Perception, 2008, volume 37, pages 1086 – 1097

doi:10.1068/p5998

Perceptual deterioration is reflected in the neural response: fMRI study of nappers and non-nappers

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Received 22 February 2007, in revised form 21 February 2008; published online 20 June 2008

Abstract. Repeated training on a perceptual task can result in performance deterioration. In the case of vision, this practice-dependent decrease, or perceptual deterioration is restored by changing the target orientation, spatial location, or by taking a daytime nap. Behavioral studies suggest the locus of these performance changes to be primary visual cortex. We used fMRI to directly probe whether perceptual deterioration and nap-dependent maintenance of performance can be detected at the level of primary visual cortex. We also asked whether these changes are due to a bottom – up, stimulus-driven response or a top – down plasticity of attentional mechanisms. Subjects were scanned while performing a texture-discrimination task. Half the subjects took a nap between sessions. We measured the relationship between changes in performance and changes in BOLD signal modulation between the two groups. Non-nappers showed performance deterioration that was significantly correlated with decreased BOLD signal modulation, exclusively in area V1 and limited to the bottom – up condition. In contrast, no change was detected in performance and BOLD response in the two conditions for nappers. These results indicate that napping prevented performance deterioration, which was reflected in the fMRI response of neurons in V1. Without a nap, perceptual deterioration was related to decreases in the stimulus-driven, bottom – up representation, rather than decreases in attentional modulation to the stimulus.

1 Introduction

Experience-dependent plasticity of cortical neurons has been shown in electrophysiological recordings in animals and with fMRI in humans. Plasticity is associated with adaptive changes to the organization of the brain due to experience with new information that leads to learning (Kandel et al 2000). These adaptive changes have been found in populations of cells (Zohary et al 1994), individual neuronal tuning functions (Schoups et al 2001; Yang and Maunsell 2004; Raiguel et al 2006), and even at the once-thought immutable level of the receptive field (Meliza and Dan 2006). Some of these changes have been associated with sleep-dependent behavioral improvements on perceptual tasks (Karni et al 1994; Walker et al 2003). Neural changes associated with sleep-dependent perceptual learning correspond to the functional nature of the particular neurons tested [eg improved orientation discrimination after a night of sleep associated with increased BOLD signal in primary visual cortex (Schwartz et al 2002; Furmanski et al 2004)].

More recently, the contrary phenomenon of performance deterioration has been investigated. Deterioration occurs, for example, on a visual texture-discrimination task following repeated within-day training (Gais et al 2000; Mednick et al 2002, 2003, 2005; Censor et al 2006). By testing whether deterioration in performance transfers to untested primitive stimulus features, these studies have made inferences regarding the exact neural group responsible for these performance changes. Perceptual deterioration does not transfer to new target locations (Mednick et al 2002) or new target orientations (Mednick et al 2005). However, deterioration is unaffected by changes to distractor orientations, or switching to the untrained eye. Interestingly, subjects are not aware of the target orientation change despite the recovery in performance. In contrast, the obvious

change to the distractor orientation is universally noted, but does not lead to recovered performance (Mednick et al 2005). These findings show that perceptual deterioration is not due to global fatigue and may not be related to conscious attention. Rather, these studies suggest the changes may be due to the fatigue of neurons early in the visual processing stream.

One intervention outside of the task parameters that can reverse perceptual deterioration is a midday nap. Previous studies have shown that napping between test sessions prevents perceptual deterioration (Mednick et al 2002). Sleep appeared necessary for reversal of the deterioration to occur, as substituting the nap with 60 min of eyes closed, or increasing subjects' motivation with monetary reward did not alter the course of the deterioration. The lack of effect of motivation supports the hypothesis that overt attentional mechanisms do not control deterioration or lack thereof.

Collectively, these results are consistent with the hypothesis that perceptual deterioration is a phenomenon occurring at the level of primary visual neurons and is not modulated with conscious attention. Indeed, previous research on perceptual learning has demonstrated that sleep-dependent improvement on this task is likely to occur at the level of primary visual cortex (Karni and Sagi 1991; Walker et al 2005). Behavioral studies of the transfer of learning or deterioration, however, may not necessarily implicate a specific underlying neuronal population. In his review, Ghose (2004) delineates the limitations of such studies with the following points: (i) orientation selectivity can be found from V1 up through inferotemporal cortex; (ii) replication of some specificity findings such as monocularity have been unsuccessful; and (iii) perceptual learning models propose that the source of improvement may just as likely be due to changes in selectivity at higher rather than lower visual areas. Similarly, one potential explanation for performance deterioration is that repeated testing reduces top–down attentional mechanisms that help modulate representation or processing of the stimulus by the primary sensory system.

In order to disentangle these competing hypotheses, the source of deterioration needs to be examined at multiple levels of the visual system with careful control of attentional modulation. Functional neuroimaging is a good method for examining the influence of top–down attention versus bottom–up stimulus-driven processing (Gandhi et al 1999).

Using fMRI, we studied subjects before and after extensive exposure to a texture-discrimination task. Half the subjects were given a daytime nap between the second and third test session. The study had two main aims. (i) To examine which areas of visual cortex (V1, V2, V3, V4v, and V3A) correlated with performance decreases due to repeated testing compared to performance maintenance after a nap. We hypothesized that these performance differences would be associated with changes to the BOLD signal in orientation-selective, retinotopically specific areas early in visual processing (ie V1). (ii) To test whether perceptual deterioration was associated with decreased bottom–up stimulus-driven response, or decreased ability of top–down attentional mechanisms to modulate that response. We hypothesized that perceptual deterioration would be associated with fatigue of bottom–up mechanisms.

2 Materials and methods

2.1 *Experimental protocol*

Each subject was tested on a version of the texture-discrimination task four times in one day: twice in the laboratory (9AM and 3:30PM) and twice inside the scanner (10:30AM and 5PM) (figure 1 for study timetable). Each session normally lasted 60–75 min.

We used essentially the same fMRI task design as in the study of spatial attention by Gandhi et al (1999). In the first condition, we measured the contrast between the fMRI response to the texture stimulus plus the attention to the task stimuli compared

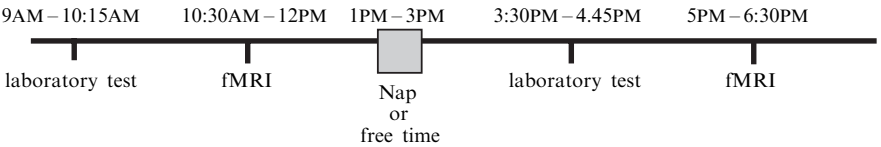

Figure 1. Timeline for experimental day.

to no stimulus (labeled 'stimulus + attention'). The task was the same as that used for training, including the full-field mask, and fixation-letter-discrimination task, with the exception that the texture stimulus on the hemifield opposite to the target hemifield was removed (see figures 2c and 2d). An arrow appeared before each trial to indicate the hemifield to which subjects were to attend. Since the mask was presented in both hemifields throughout the scan, we expected the fMRI activation in each brain hemisphere to be modulated both by attention and the presence of the texture stimulus versus the absence of both attention and stimulus.

In the second condition, we measured the effect of attention alone (labeled 'attention only'). A block design was used in which the texture stimulus, including the peripheral target array, appeared in both hemifields simultaneously, while an arrow directed the subject to alternate attention to one hemifield at a time (see figures 2a and 2b). Thus fMRI modulation in a given hemisphere was due only to the attentional modulation to the hemifield, since the physical properties of the stimulus remained constant throughout the scan.

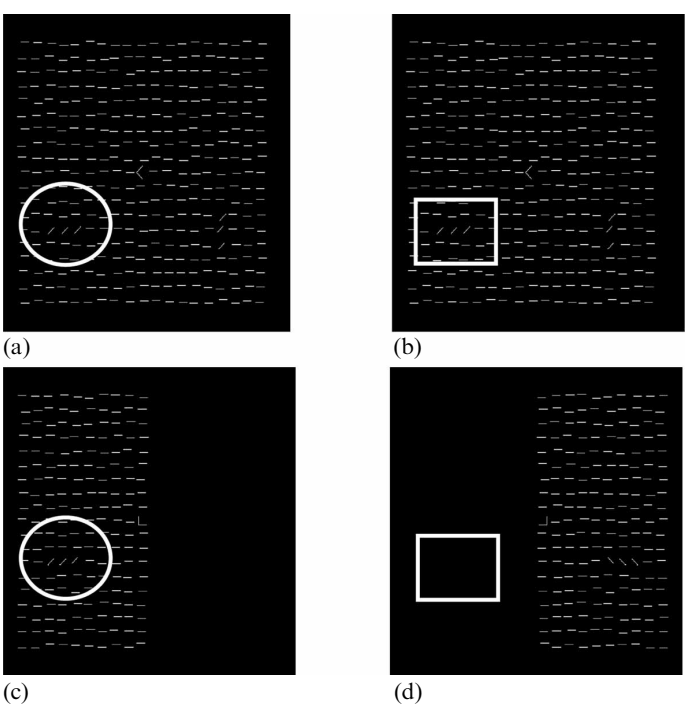

Figure 2. fMRI conditions: Scans were structured in a blocked design in which half of the trials directed the subject to perform the task with the target on the trained side and half on the untrained side. In the attention-only condition [(a) and (b)] measurements were made of top–down modulation to a region of interest where there was an attended stimulus (indicated by circle) versus an unattended region with a stimulus (indicated by square). In the stimulus + attention condition [(c) and (d)] measurements were made of bottom–up modulation to a region of interest where there was an attended stimulus (indicated by circle) versus an unattended region with no stimulus (indicated by square).

In order to test our a priori hypothesis that perceptual deterioration was produced by a stimulus-driven (bottom – up) fatigue of V1 neurons, we devised four difference scores. For each of the two conditions, one difference score was devised to test the change in BOLD signal modulation to the trained target from fMRI session 1 to session 2. The other score was the same subtraction but to the untrained target and served as a retinotopic control condition for the first difference score. These difference scores were calculated for the selected visual areas: V1, V2, V3, V4v, V3A.

2.2 *Subjects and procedures*

A total of thirty-four subjects gave informed consent to participate in the study, which was approved by the institutional review boards of both the University of California San Diego (UCSD) and the Salk Institute for Biological Studies. All subjects, 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, alcohol starting the evening before test day, and were asked to get at least 7 h of sleep the night before the study.

2.2.1 *Nap procedures.* Half of the subjects ($n = 17$) were randomly assigned to a napping group. At 12:30PM, nappers were taken to the UCSD Gillin Laboratory for Sleep and Chonobiology where they were fitted with standard monitors for polysomography and were in bed by 1PM. Sleep stages and nap duration was visually monitored and scored in real time. Subjects got out of bed after 90 min of sleep or 2 h in bed, whichever came first.

2.2.2 *Data elimination.* We tested seventeen nappers and sixteen non-nappers. Functional data from two nappers and two non-nappers contained an uncorrectable artifact (apparently produced by the head coil) confined to the occipital pole. We excluded these subjects in the analysis of the behavioral and fMRI data.

2.3 *Texture discrimination task*

2.3.1 *In-laboratory testing.* Laboratory testing was performed with a simulator that matched the optical conditions used in the fMRI environment. The simulator included the same LCD projector (NEC, Rancho Cordova, CA), back-projection screen, stimulus-generating computer (Macintosh Powerbook G3 laptop), and viewing distances as those in fMRI environment. Laboratory testing took place in a dimly lit room with a chin-rest, at a distance of 57.5 cm from the back-projection screen. The task was programmed in Matlab and PsychToolbox (Pelli 1997).

Participants performed a texture-discrimination task similar to that developed by Karni and Sagi (1991). They 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 $2.5^\circ - 5.9^\circ$ 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 horizontally oriented bars, which created a texture difference between the target and background (see figure 2a).

An experimental trial consisted of the following sequence: central fixation cross, target screen for 32 ms, blank screen for a duration between 0 and 600 ms (the interstimulus-interval, ISI), 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. The central task controlled for eye movements.

Each block consisted of 50 trials, each with the same ISI, and lasting approximately 2 min. A threshold was determined from the performance across 20 blocks, with a progressively shorter ISI, starting with 600 ms and ending with 0 ms. The specific sequence of ISIs across an entire session was: 600, 500, 400, 350, 300, 250, 200,

175, 150, 125, 100, 80, 60, 40, 20, 0 ms. A psychometric function of percentage correct for each block was fit with a Weibull function to determine the ISIs at which performance yielded 80% accuracy.

Participants controlled the onset of each block and were instructed to take as many breaks as they needed between blocks. Once a block began, a new trial was initiated every 2 s, regardless of whether or not the subject made a response. Training, which occurred at the beginning of the 9AM test session, consisted of 15 trials of an easy version of the task (ISI of 1000 – 1500 ms) and 50 trials of the easiest block of the actual task (ISI of 600 ms). 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.

2.4 *Performance difference scores*

Difference scores were calculated to measure the change in performance by subtracting the second in-laboratory test session threshold from the first in-laboratory test session threshold. Negative difference scores indicate perceptual deterioration.

2.5 *In-scanner testing*

The task design described in the experimental-procedures section was adapted for administration in the scanner to measure the fMRI responses to the texture stimulus. fMRI requires incorporating a contrast within each scan session, which eliminated the possibility of using the same behavioral task inside and outside the scanner. This requirement, however, allowed us to design a contrast that compared BOLD signal modulation in both the trained and untrained (ie control) hemifield. Each scanning session lasted 60 – 75 min. Scans alternated between two conditions of the task. Each condition was administered four times, for a total of eight functional scans. In both conditions of the test, block designs were used in which the texture stimulus alternated between the trained and untrained visual hemifield every 20 s (ie every 10 trials). A reference scan ended each scanning session.

The task parameters were also altered to conform to the scanner. Each fMRI session consisted of eight 4 min scans. Within each scan there were six 40 s cycles. Each cycle consisted of a block of trials in the trained hemifield and a block of trials in the untrained hemifield. Whether the first block of a scan was in the trained or untrained hemifield was counterbalanced across scans and subjects. Each block contained ten 2 s trials. Each trial consisted of a 100 ms fixation interval with a cue, a texture stimulus presented for 17 ms, a blank ISI (duration of the ISI was determined with an online three-up/one-down staircase procedure), a 17 ms mask, and a 1.5 s response interval during which subjects made a response to the fixation (T versus L) and texture (vertical versus horizontal) targets. Again, the fixation target controlled for eye movements.

The staircase procedure was implemented inside the scanner in order to maximize the number of trials (and thus BOLD signal modulation) at threshold (80% correct). These thresholds, however, were not used in the statistical analysis comparing changes in performance and changes in BOLD for three reasons. First, the staircase procedure produced extremely noisy data. Second, the thresholds obtained in the laboratory were used instead in order to have an independent measure of performance change. Third, perceptual deterioration has been shown to increase linearly with the amount of training. In the present study, performance deterioration in the second in-laboratory session (third session overall) showed the same linear increase in ISI that we have previously reported (Mednick et al 2005), a difference score of 43 ms after second training session, while in the present study a difference score of 63 ms was found after third session). Since behavioral data from inside the scanner were not used, we were also unable to analyze performance in the untrained hemifield.

2.6 *Statistical analysis*
To evaluate the relationship between changes in behavioral performance with changes in BOLD signal modulation, multiple regression tests were run with one dependent variable: the behavioral difference score—TDT difference and two independent variables: group (napper versus non-napper) and the difference score for BOLD signal modulation associated with each condition. The results are presented by visual area.

3 MRI data collection

3.1 *Functional images*
fMRI experiments were conducted at the Center of Functional Magnetic Resonance Imaging at the University of California San Diego. Echo-planar imaging was performed on a whole-body 3 T GE MR scanner with a low-bandwidth echo-planar pulse sequence. An eight-channel array surface coil was used to maximize signal-to-noise in the occipital areas. 150 volumes of 32 axial slices were acquired per run with repetition time (TR) = 2 s, echo time (TE) = 30 ms, field of view (FOV) = 25 cm, in-plane resolution = 64×64.

3.2 *Retinotopic mapping*
Prior to the experimental scans, all subjects had their visual areas mapped by standard retinotopic mapping techniques to segregate the subjects' retinotopic visual areas (V1, V2, V3, V3A, and V4v). The polar angle and eccentricity components of the retinotopic maps were measured by recording the fMRI response to slowly rotating wedge and expanding ring stimuli, respectively. These retinotopy measurements were visualized on a computationally flattened region of the gray matter in the occipital lobe from a high-resolution MRI of each subject's brain (Engel et al 1997). fMRI data from subsequent sessions were then aligned to a common three-dimensional coordinate grid, which allowed us to project regions of interest across sessions.

3.3 *Reference scan*
Each experimental session ended with a reference scan that determined the region within each retinotopic area associated with the textured target. This also served to eliminate inactive voxels suffering from partial volume effects. The reference scan consisted of a contrast-reversing 8.3 Hz, 1 cycle deg^{-1} checkerboard restricted to the same peripheral apertures as the texture target in the main experiments. The stimulus alternated (20 s on, 20 s off) with a uniform gray field. Active voxels that correlated with a 40 s sinusoid ($r > 0.23$) were included for analysis in the subsequent scans.

3.4 *Post-processing of data and determining response amplitude*
A total of nine functional scans, including the reference scan, were acquired from each subject during each scanning session. This reference scan also served as a baseline response to assess hemodynamic lag (phase) and to measure maximal response (amplitude) for each visual area. Each scanning session ended with an anatomical scan, used to align all functional data across multiple scanning sessions to a reference volume, allowing us to identify predefined regions of interest (ROIs) in each data set. All subjects used a bite-bar during all scans and as a result no motion correction was performed for any of the functional scans.

Functional MR response was quantified by (i) dividing each voxel's time series by its mean intensity; (ii) subtracting any linear trend from each voxel's time series; (iii) averaging the time series over a set of voxels corresponding to a particular brain region; and (iv) calculating the amplitude of the response relative to a fixed variable phase delay, equivalent to the best-fitting sinusoid for the ON versus OFF cycles of the reference scan. We then measured the magnitude of the hemodynamic response as a result of visual stimulation in the predefined, restricted ROIs.

4 Results

4.1 *Task performance*

Replicating earlier findings that napping prevents perceptual deterioration, we found significant differences between nappers and non-nappers on the difference score ($t = 2.56$, $p = 0.01$, -7.3 ms and -63.0 ms, nappers and non-nappers respectively, figure 3).

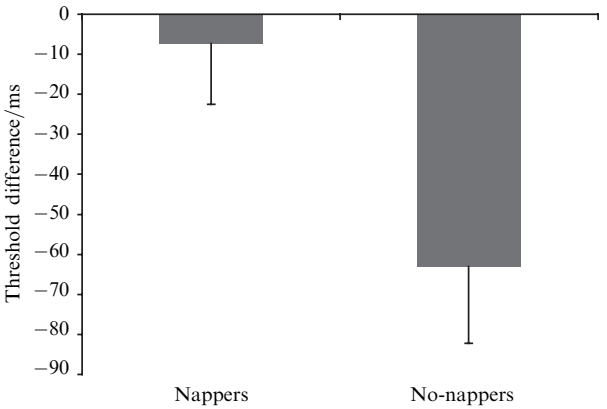

Figure 3. Texture discrimination difference threshold in nappers and non-nappers.

4.2 *BOLD fMRI data, V1*

We tested the difference between nappers and non-nappers on the two conditions in the scanner, using behavioral performance as the dependent measure, modeling the effects of group, attention-only condition, stimulus + attention condition, and the interactions between group × attention-only, and group × stimulus + attention. A significant relationship was found between the change in behavioral performance (TDT difference) and BOLD signal modulation across sessions (omnibus $F = 3.39$, $p = 0.01$, $r^2 = 0.41$). Amongst the terms, there was a significant effect of group ($F = 6.88$, $p = 0.01$), and significance in the interaction group × stimulus + attention ($F = -2.05$, $p = 0.05$). There were no further significant terms: attention-only ($F = 0.95$, $p = 0.34$); stimulus+attention ($F = 2.9$, $p = 0.10$), or the interaction group × attention-only ($F = 0.67$, $p = 0.42$).

4.2.1 *Stimulus + attention/trained-side.* The stimulus + attention condition measures the response associated with attention and the target stimulus compared to the response to no stimulus. Since the above-mentioned omnibus F statistic was significant, we repeated the regression separately for nappers and non-nappers. In the nappers, we found no relationship between TDT difference and changes in BOLD signal modulation ($F = 0.08$, $p = 0.77$) (figure 4, black diamonds).

Non-nappers, however, showed a significant relationship ($F = 10.95$, $p = 0.005$, $r^2 = 0.47$), such that the decrement in perceptual deterioration in the second session was positively correlated with the decrement in BOLD signal in the second session (figure 4, gray squares). We examined the behavioral and BOLD signal data to ensure that this significant correlation was not due to outliers (values more than three standard deviations from the mean). No data fit this outlier definition indicating that the correlation between BOLD signal modulation and performance was not skewed by individual data points.

4.2.2 *Stimulus + attention/untrained side.* In the untrained side of V1, the omnibus test was not significant ($F = 2.11$, $p = 0.11$, $r^2 = 0.19$). Amongst the modeling effects, group was significant ($F = 5.13$, $p = 0.04$) but neither the condition ($p = 0.83$) nor interaction ($p = 0.30$) were significant, indicating a lack of a relationship between performance and BOLD signal modulation on the untrained side in nappers and non-nappers. By considering the untrained side as a control, we found that the relationship between changes in performance and in BOLD signal was present in the trained side of V1 only.

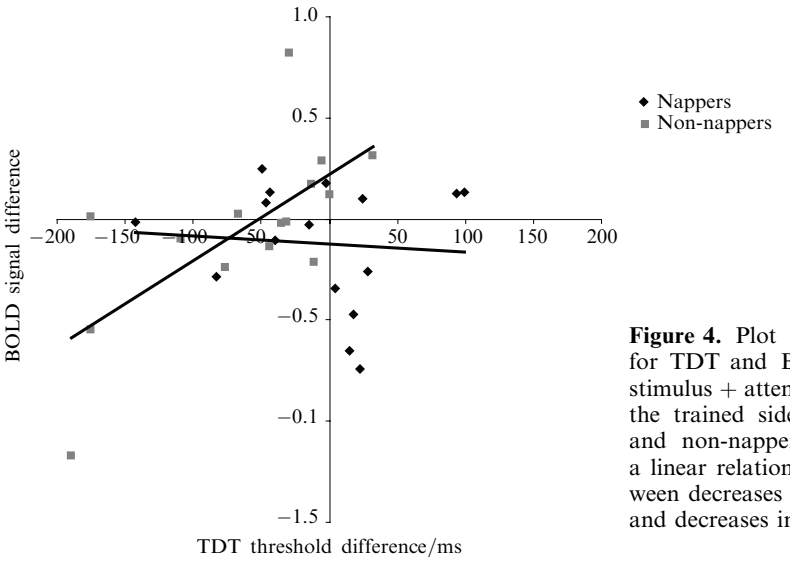

Figure 4. Plot of difference scores for TDT and BOLD signal of the stimulus + attention condition on the trained side of V1 in nappers and non-nappers. In non-nappers, a linear relationship was found between decreases in task performance and decreases in BOLD signal.

4.2.3 *Attention-only/trained side.* The attention-only condition measured the brain response to an attended versus an unattended target. The omnibus regression of group and session on TDT difference was not significant ($F = 1.71$, $p = 0.18$). The term group was significant ($F = 4.96$, $p = 0.03$). But no other terms reached significance: attention-only ($F = 0.02$, $p = 0.86$), interaction ($F = 0.2$, $p = 0.65$). When each group was analyzed separately, there was no relationship between the performance change and the change in BOLD signal to the attention condition for either condition of either group (nappers: $F = 0.05$, $p = 0.8$—figure 5, black diamonds; non-nappers $F = 0.13$, $p = 0.72$—figure 5, gray squares). Thus, the top–down condition was not correlated with the decreases in performance in the non-nappers.

4.2.4 *Attention-only, untrained-side.* In the untrained side of V1, there was no significant relationship between TDT difference and changes in BOLD signal modulation between session one and two (omnibus $F = 1.98$, $p = 0.14$, $r^2 = 0.18$). The term group was significant ($F = 5.12$, $p = 0.02$), but none of the other terms reached significance—

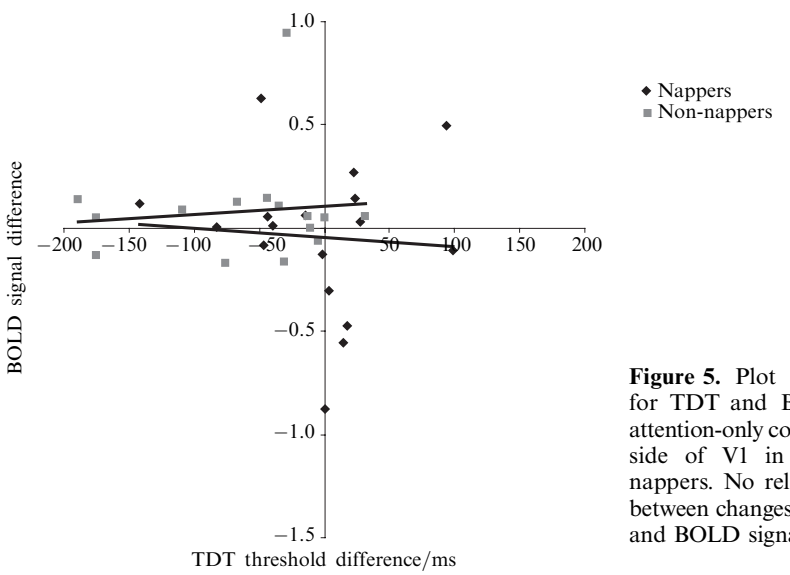

Figure 5. Plot of difference scores for TDT and BOLD signal of the attention-only condition on the trained side of V1 in nappers and non-nappers. No relationship was found between changes in task performance and BOLD signal modulation.

attention-only ($p = 0.35$), interaction ($p = 0.37$)—indicating a lack of a relationship between performance and BOLD signal modulation on the untrained side in nappers and non-nappers.

4.3 *BOLD fMRI data, V2 – V4*

No significant differences were found for any of the analyses conducted within the other of the visual areas examined (V2, V3, and V4) (all ps > 0.2).

5 Discussion

5.1 *Neural correlates of perceptual deterioration*

We found that performance decrease due to repeated, within-day testing was reflected in fMRI response in the trained hemisphere of primary visual cortex. This relationship was not seen in higher visual areas of V2, V3, V4v, V3A, or in the untrained side of V1. Decreased BOLD signal in the non-nappers was found in the bottom – up condition, which compared fMRI signal modulation to the stimulus in the attended side with no stimulus in the unattended side. No such relationship was found between behavioral performance and BOLD signal in the top – down condition, which compared fMRI signal modulation to the stimulus in the attended side with the stimulus in the unattended side. These data suggest perceptual deterioration is a stimulus-driven effect that is related to the fatigue of early visual neurons. We did not find evidence that deterioration is due to an inability to allocate attention to the visual stimulus.

Prior behavioral studies suggested that perceptual deterioration is due to fatigue of target-selective, orientation-specific, binocular neurons. Perceptual deterioration does not appear to be affected by subject motivation or quietly resting (without sleep) (Mednick et al 2003). Further, even though deterioration can be eliminated by changing the target orientation, subjects are not aware of these stimulus changes. The present study adds to the characterization of this phenomenon by demonstrating that deterioration involves bottom – up fatigue of V1 neurons and is not modulated by top – down attentional processes. This finding shows further evidence of a discrepancy between the activity of V1 neurons and awareness, since perceptual deterioration (occurring in V1) does not involve awareness.

The relationship between BOLD signal modulation and performance decreases was not found in areas outside of V1. Other findings also support a dissociation between V1 and conscious awareness. Sasaki and Watanabe (2004) recently reported that attentional modulation on a color filling-in task enhanced BOLD signal modulation only in the primary visual cortex. The activity of later visual areas is not necessary for the generation of the motor signal needed for the behavioral response, as the signals that drive the motor system do not originate in the visual cortex regardless of the stimuli or induced perception. The stimulus-driven signals generated in the visual system are sent to the frontal-eye-fields (FEFs), an area implicated in decision-making (Glimcher 2001). Studies have shown that the final stimulus-based response is determined by the output of the FEFs (Hanes and Schall 1996; Schall and Thompson 1999). The observed activation pattern of visual cortical areas beyond V1 is consistent with the notion that subjects are deliberately attending to a target which was texturally different from a uniform background (Zipser et al 1996). The fact that BOLD signal in higher visual areas V2, V3, V4v did not correlate with performance indicates that, given the stimuli used, V1 is sufficient for process target features, but that the attentional resources of this area were not able to overcome the build up of training-induced fatigue.

5.2 *Perceptual and neural maintenance*

Napping prevented deterioration from occurring both at the level of behavior and the fMRI response. Nappers maintained baseline performance and BOLD signal for each visual area in both task conditions. These results replicate previous findings that an

hour nap restored performance to baseline on the texture-discrimination task (Mednick et al 2002), and go further to demonstrate the neural consequence of napping versus not napping. A recent surge in examination of the benefits of napping has produced a wide range of results in learning and memory research. Along with the benefits to perceptual learning (Mednick et al 2003), napping has been shown to produce the same amount of memory increases as a full night's sleep on tasks of declarative memory (Takashima et al 2006; Tucker et al 2006), motor memory (Walker et al 2003), and spatial memory (Peigneux et al 2004). The present results suggest that napping can also prevent early sensory cortical areas from succumbing to fatigue that would otherwise have happened without a nap.

One difference between perceptual deterioration and perceptual learning may be the cortical level of processing that drives both phenomena. We have shown that performance decreases correlated with the BOLD signal in the bottom–up stimulus-driven condition in V1, but no evidence for influence of top–down processes or higher visual areas. Contrasting these results with models of perceptual learning, it appears that these two phenomena (learning and deterioration) may be opposing forces acting in parallel. Current theories of perceptual learning have shifted from strictly bottom–up models of plasticity of early visual neurons (Fiorentini and Berardi 1980; Fahle and Edelman 1993) to the proposal that learning is governed by top–down mechanisms (Ahissar and Hochstein 2004; Polley et al 2006).

Generally speaking, top–down models propose that performance improvement is shaped by the task and environmental demands, as well as the state of expectation and attention of the subject, which refine access to sensory input via top–down mechanisms. Li et al (2004) showed that, for monkeys trained in a shape-discrimination task, V1 neurons took on novel functional properties that were specifically related to the task demands and not tied to the primitive stimulus features of the task. Walker and co-workers (2005) employed fMRI with the same task as that used here to show that nocturnal sleep-dependent improvement was related not only to enhanced BOLD signal in primary visual cortex, but also in regions associated with higher levels of processing such as the occipital temporal junction, the medial temporal lobe, and the inferior parietal lobe. While only focusing on the visual system, our data are consistent with those of Walker, showing that a nap produced parallel results for both behavior and BOLD signal. In our case, however, this was perceptual and neural maintenance, not improvement.

An interesting extension of these findings would be an investigation into the dynamics of these two processes. For example, it is not clear to what extent increasing levels of perceptual deterioration may affect perceptual learning. A parallel example of a deterioration in processing with repeated training in the motor system may be motor dystonia, a movement disorder characterized by sustained involuntary muscle contractions that often requires extensive repetition of a stereotypic movement to emerge (eg writer's cramp) (Hallett 1998). People with this disorder show higher thresholds in a task involving discrimination of two electric stimuli closely related temporally, an abnormality that correlates with the degree of severity of dystonia (Bara-Jimenez et al 1998). Further, deficient activation of premotor cortex and decreased correlation between premotor cortical regions and putamen suggest a dysfunction of the premotor cortical network in patients with writer's cramp (Ibanez et al 1999). Perhaps submitting a local region of primary visual cortex to an orientation-discrimination task over an extended period of time may slow the neural response and decrease perception. Further research in this area may have implications for occupational related injuries due to repetitive visual processing, and in planning optimized training strategies integrating napping with learning schedules.

In summary, we have conducted the first study with functional neuroimaging to demonstrate that napping can prevent training-induced fatigue of early visual neurons. Some limitations of the present study include (i) performance inside the scanner was not used in the regression with BOLD signal; (ii) although the overall tasks inside and outside the scanner were similar, the exact stimuli were not the same across conditions; (iii) low power of the study. Future studies will address these issues. Nevertheless, these perceptual changes may be fundamental to sensation and perception in everyday life. The specificity of deterioration to spatial location and configuration of the stimulus indicates that this phenomenon is not simply the result of general fatigue or changes in arousal. The results presented here suggest that perceptual deterioration is manifested as decreased activity in V1, the earliest stages of visual processing. This is caused by degradation in the feedforward stimulus-driven, or bottom – up representation of the stimulus, rather than by a decrease in the ability of attentional mechanisms to modulate the representation of the attended stimulus. This implies that once perceptual deterioration has occurred, performance cannot be recovered simply through increasing attention or effort, because information is lost at the sensory level.

Acknowledgments. This work was supported by NIH grant EY12925 and Ruth L Kirschstein National Research Service Award (NIH F32 EY015564) to S C Mednick.

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