

Response feedback triggers long-term consolidation of perceptual learning independently of performance gains

Jonathan Dobres

Department of Psychology, Boston University,
Boston, MA, USA



Takeo Watanabe

Department of Psychology and Program of
Neuroscience, Boston University, Boston, MA, USA



Visual perceptual learning (VPL) is defined as a long-term performance enhancement on a visual task, and is typically thought of as a manifestation of plasticity in visual processing. It is thought that neural representations relevant to a recently learned task are consolidated over the course of hours or days and made robust against the effects of deterioration and interference. However, recent work has shown that when these representations are reactivated by further task exposure, they become plastic again and are vulnerable to deterioration effects. Here we used a perceptual learning paradigm in combination with performance feedback (knowledge of task accuracy provided to the observer in real-time) to investigate behavioral factors that influence consolidation. Subjects were trained to detect two coherent motion directions embedded in noise over several days. It was found that without feedback, performance improvements accrued during training rapidly deteriorated upon exposure to novel, neighboring motion directions. However, when one of the two directions was consistently paired with feedback during training, the paired direction was resilient against the effects of deterioration. This benefit coincides with a gradual inhibition of learning for the unpaired stimuli. Furthermore, this stabilizing effect operates independently of the magnitude of performance gains during training and suggests a useful behavioral marker for the study of consolidation processes.

Keywords: consolidation, interference, perceptual learning, feedback, motion

Citation: Dobres, J., & Watanabe, T. (2012). Response feedback triggers long-term consolidation of perceptual learning independently of performance gains. *Journal of Vision*, 12(8):9, 1–10, <http://www.journalofvision.org/content/12/8/9>, doi:10.1167/12.8.9.

Introduction

Visual perceptual learning (VPL) is defined as long-term performance enhancement on a visual task as a result of visual experiences, and is regarded as a manifestation of neuroplasticity related to visual processing (Adini, Sagi, & Tsodyks, 2002; Ahissar & Hochstein, 1997; Fahle & Poggio, 2002; Furmanski & Engel, 2000; R. W. Li, Klein, & Levi, 2008a; W. Li, Piëch, & Gilbert, 2004; 2008b; Z. Liu, 1999; Lu & Doshier, 2004; Lu, Chu, Doshier, & Lee, 2005; Mukai et al., 2007; Sagi, 2010; Sasaki, Nanez, & Watanabe, 2009; Schoups, Vogels, Qian, & Orban, 2001; A. R. Seitz & Dinse, 2007; A. Seitz & Watanabe, 2003; Tsodyks & Gilbert, 2004; Watanabe, Nanez, & Sasaki, 2001; Xu, He, & Ooi, 2010; Yang & Maunsell, 2004; Yotsumoto, Watanabe, & Sasaki, 2008). Research has shown that VPL can be strengthened by two mechanisms: response feedback (M. Herzog & Fahle, 1997, 1999; M. H. Herzog & Fahle, 1998; A. R. Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006; Shibata, Yamagishi, Ishii, & Kawato, 2009; Weiss, Edelman, & Fahle, 1993) and stabilization/consolidation (Censor, Karni, & Sagi,

2006; Censor & Sagi, 2008; S. C. Mednick et al., 2002; S. Mednick, Nakayama, & Stickgold, 2003; A. R. Seitz et al., 2005; Stickgold, James, & Hobson, 2000). It is thought that these two mechanisms operate independently of one another.

Response feedback is information about the accuracy of observers' responses that is provided to observers as they perform a task. Feedback is an important reinforcing factor that enables an observer to efficiently adapt to his environment. In VPL paradigms, it has commonly been found that feedback significantly increases the speed and magnitude of learning effects (M. Herzog & Fahle, 1997, 1999; M. H. Herzog & Fahle, 1998; Seitz et al., 2006; Shibata et al., 2009; Weiss et al., 1993). So far the research on feedback has concentrated on examining how feedback affects the magnitude of VPL, to establish a link between VPL and general learning principles such as supervisory/non-supervisory learning and reinforcement learning (Chubb, Lu, & Sperling, 1997; Dayan & Balleine, 2002; Doya, 1999; Poggio, Fahle, & Edelman, 1992; Shibata et al., 2009). More recent models of perceptual learning conceive of feedback not as a supervisory or

teaching signal, but as an additional statistical parameter that enhances Hebbian learning processes in situations where the visual system is especially taxed (J. Liu, Lu, & Doshier, 2010; Petrov, Doshier, & Lu, 2005, 2006).

Stabilization/consolidation is the process by which a trace of developing VPL is strengthened so that it becomes permanently established. Generally speaking, this stabilization process occurs in two steps. The first step occurs within approximately 1 hour after completion of visual training. If training of a visual task is immediately followed by a different but similar task, VPL of the initial task is disrupted or interfered with. However, if there is at least a 1-hour interval between training of the two tasks, no interference is observed (A. Seitz et al., 2005; Yotsumoto et al., 2008). The second step occurs during sleep subsequent to training of a visual task. Sleep or nap reduces deterioration or adaptation caused by excessive training of VPL (Censor & Sagi, 2008; Censor et al., 2006; S. C. Mednick et al., 2002). For at least 1 hour after the onset of sleep subsequent to training of VPL, blood-oxygen-level-dependent (BOLD) signals are activated only in the regions of V1 that correspond to the retinotopic locations of trained features. The magnitude of activation is strongly correlated with the degree of improvement of VPL on subsequent days (Yotsumoto et al., 2009). Conversely, deprivation of REM and NREM sleep leads to abolishment of VPL (Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Stickgold et al., 2000). These results suggest that sleep plays an important role in stabilizing or consolidating VPL in the long term. It is generally thought that these two stages of consolidation make a fragile trace of VPL permanent (Yotsumoto et al., 2008).

However, further research has shown that even thoroughly consolidated learning can be disrupted or interfered with. Just as the neural representations associated with a task are presumably activated and modified during training, that representation is also reactivated during subsequent testing. Work in both motor learning and episodic memory has shown that this reactivation can make a consolidated neural representation vulnerable to interference effects once again (Diekelmann, Büchel, Born, & Rasch, 2011; Walker, Brakefield, Hobson, & Stickgold, 2003). This retest lability presents a potentially serious obstacle for experimental paradigms that rely on retesting previously consolidated learning with new stimuli, as is common in perception research.

There are several lacunae in the literature. Stabilization/consolidation is typically examined in the context of sleep paradigms, with more purely behavioral studies being relatively sparse. Feedback is usually discussed in terms of its performance benefits, but examinations of the underlying mechanisms of such benefits are

relatively rare. Research on factors that might ameliorate retest lability has focused on the effects of sleep consolidation. Lastly, no study has examined the relationship between feedback and stabilization/consolidation of learning. In the present study, we examined the effects of feedback on consolidation using a motion detection paradigm and training regimens of varying lengths. Subjects were trained to detect two target motion directions over the course of several days, with and without feedback. Stability of learning was probed by testing the observer with several novel motion directions.

Materials & methods

Participants

All subjects had normal or corrected-to-normal vision. Subjects provided informed consent and were tested under conditions that conformed to the Boston University Office of Research Compliance's guidelines for research on human subjects. A total of 12 subjects participated in Experiment 1 (four female), 14 subjects (nine female) participated in Experiment 2, and 13 (eight female) participated in Experiment 3. One female participant in Experiment 3 was excluded from analysis due to a failure to complete all sessions, leaving a total of 12 subjects.

Apparatus

All experiments were conducted using a 2.53 GHz Mac Mini running Matlab (Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were displayed on a 17-inch ViewSonic CRT monitor (ViewSonic, Walnut, CA) with a resolution of 1024×768 pixels and a 100 Hz refresh rate. Subjects' heads were secured in a chin rest throughout the experiment, ensuring that the monitor was at a consistent viewing distance of 24 inches. Subjects responded to each trial of the experiment using the numeric keypad of a standard U.S. keyboard.

Stimuli

In all experiments, subjects participated in a two-interval forced choice motion detection task. Motion stimuli were random dot cinematograms displayed in a circular aperture, 10° in diameter, centered on a fixation point. Dots measured 0.08° in diameter and were plotted using a white noise motion algorithm (Newsome & Pare, 1988; Pilly & Seitz, 2009) with a dot

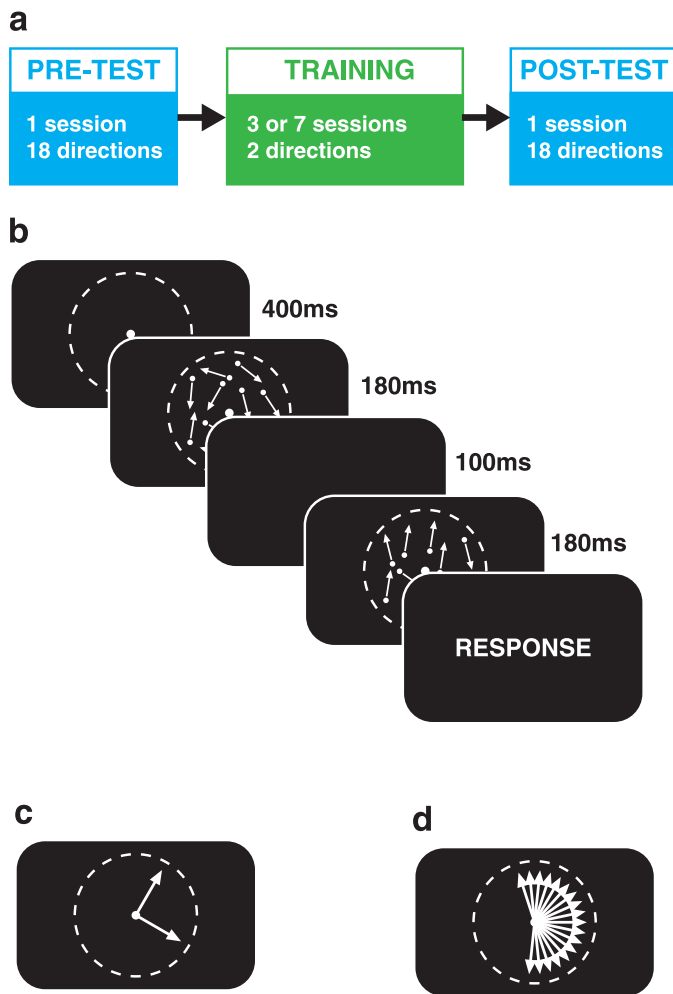


Figure 1. Methods of the study. **(A)** Schedule of experimental sessions. Each session of the experiment was conducted on a separate day. **(B)** Schematic of a single trial. Each trial included a noise-only and a signal+noise interval presented consecutively. The observer's task was to determine which of the two intervals contained the signal. The dashed circle represents the circular aperture used to confine the display of motion stimuli, and was not visible in the experiment. **(C)** An illustration of the number of motion directions shown during training sessions. The two directions were counterbalanced across subjects and always separated by 90° . In experiments in which feedback was provided, the feedback-paired direction was always the more clockwise of the two directions. **(D)** An illustration of the number of motion directions shown during pre-test and post-test sessions. None of the directions was paired with feedback during these sessions.

density of approximately 1 dot/deg² (approximately 80 dots in any single frame). The structure of each trial is illustrated in [Figure 1B](#). A fixation point was displayed alone for 400 ms, then the first stimulus was displayed for 180 ms, followed by a 100-ms interstimulus interval. The fixation point would then reappear alone for another 400 ms, followed by the second stimulus. On each trial, one of the two stimuli was designated as the

signal interval and had 10% of its dots selected for coherent movement in a uniform direction at a speed of $7.1^\circ/\text{sec}$. After the presentation of both stimuli, subjects had up to 2 seconds to respond by indicating which of the two intervals contained the signal stimulus.

Training sessions

During training sessions, subjects were exposed to two possible signal directions, separated by an angle of 90° ([Figure 1C](#)). Signal directions were always 30° off-cardinal and the combination of directions used was counterbalanced across subjects. In Experiments 1 and 3, the more clockwise of the two directions was always paired with a feedback tone that indicated to the observer whether he/she had made a correct or incorrect choice of signal interval, while the other direction was never paired with feedback. The two trial types were randomly interleaved throughout the session. In Experiment 2, no feedback was given for either direction. Each session consisted of 540 trials (270 trials per direction). In Experiments 1 and 2, subjects participated in seven training sessions, while in Experiment 3, they participated in three training sessions. Training sessions were always conducted on separate days.

Test sessions

Subjects participated in a pretest session the day before their training sessions and a posttest session the day after the final training session was completed. Subjects were presented with the two directions of training as well as a spread of directions $\pm 48^\circ$ away from these directions in increments of 12° , for a total of 18 exposed directions ([Figure 1D](#)). Trials of different directions were randomly interleaved throughout the session. No feedback was given during pretest and posttest sessions. Each session consisted of 540 trials (30 trials per direction).

Tuning functions

Performance tuning functions were computed for each observer to gauge the specificity and stability of learning effects. Percent correct was calculated for each exposed direction of the pretest and posttest. Pretest values were then subtracted from their corresponding posttest values to establish tuning functions. “Early” tuning functions were computed by calculating these measures from only the first 15 presentations of each direction in pretest and posttest. Likewise, “late” tuning functions include data from the latter 15 presentations of each direction.

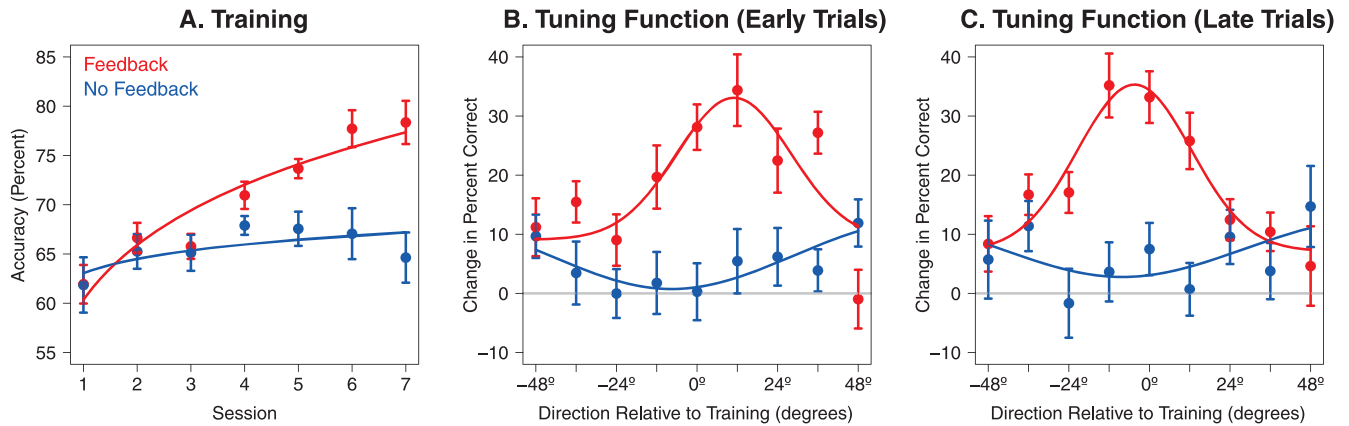


Figure 2. Performance change functions for subjects in Experiment 1 ($N = 12$). Performance change functions are computed by subtracting pre-test measurements from their corresponding post-test measurements. For details, see the [Materials & methods](#) section. (A) Accuracy measures ($\pm SEM$) for the feedback-paired and feedback-absent directions across training sessions of Experiment 1. (B) Performance improvement ($\pm SEM$) for “early” trials of Experiment 1. (C) Performance improvements ($\pm SEM$) for “late” trials of Experiment 1. Note the stability of the learning effects between early and late trials.

Note on reporting percent correct

Percent (or proportion) correct performance on a two-interval forced choice detection task is the primary metric used throughout this study (or the subtraction of percent correct measures for the tuning functions). Measures are not converted to a d' -prime score because both signal and noise stimuli are present on each trial, making it impossible to separate false positives and false negatives, thereby limiting the usefulness of the d' -prime scale and making percent correct the most straightforward measure of accuracy. Since our measures are presented as raw percentages (or subtractions of percentages), it is important to bear in mind that when we state that “learning improved by 30%,” we mean the *absolute* change on the scale of percent correct, not a 30% improvement relative to baseline. For example, a reported improvement of 30% reflects a change in performance from 50% to 80% accuracy (30% absolute improvement), not a change of 50% to 65% (30% improvement relative to baseline).

Results

Experiment 1: Feedback augments the learning of paired directions

In Experiment 1, subjects underwent 7 days of training in which one of the trained motion directions was consistently paired with a feedback tone, while no feedback was given for the other direction. As shown in [Figure 2A](#), observers demonstrate a steady increase in performance for the feedback-paired direction over the

7 days of training, but not for the feedback-absent direction (significant effect of training session [$F(6, 66) = 6.08, p < 0.0001$] and a significant interaction between training session and motion direction [$F(6, 66) = 3.96, p < 0.002$], and a borderline effect for motion direction alone [$F(1, 11) = 3.54, p = 0.087$]; 16.4% absolute increase in proportion correct for feedback-paired direction [$p = 0.001, t$ test], 2.78% increase for feedback-absent direction [$p = 0.569, t$ test]). An examination of the early-trial and late-trial tuning functions that resulted from this training regimen shows that this experimental manipulation had striking effects on the learning of the two stimulus types ([Figure 2B](#) and [C](#)). Analyzing the tuning functions in a two-factor repeated-measures ANOVA reveals that early-trial data show significant differences between the two tuning functions, relative testing directions, and their interaction (significant difference between the two sets of direction [$F(1, 11) = 12.22, p = 0.005$], significant difference among tested directions around each trained direction [$F(8, 88) = 2.15, p = 0.039$], and a significant interaction between the two factors [$F(8, 88) = 3.34, p = 0.002$]; significant performance gain at the direction paired with feedback [28.1%, $p < 0.001, t$ test], but not the feedback-absent direction [0.2%, $p = 0.973, t$ test]). The same pattern of results is evident when the late-trial data are examined (significant difference between the two sets of direction [$F(1, 11) = 12.62, p = 0.005$], significant difference among tested directions around each trained direction [$F(8, 88) = 2.36, p = 0.023$], and a significant interaction between the two factors [$F(8, 88) = 2.89, p = 0.007$]; significant performance gain at the direction paired with feedback [33.2%, $p < 0.001, t$ test], but not the feedback-absent direction [7.5%, $p = 0.354, t$ test]).

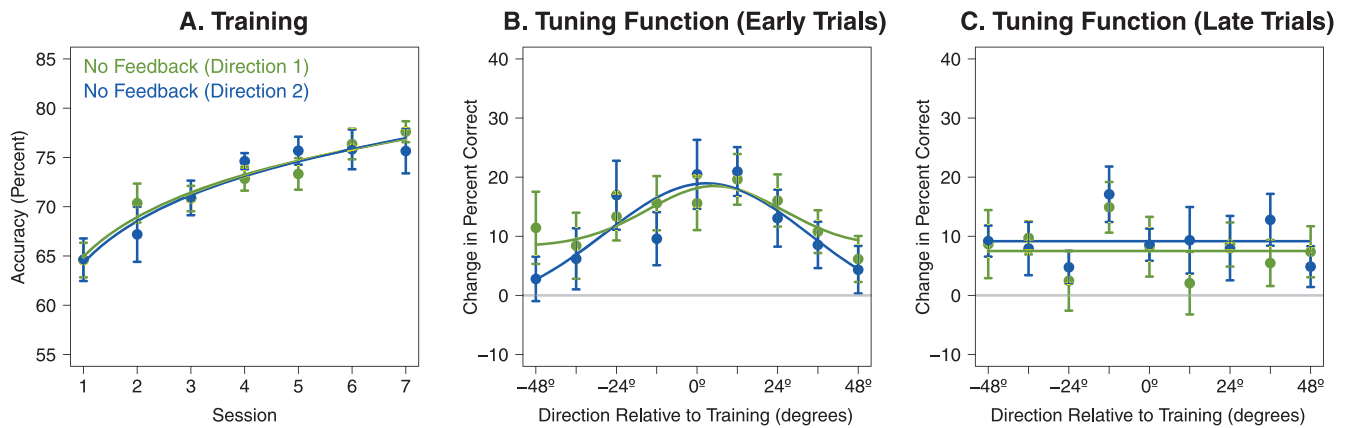


Figure 3. Performance change functions for subjects in Experiment 2 ($N = 14$). Labeling as in Figure 2. Note the collapse of performance improvements in the later trials of this experiment.

In other words, the tested directions in the vicinity of the direction paired with feedback demonstrate a strong Gaussian-shaped pattern of improvement centered on the trained direction, while there appears to be no learning at directions in the vicinity of the feedback-absent training direction. Moreover, this pattern remains stable between early and late trials of the testing sessions, showing no signs of deterioration or interference.

Experiment 2: Learning without feedback remains vulnerable to deterioration

The results of Experiment 1 demonstrate that feedback exerts powerful effects on learning. However, it is unclear whether the difference between learning trends of feedback-paired and feedback-absent tuning functions is merely a byproduct of task difficulty (A. R. Seitz et al., 2006), fatigue or neural saturation (S. Mednick, Arman, & Boynton, 2005), or a perceptual interference effect (Diekelmann et al., 2011; A. Seitz et al., 2005; Walker et al., 2003). To clarify the role of feedback, we undertook Experiment 2. All parameters and conditions in this experiment are identical to those of Experiment 1, except that no feedback is provided at any point during training or testing.

In contrast to Experiment 1, observers in Experiment 2 (Figure 3) demonstrated equal learning for both motion directions across the training sessions (significant effect of training session [$F(6, 78) = 8.11, p < 0.0001$], but no significant difference between trained motion directions [$F(1, 13) = 0.003, p = 0.955$], and no interaction [$F(6, 78) = 0.724, p = 0.631$]; 13.0% absolute increase in proportion correct for one trained motion direction [$p < 0.001, t$ test], 11.0% increase in proportion correct for the other trained direction [$p = 0.014, t$ test]). In the tuning functions, the results of early trials (Figure 3B) show equal and significant

learning effects for both trained directions and their vicinities (significant difference among tested directions around each trained direction [within each set, $F(8, 104) = 2.04, p = 0.049$], no significant difference between the two sets of directions [$F(1, 13) = 0.24$, between two sets, $p = 0.632$] and no significant interaction between the two factors [$F(8, 104) = 0.42, p = 0.908$] in two-way repeated measures ANOVA; significant performance gain at both trained directions [15.6% and 20.5%, $p = 0.02$ and $0.013, t$ test]). In contrast, results of the late trials (Figure 3C) did not show significant improvement at either trained direction or differences across the tested directions (no significant effects within each set [$F(8, 104) = 1.19, p = 0.314$], between two sets, [$F(1, 13) = 0.42, p = 0.529$] or their interaction [$F(8, 104) = 0.28, p = 0.973$] in two-way repeated measures ANOVA; no significant performance gain at both trained directions [8.2% and 8.6%, $p = 0.212$ and $0.092, t$ test]). That is, the learning effect shown for both trained directions and their vicinities in the early trials disappeared in the later trials.

Note that the posttest was conducted after 7 days' training and therefore the VPL must have been well consolidated during wakefulness and sleep. Nevertheless, in the current experiment VPL was severely disrupted when detection of the trained motion directions was interleaved with new motion directions. There are at least two possible explanations for this result. The magnitude of VPL may not have been sufficiently large to survive interference during the later trials, irrespective of feedback. Alternately, irrespective of the magnitude of VPL, the abolishment of VPL in the later trials occurred because of the absence of feedback during the training stage. Since the magnitude of learning effects observed in Experiments 1 and 2 are quite different, it is difficult to compare them directly. If VPL of a direction trained with feedback is of the same or smaller magnitude than the VPL in this experiment (without feedback), and nevertheless sur-

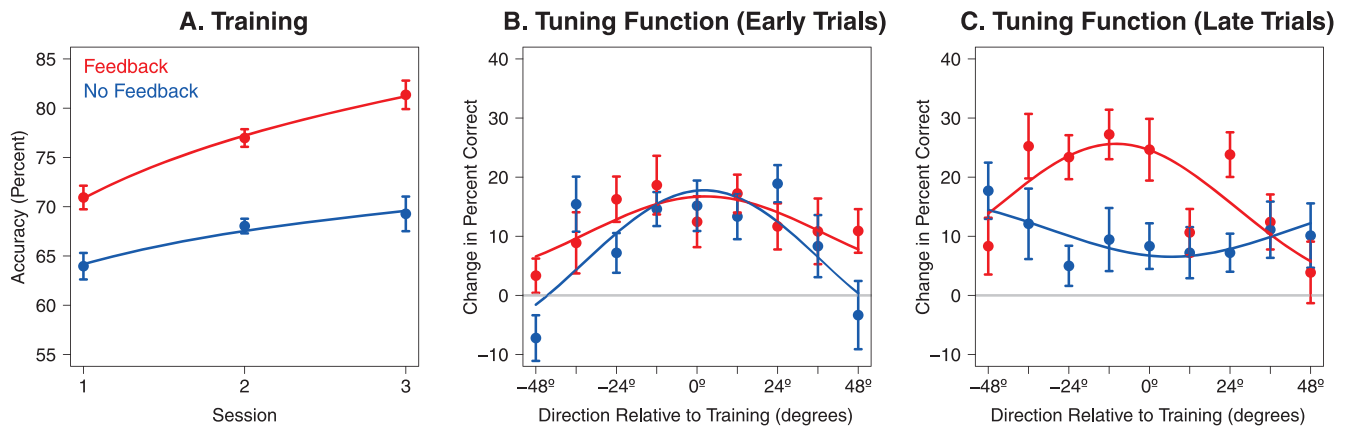


Figure 4. Performance change functions for subjects in Experiment 3 ($N = 12$). Labeling as in Figure 2. Note the pattern of results here: the early tuning function is similar to the early tuning function of Experiment 2, and the late tuning function is similar to the tuning functions of Experiment 1.

vives interference during the later trials, this would indicate that the second possibility is the case.

Experiment 3: Feedback stabilizes learning irrespective of the magnitude of performance gains

To test which possibility is more likely, we undertook Experiment 3 with a new group of 12 subjects. As previously mentioned, it has been reported that in some cases the magnitude of VPL attained with feedback is larger than without feedback (M. Herzog & Fahle, 1997; Shibata et al., 2009). Thus, to equalize the magnitude of VPL trained with feedback in this third experiment to that of the VPL without feedback in the second experiment, the number of training days was reduced from 7 to 3. In addition, to directly compare effects of feedback within the same group of subjects, during training one motion direction was always paired with feedback, while the other was not.

Observers in Experiment 3 (Figure 4) demonstrated significant learning during training for the feedback-present direction, but not the feedback-absent direction, as in Experiment 1 (significant effect of training session [$F(2, 22) = 11.95, p = 0.0003$], significant effect of motion direction [$F(1, 11) = 7.40, p = 0.02$], no interaction between these effects [$F(2, 22) = 1.49, p = 0.247$]; 10.4% absolute increase in proportion correct for the feedback-paired direction [$p = 0.002, t$ test], 5.3% increase for the feedback-absent direction [$p = 0.109, t$ test]). As shown in Figure 4B, for early trials of the post-test, the learning effect was significant for both the feedback-paired and feedback-absent directions (significant difference among tested directions [$F(8, 88) = 4.00, p = 0.0004$], not significant between sets [$F(1, 11) = 3.20, p = 0.101$], and not significant in their interaction [$F(8, 88) = 1.22, p = 0.298$], in two-way

repeated measures ANOVA; significant performance gain both at the feedback-paired direction [12.5%, $p = 0.02, t$ test] and at the feedback-absent direction [15.2%, $p = 0.022, t$ test]). Note that the magnitude of VPL of the feedback-absent direction was roughly equal to that of the feedback-paired direction, and that the magnitudes of these effects are similar to those obtained for the early-trial tuning functions of Experiment 2.

For the later trials (Figure 4C), VPL at and around the feedback-paired direction was retained, whereas VPL at the feedback-absent direction was not (overall non-significant effects of test direction [$F(8, 88) = 1.53, p = 0.16$] and training direction [$F(1, 11) = 4.46, p = 0.058$], but a significant interaction [$F(8, 88) = 2.19, p = 0.036$], in two-way repeated measures ANOVA; significant performance gain at the feedback-paired direction [24.6%, $p < 0.001, t$ test] and no significant performance gain at the feedback-absent direction [8.3%, $p = 0.231, t$ test]).

Since the magnitude of VPL at the feedback-paired direction in this experiment was equivalent to the feedback-absent directions in the second experiment and in the current experiment, we conclude that VPL of a motion direction survives exposure to new motion directions as long as the trained direction is paired with feedback, irrespective of the magnitude of learning.

Discussion

In the present study, we examined the role that feedback plays in the consolidation of VPL. We found that feedback had pronounced effects on the learning of stimuli that were trained for many days. After a 7-day training regimen, a strong learning effect was observed for feedback-associated stimuli, while no

learning was observed for feedback-absent stimuli. We also found that without feedback during the training stage, accrued learning is equal for both trained directions, but learning is disrupted upon exposure to motion directions in the vicinity of the trained ones. Critically, no such disruption was observed for VPL of the direction trained with feedback, even when the length of the training stage is reduced to equalize the magnitude of VPL with those of the motion directions trained without feedback. These results indicate that feedback given during training makes VPL resilient against disruption that occurs even after VPL has been consolidated.

The role of consolidation

Stabilization/consolidation and feedback, phenomena that are usually studied independently of each other, in fact, interact powerfully. In skill-learning paradigms such as VPL and motor sequence learning there are at least two stages of consolidation. Within a few hours after training during wakefulness, the first stage of consolidation occurs and makes a fragile learning trace resilient against disruption or interference from training of a new task (A. Seitz et al., 2005; Shadmehr & Holcomb, 1997). During sleep following training, the second stage of consolidation occurs, mainly resulting in performance gains during subsequent training (Censor & Sagi, 2008; Gais, Plihal, Wagner, & Born, 2000; Karni & Sagi, 1993; S. C. Mednick et al., 2002). However, even after these consolidation stages, performance of the trained task can reactivate corresponding neural representations and make the learning trace labile and vulnerable to disruption or interference (Walker et al., 2003). In the present study, feedback-absent motion directions were trained for several days and thus the learning must have gone through the two types of consolidation stages (one for wakefulness and the other for sleep). In the post-test, it is possible that VPL was reactivated and then disrupted when exposed to new, similar motion directions. Our results show that training with feedback makes VPL resilient to this type of disruption. Since the stabilizing effects of feedback occur independently of the magnitude of associated performance gains, as demonstrated in Experiments 1 and 3, this suggests that stabilization or consolidation may be fundamental to feedback's beneficial effects.

The data may appear consistent with two alternative hypotheses. The first is that differences between experiments might have arisen due to differences in baseline performance levels, some evidence of which can be seen in the training data of Experiment 3. However, the differences in sensitivity between the two trained directions at the start of training are nonsignificant in all experiments ($p = 0.985, 0.995, \text{ and } 0.137$

in paired t tests for Experiments 1–3, respectively). Moreover, given the well-known facilitative effects of feedback, the initial difference in sensitivity in Experiment 3 is not unexpected (if anything, the lack of a facilitative effect of feedback on day one of Experiment 1 is somewhat unusual). Although there is some fluctuation in baseline performance between experiments, these differences are nonsignificant and unlikely to account for the observed experimental effects (for further discussion of variability in the data, see [Supplemental Materials](#)).

Secondly, the interference effect may have been a byproduct of neural saturation or fatigue (S. Mednick et al., 2005). However, sessions were relatively short (25–40 minutes, depending on the subject), and there is no evidence of a deterioration of performance in the training sessions when “early” and “late” trials are compared ($F(1, 11) = 1.81, p = 0.205$ for Experiment 1; $F(1, 13) = 0.31, p = 0.587$ for Experiment 2; $F(1, 11) = 1.36, p = 0.269$ for Experiment 3). This suggests that deterioration occurred only in the presence of novel testing stimuli, lending support to the interference hypothesis. Moreover, because testing sessions were conducted without feedback across all experiments, all posttests were equivalent. If fatigue had influenced the testing sessions, we would expect to see evidence of fatigue in all three experiments, which is not the case here.

While our psychophysical data make it impossible to definitively reveal a physiologic mechanism, there is some recent work in mice suggesting that certain proteins produced in the brain act as a “plasticity break” that modulates neuroplasticity and, consequently, the stability of accrued changes in the brain (Morishita, Miwa, Heintz, & Hensch, 2010). It is possible that feedback could promote the production of a similar protein in human observers.

Feedback-induced inhibition of perceptual learning

Experiment 1 demonstrated dramatic and very different learning effects for the two trained stimuli. The feedback-associated test directions showed a strong learning trend, while the feedback-absent test directions showed no learning at all. Viewing this experiment in isolation, it would be tempting to conclude that feedback exerted effects only on its paired direction. However, our subsequent experiments reveal a more complex effect: the feedback-associated learning improvements remain stable during testing, while the feedback-absent directions initially show evidence of a sensitivity improvement, which later collapses, as shown in Experiments 2 and 3. This suggests that the results of Experiment 1 represent an

endpoint in the development of not one, but two learning profiles. Feedback augments or boosts learning at its paired direction, and also inhibits the learning of unpaired directions. Since the post-test is administered earlier in Experiment 3 (after just 3 days of training), facilitative effects are captured in the sensitivity functions before the development of complete suppression of the feedback-absent direction. Experiment 3's early-trial posttest data reveal a sensitivity increase for both trained directions, but in later trials a "collapse" effect similar to Experiment 2's can be seen for the feedback-absent tuning function. We speculate that the presence of feedback over a longer time course, as in Experiment 1, eventually suppresses sensitivity improvements for feedback-absent stimuli in favor of the more stabilized feedback-paired stimuli. In Experiment 2, in which no feedback was given, both trained directions exhibited equal but unstable improvements in sensitivity, lending further support to the idea that the presence of feedback on one stimulus inhibits learning on others. Such an inhibitory effect has not been reported previously.

A promising model of perceptual learning known as the Augmented Hebbian Reweighting Model, or AHRM, posits that feedback results from changes in weights between sensory channels and higher-level decision units (J. Liu et al., 2010; Petrov et al., 2005, 2006). According to this model, VPL can occur in the absence of feedback, but feedback can augment learning if it is provided in situations where the visual system is not able to "solve" the present task through purely Hebbian mechanics. The AHRM elegantly explains much of the complex and seemingly contradictory data in the feedback literature, but the present data are somewhat difficult for the model to explain, at least in its present form. The AHRM conceives of feedback in a facilitative role and thus does not account for inhibitory learning trajectories, as reported here. Data from the AHRM studies suggest that one of the unique benefits of performance feedback is to reduce response bias. The results reported in the present study would in fact be consistent with the opposite conclusion: the presence of feedback for one of two presented directions *increases* response bias (or preference) for that direction. Even so, the deterioration effects reported here are inconsistent with a simple perceptual preference or response bias. It is worth keeping in mind that the AHRM studies employ a methodology significantly different from the one used here. Those studies used discrimination tasks (not detection), manipulated the noise contexts of stimuli (here we manipulated the signal components), and alternated task stimulus types in large blocks (the present study randomly interleaved different trial types). Incorporating the results of the present study into the AHRM, or vice versa, presents a promising avenue for future research.

Conclusions

Here we have shown that knowledge of performance accuracy (feedback) stabilizes associated visual perceptual learning and makes it robust against the effects of interference and deterioration. However, this feedback-associated stabilization also inhibits the learning of unpaired stimuli presented during the same training sessions. Without feedback, all presented stimuli show evidence of learning, though this learning is unstable. Stabilization occurs irrespective of the effect size of learning and does not generalize to orthogonal stimulus types. The present research suggests a complex relationship between the time course of visual learning, length of training, and the probe stimuli that are used to test learning. The psychophysical methods used here, such as providing feedback and exposing variations of trained stimuli, are ubiquitous in the field. As such, it is beneficial for researchers to be aware of the epiphenomenal effects and potential confounds introduced along with these common methods.

Acknowledgments

This study was supported by NIH grant R01EY019466 to TW.

Commercial relationships: none.

Corresponding author: Takeo Watanabe.

Email: takeo@bu.edu.

Address: Department of Psychology and the Program of Neuroscience, Boston University, Boston, MA, USA.

References

- Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790–793.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*(6631), 401–406.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Censor, N., Karni, A., & Sagi, D. (2006). A link between perceptual learning, adaptation and sleep. *Vision Research*, *46*(23), 4071–4074.
- Censor, N., & Sagi, D. (2008). Benefits of efficient consolidation: Short training enables long-term resistance to perceptual adaptation induced by intensive testing. *Vision Research*, *48*(7), 970–977.

- Chubb, C., Lu, Z. L., & Sperling, G. (1997). Structure detection: A statistically certified unsupervised learning procedure. *Vision Research*, 37(23), 3343–3365.
- Dayan, P., & Balleine, B. W. (2002). Reward, motivation, and reinforcement learning. *Neuron*, 36(2), 285–298.
- Diekelmann, S., Büchel, C., Born, J., & Rasch, B. (2011). Labile or stable: Opposing consequences for memory when reactivated during waking and sleep. *Nature Neuroscience*, 14(3), 381–386.
- Doya, K. (1999). What are the computations of the cerebellum, the basal ganglia and the cerebral cortex. *Neural networks*, 12(7-8), 961–974.
- Fahle, M., & Poggio, T. (2002). *Perceptual Learning* (1st ed., p. 455). Cambridge, MA: The MIT Press.
- Furmanski, C. S., & Engel, S. A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. *Vision Research*, 40(5), 473–484.
- Gais, S., Plihal, W., Wagner, U., & Born, J. (2000). Early sleep triggers memory for early visual discrimination skills. *Nature Neuroscience*, 3(12), 1335–1339.
- Herzog, M., & Fahle, M. (1997). The role of feedback in learning a vernier discrimination task. *Vision Research*, 37(15), 2133–2141.
- Herzog, M., & Fahle, M. (1999). Effects of biased feedback on learning and deciding in a vernier discrimination task. *Vision Research*, 39(25), 4232–4243.
- Herzog, M. H., & Fahle, M. (1998). Modeling perceptual learning: Difficulties and how they can be overcome. *Biological Cybernetics*, 78(2), 107–117.
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, 365(6443), 250–252.
- Karni, A., Tanne, D., Rubenstein, B. S., Askenasy, J. J., & Sagi, D. (1994, July 29). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*, 265(5172), 679–682.
- Li, R. W., Klein, S. A., & Levi, D. M. (2008a). Prolonged perceptual learning of positional acuity in adult amblyopia: Perceptual template retuning dynamics. *Journal of Neuroscience*, 28(52), 14223–14229.
- Li, W., Piëch, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651–657.
- Li, W., Piëch, V., & Gilbert, C. D. (2008b). Learning to link visual contours. *Neuron*, 57(3), 442–451.
- Liu, J., Lu, Z.-L., & Doshier, B. A. (2010). Augmented Hebbian reweighting: Interactions between feedback and training accuracy in perceptual learning. *Journal of Vision*, 10(10): 1–14, <http://www.journalofvision.org/content/10/10/29>, doi:10.1167/10.10.29. [PubMed] [Article]
- Liu, Z. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences of the United States of America*, 96(24), 14085–14087.
- Lu, Z.-L., Chu, W., Doshier, B. A., & Lee, S. (2005). Independent perceptual learning in monocular and binocular motion systems. *Proceedings of the National Academy of Sciences of the United States of America*, 102(15), 5624–5629.
- Lu, Z.-L., & Doshier, B. A. (2004). Perceptual learning retunes the perceptual template in foveal orientation identification. *Journal of Vision*, 4(1):5, 44–56, <http://www.journalofvision.org/content/4/1/5>, doi:10.1167/4.1.5. [PubMed] [Article]
- Mednick, S., Arman, A., & Boynton, G. (2005). The time course and specificity of perceptual deterioration. *Proceedings of the National Academy of Sciences of the United States of America*, 102(10), 3881–3885.
- Mednick, S., Nakayama, K., & Stickgold, R. (2003). Sleep-dependent learning: A nap is as good as a night. *Nature Neuroscience*, 6(7), 697–698.
- Mednick, S. C., Nakayama, K., Cantero, J. L., Atienza, M., Levin, A. A., Pathak, N., et al. (2002). The restorative effect of naps on perceptual deterioration. *Nature Neuroscience*, 5(7), 677–681.
- Morishita, H., Miwa, J. M., Heintz, N., & Hensch, T. K. (2010, November 26). Lynx1, a cholinergic brake, limits plasticity in adult visual cortex. *Science*, 330(6008), 1238–1240.
- Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marrett, S., & Ungerleider, L. G. (2007). Activations in visual and attention-related areas predict and correlate with the degree of perceptual learning. *Journal of Neuroscience*, 27(42), 11 401–11 411.
- Newsome, W., & Pare, E. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, 8(6), 2201.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Petrov, A. A., Doshier, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, 112(4), 715–743.

- Petrov, A. A., Doshier, B. A., & Lu, Z.-L. (2006). Perceptual learning without feedback in non-stationary contexts: Data and model. *Vision Research*, 46(19), 3177–3197.
- Pilly, P. K., & Seitz, A. R. (2009). What a difference a parameter makes: A psychophysical comparison of random dot motion algorithms. *Vision Research*, 49(13), 1599–1612.
- Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, 256(5059), 1018–1021.
- Sagi, D. (2010). Perceptual learning in Vision Research. *Vision Research*, 51(13), 1552–1566.
- Sasaki, Y., Nanez, J. E., & Watanabe, T. (2009). Advances in visual perceptual learning and plasticity. *Nature Reviews Neuroscience*, 11(1), 53–60.
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549–553.
- Seitz, A., & Watanabe, T. (2003). Psychophysics: Is subliminal learning really passive? *Nature*, 422(9), 36.
- Seitz, A., Yamagishi, N., Werner, B., Goda, N., Kawato, M., & Watanabe, T. (2005). Task-specific disruption of perceptual learning. *Proceedings of the National Academy of Sciences*, 102(41), 14895.
- Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, 17(2), 148–153.
- Seitz, A. R., Nanez, J. E., Holloway, S., Tsushima, Y., & Watanabe, T. (2006). Two cases requiring external reinforcement in perceptual learning. *Journal of Vision*, 6(9):9, 966–973, <http://www.journalofvision.org/content/6/9/9>, doi:10.1167/6.9.9. [PubMed] [Article]
- Shadmehr, R., & Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. *Science*, 277(5327), 821–825.
- Shibata, K., Yamagishi, N., Ishii, S., & Kawato, M. (2009). Boosting perceptual learning by fake feedback. *Vision Research*, 49(21), 2574–2585.
- Stickgold, R., James, L., & Hobson, J. A. (2000). Visual discrimination learning requires sleep after training. *Nature Neuroscience*, 3(12), 1237–1238.
- Tsodyks, M., & Gilbert, C. (2004). Neural networks and perceptual learning. *Nature*, 431(7010), 775–781.
- Walker, M. P., Brakefield, T., Hobson, J. A., & Stickgold, R. (2003). Dissociable stages of human memory consolidation and reconsolidation. *Nature*, 425(6958), 616–620.
- Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, 413(6858), 844–848.
- Weiss, Y., Edelman, S., & Fahle, M. (1993). Models of perceptual learning in vernier hyperacuity. *Neural Computation*, 5(5), 695–718.
- Xu, J. P., He, Z. J., & Ooi, T. L. (2010). Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. *Current Biology*, 20(20), 1864–1868.
- Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24(7), 1617–1626.
- Yotsumoto, Y., Sasaki, Y., Chan, P., Vasios, C. E., Bonmassar, G., Ito, N., et al. (2009). Location-specific cortical activation changes during sleep after training for perceptual learning. *Current Biology*, 19(15), 1278–1282.
- Yotsumoto, Y., Watanabe, T., & Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron*, 57(6), 827–833.