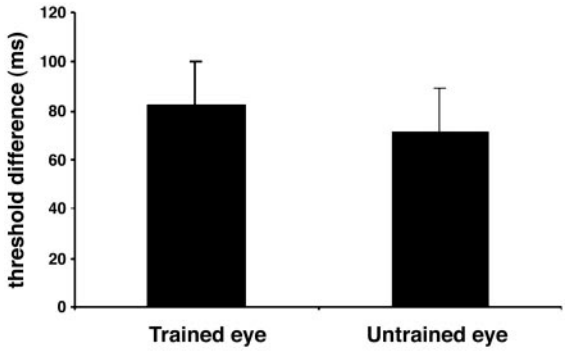

Fig. 5. Transfer of deterioration in trained eye (T2 − T1) and the untrained eye (T3 − T1).

eye (236 vs. 319 ms, session one and two, respectively; paired *t* test, $P = 0.009$). Difference scores were calculated to measure threshold (T) changes in the same eye across sessions (Session 2(T2) − Session 1(T1)) and in different eyes across sessions (Session 3(T3) − Session 1(T1)). If deterioration were binocular, performance decreases in the trained eye would transfer to the untrained eye. No significant differences were found between thresholds obtained with the trained versus the untrained eye (paired *t* test, $P = 0.39$) (mean and standard error shown in Fig. 5). Thus, deterioration appears to occur at least at the level of binocular neurons of early visual cortex.

Conclusions

Herein, we have described the time course and specificity of perceptual deterioration that develops with repeated, within-day testing on a texture discrimination task. Deterioration occurred within the first testing session and continued to increase in a linear fashion with continued training. Thresholds remained dynamic throughout the entire testing period. An initial improvement, perhaps due to procedural (13) or perceptual (14) learning, was followed by a steady increase in subsequent thresholds. At no time during testing did performance remain stable. Thus, the concept of an average threshold becomes difficult to define for these data.

Previous studies using the texture discrimination task have shown performance improvement when participants were allowed a period of sleep between training and retesting (7, 11, 15). This sleep-dependent learning was specific to the eye of origin (7) (not replicated in ref. 16), the orientation of the background (but not the target) elements (7), and the retinotopic location of the target (7, 10), indicating slow, sleep-dependent plasticity of early visual cortex.

This study uses the same task as above but shows very different results. We report that unlike learning, deterioration is not specific to the eye of origin or the orientation of the background elements, but it is specific to the orientation of the target elements. These results indicate that deterioration is likely driven by rapid plasticity of early visual cortical areas. Thus, the processes pertaining to learning and deterioration appear to share the same brain areas but are mediated by different types of neuronal plasticity. This temporal difference in development (rapid for deterioration versus slow for learning), along with the difference in specificity (target versus background, binocular versus monocular), suggests two separate mechanisms underlying perceptual learning and deterioration, each sensitive to different visual information.

It has been suggested that the dependence of learning on the background orientation involves plasticity in contextual interactions between background and target (refs. 7 and 17; for a contrary view, see ref. 18). In contrast, deterioration appears to develop solely for the attended target. Deterioration recovers when the target is moved to a new spatial location, even though oriented elements had been placed at this ignored location throughout previous training sessions (10). Thus, deterioration only seems to occur in mechanisms representing attended stimuli.

We noted a dissociation between subjective report and perceptual performance in the test of specificity. In agreement with behavioral data, most participants experienced the second session as harder than the first. In the third session, however, all participants were aware of the change in orientation of the background, but performance in this condition was no different from the control condition. On the other hand, not a single participant accurately noted the change in the target, even though the target change led to a complete restoration of performance to baseline levels. Three aspects of these data underscore the perceptual nature of these deterioration results and argue against a generalized fatigue principle proposed by Hull (1). First, an undetected change of the target components restored performance to baseline levels. Second, a detected, full visual field change of the background did not affect performance. Last, subjective sleepiness ratings did not increase significantly across the day.

The extent to which these unstable thresholds may have depended on the participant pool (mostly comprised of university undergraduates inexperienced with psychophysical testing and this particular task) is unknown. Studies of the dynamics of skill acquisition have reported differences on a variety of performance measures between naïve and expert subjects (19, 20). Future studies comparing experienced and naïve subjects on a similar deterioration-producing task can test the hypothesis that expertise may serve as a protection against rapid perceptual deterioration.

These results have implications for interpreting performance decreases reported by more applied areas of study. Investigations of the ''useful visual field'' (21), or the region of the visual field from that we can extract information during eye fixation, report degradation (i.e., driving simulator task shows response time slowing and decreased accuracy) under a variety of circumstances and individual characteristics (22, 23). Compared with the complex behavioral patterns required for driving, this study of performance deterioration at the perceptual level can be useful in describing what specific components of the driving task may be susceptible to deterioration. In this light, perceptual deterioration may have applications beyond being just a nuisance for psychophysicists planning an experimental design.

An analogous body of research to perceptual deterioration of the visual system can be found in sensory motor research showing practice-dependent performance decreases that are linked with cortical plasticity. It has been shown that even a small amount of tactile finger stimulation can produce rapid alteration of the orderly topographic digit representation of primary somatosensory cortex (24). Moreover, repetitive stereotyped hand movements have been shown to produce mild to severe motor deficits leading to acquired focal hand dystonia, associated with writer's cramp, typist's cramp, and musician's cramp (25). FMRI studies have shown that focal hand dystonia has been correlated with altered somatotopic finger representations in humans (26). Further, physiological studies in monkeys have shown massive receptive field expansion, spreading of receptive fields from single digits to multiple digits, and dedifferentiation of the normally sharply segregated areas of the hand representation in area 3b (27, 28). It has also been noted that people with focal hand dystonia show impaired spatial and temporal tactile discrimination (29, 30). Thus, a repeated motor task can lead to performance decreases matched with distortions of neural representations.

Interestingly, intensive physical therapy of the affected hand can cause resegregation of somatotopic finger representations to normal borders and improve functioning of the affected hand (31), indicating a wide range of experience-dependent plasticity in the adult human cortex from learning to deterioration. These studies show that the experience-dependent neural plasticity underlying both learning and deterioration may be adaptive in terms of learning and maladaptive in terms of deterioration. An interesting speculation is that such neural plasticity may be occurring in visual cortex throughout the day.

Attention could lead to enhanced deterioration simply because attention enhances the response to the stimulus and, like adaptation, greater responses may cause more deterioration. Neuroimaging and physiological studies of attention both show that attention affects the magnitude of response as early as primary visual cortex (V1) (32–34). These attentional effects, however, are relatively small. Early visual areas still respond well to unattended (35), and even unseen,[†] stimuli, whereas the unattended stimuli (background elements) in the present study had no effect on perceptual deterioration. Thus, it appears that attentional gain alone cannot explain the relationship between attention and deterioration.

Prolonged performance on a task may lead to deterioration in the ability to allocate attention to a stimulus attribute. Such a mechanism has been proposed for perceptual learning, wherein observers "learn to pay attention to the set of neurons that is most sensitive to the task" (36). Further, a recent neurophysiological study in the macaque shows that attention to a specific aspect of a stimulus selectively enhances the responses of V1 neurons in a very task-specific manner (37). Perhaps it is this task-specific mechanism of attention that is deteriorating over time.

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