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Boosting perceptual learning by fake feedback

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ABSTRACT

How does the brain control its sensory plasticity using performance feedback? We examined this question using various types of fake feedback in perceptual learning paradigm. We demonstrated that fake feedback indicating a larger performance improvement facilitated learning compared with genuine feedback. Variance of the fake feedback modulated learning as well, suggesting that feedback uncertainty can be internally evaluated. These results were explained by a computational model which controlled the learning rate of the visual system based on Bayesian estimation of performance gradient incorporating an optimistic bias. Our findings suggest that sensory plasticity might be controlled by high-level cognitive processes.

1. Introduction

Sensitivity in various modalities, such as vision, improves after extensive training (Fahle, 2005; Gilbert, 1994; Karmarkar & Dan, 2006; Seitz & Dinse, 2007). This 'perceptual learning' enables us to adapt to new sensory environments. Psychophysical studies of perceptual learning in vision have shown that improvements are often specific to stimulus attributes used in training (e.g., orientation, spatial frequency, and motion direction; Karni & Sagi, 1993; Watanabe et al., 2002). This finding suggests that the neural locus of perceptual learning may lie in the early stages of the visual processing (i.e., the visual cortex). Indeed, neuroimaging studies have provided evidence in support of this proposition (Mukai et al., 2007; Schoups, Vogels, Qian, & Orban, 2001; Yotsumoto, Watanabe, & Sasaki, 2008).

Although the neural locus of perceptual learning could be found in the visual cortex, it has been reported that the learning can be modulated by some cognitive factors. These factors include selective attention (Karni & Sagi, 1993; Li, Piech, & Gilbert, 2004), successful recognition of a concurrent task target (Seitz, Lefebvre, Watanabe, & Jolicoeur, 2005), and performance feedback (Herzog & Fahle, 1997; Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006). These findings suggest that high-level cognitive processes as well as low-level sensory inputs can impact on perceptual learning (Seitz & Watanabe, 2005; Yotsumoto & Watanabe, 2008).

1.1. Role of performance feedback in perceptual learning

We constantly adapt to new environments, and an appropriate learning strategy (e.g., controlling learning rate) can facilitate sensory adaptation. Utilizing performance feedback is one way of evaluating whether a current learning strategy is appropriate. Herzog and Fahle proposed a computational model that describes how the performance feedback guides perceptual learning (Herzog & Fahle, 1997; Herzog & Fahle, 1998). In their model, the performance feedback is utilized as a signal to control unsupervised learning in the visual system, not as a direct teaching signal for a task. A similar idea has been proposed in theoretical studies of learning using neural networks (Bishop, 1995; Vogl, Mangis, Rigler, Zink, & Alkon, 1988). According to this theory, the speed of weight update (learning rate) is proportional to the recent performance gradient. That is, the learning rate is set large while performance keeps improving. Information regarding the performance gradient is particularly useful for the efficient control of learning rates in new environments (Bishop, 1995).

Although using performance gradient might be an efficient way to control sensory plasticity, the question of how it is obtained remains unanswered. Performance feedback inherently contains uncertainty because performance fluctuates over time, and performance is measured over a limited number of trials. Thus, the overall performance gradient cannot be precisely calculated by observing performance feedback alone. Rather, performance feed-

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back can only be used to estimate the performance gradient. To deal with the uncertainty inherent in performance feedback, it is necessary to extend existing models in a probabilistic manner.

1.2. Cognitive bias on performance feedback

Performance feedback acts as a teaching signal for a task and can also affect the learner's emotional status (O' Leary & O' Leary, 1977). Giving accurate feedback is not always the most effective way to maximize a person's learning. Very complex interactions exist between performance feedback and learners' psychological states (Kluger & DeNishi, 1996; Schunk, Pintrich, & Meece, 2008). Studies in educational psychology have demonstrated that people exhibit cognitive biases in response to performance feedback. For example, people tend to undervalue performance feedback if it is worse than they expected, showing an optimistic 'self-serving bias' (Alloy & Abramson, 1979; Sedikides & Campbell, 1998). In addition, a neuroimaging study showed that cortical responses to positive and negative performance feedback are different even if the information contained in the feedback is identical (van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). This cognitive bias in response to performance feedback might affect perceptual learning processes.

1.3. Objectives

To investigate the role of performance feedback in perceptual learning and the mechanisms underlying it, we generated fake feedback and tested whether its manipulation could modulate perceptual learning. Several previous studies found no effect of fake feedback in perceptual learning (Herzog, Ewald, Hermens, & Fahle, 2006; Herzog & Fahle, 1997, 1999). However, in these studies, the gradient of the fake performance feedback was not manipulated. If the brain controls sensory plasticity based on a recent performance gradient estimated from observed performance feedback, it is possible that manipulating the gradient of the predefined fake feedback could affect perceptual learning. In addition, we developed a computational model of feedback effects on perceptual learning. Simulation results were compared with behavioral results to verify the model.

In this study, we show that the fake performance feedback actually modulates perceptual learning with a same/different task using two complex gratings. In psychophysical experiments, the fake feedback indicating a larger performance improvement facilitated learning compared with genuine feedback. Modulating the variance of the fake feedback also affected learning. On the other hand, the fake feedback generated based on smaller performance gradient had no effect on learning compared with the genuine feedback. All subjects reported that they were not aware of the fake feedback. This implies that the learning was implicitly controlled by the fake feedback. A computational model that we proposed successfully supported this idea. The model controls a learning rate of a visual system based on two processes: Bayesian estimation of performance gradient and optimistic bias against worse feedback compared to expectation. Our findings suggest that top–down control signals may modulate sensory plasticity in the brain, and that perceptual learning can be improved by manipulating performance feedback.

2. Psychophysical experiment

2.1. Methods

2.1.1. Subjects

One hundred and seventeen naive subjects, aged 18–29 years, participated in the experiment, which was approved by the ATR Human Subjects Review Committee. All subjects gave informed consent and had normal or corrected-to-normal visual acuity. Each subject was randomly assigned to one of nine conditions: genuine-feedback, no-feedback, self-rating, and six fake-feedback conditions. The data sets of nine subjects were omitted from subsequent analysis because their mean accuracy was not significantly better than chance (0.5; one-sample t-test, $P > 0.05$). In consequence, 12 subjects participated in each condition.

2.1.2. Stimulus and procedure

We used a same/different task using complex gratings developed by Fiorentini and Berardi (1980) and Fiorentini and Berardi (1981) (Fig. 1a). Previous studies using these stimuli have shown that performance improvements were specific to the orientation and spatial location of the stimuli (Fiorentini & Berardi, 1980, 1981), and that neural modulations can be observed in early visual cortex during learning (Mukai et al., 2007). Subjects maintained central fixation (a white point [20 cd m^{-2}] on a 1° diameter black

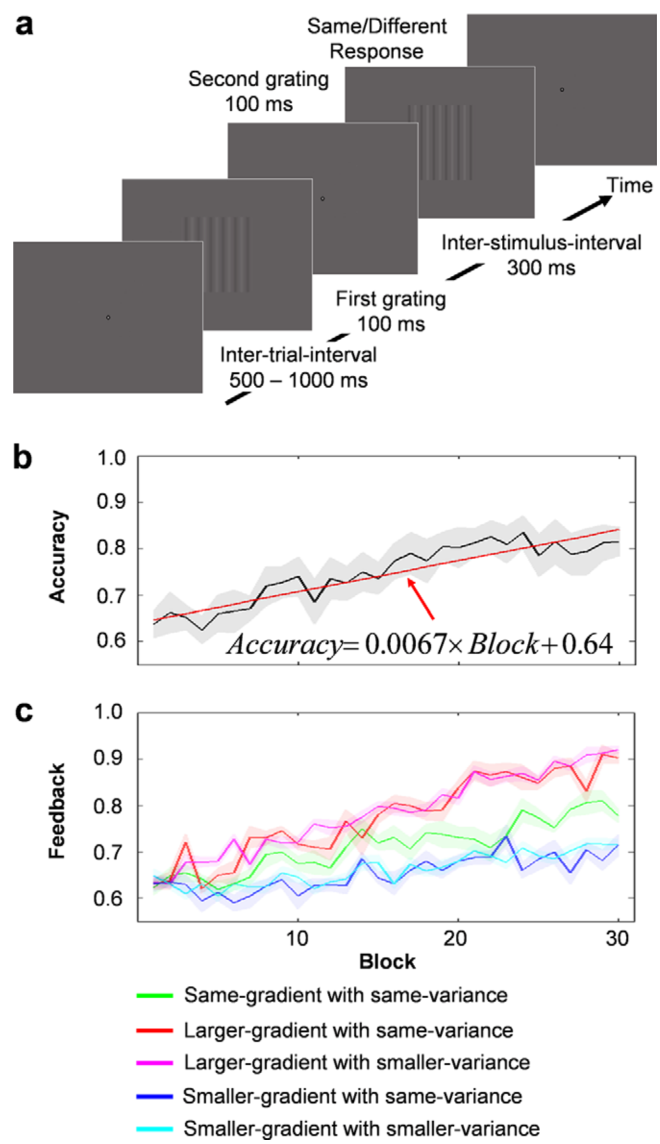

Fig. 1. Experimental design. (a) Same/different task for two gratings. Subjects were asked to report whether two gratings were the same or different. (b) Time-course of mean accuracy across 12 subjects in genuine-feedback condition (black) with a regression line (red) (gray shade reflects s.e.). (c) Time-courses of mean feedback across 12 subjects used in fake-feedback conditions (colored shades reflect s.e.). Each color represents each different condition.

circle [0.2 cd m^{-2}]) throughout each block of trials. The background color was gray and luminance was 10 cd m^{-2}. After the presentation of two gratings, subjects were asked to report whether the gratings were the same or different.

Two types of complex gratings were used. They consisted of the sum of two sinusoids of spatial frequency f and $3f$, and contrast c_1 and c_2. Two grating types differed only in the contrast c_2. The contrast pattern of the grating s at each retinal position (x,y) was calculated by

$$s(x,y) = c_1 \sin(fx\cos\theta + fy\sin\theta) + c_2 \sin(3fx\cos\theta + 3fy\sin\theta),$$

where f represents spatial frequency (0.5 cycles/deg), and θ represents spatial orientation. The contrast c_1 was always 0.4 while c_2 was randomly chosen from 0.13 or 0.20 for each trial. These contrasts were kept constant across trials/subjects and were predetermined using subjects who did not participate in the main experiments to yield an accuracy score of approximately 0.65 without learning. Horizontal gratings ($\theta = 0$) were presented to half of the subjects, and vertical gratings ($\theta = \pi/2$) were presented to the other half. The stimuli were generated using VSG2/5 graphics board (Cambridge Research Systems, Rochester, UK).

Before the experiment, each subject received detailed instructions about the task procedure and a few tens of practice trials. To ensure the practice did not affect learning in the subsequent main experiment, gratings that consisted of only one sine wave were used for the practices. It has previously been shown that exposure to this type of grating for this number of trials did not lead to learning (Fiorentini & Berardi, 1981), so no learning transfer to the main experiment would be expected. The main experiment comprised 30 blocks of trials and each block contained 40 trials. The experiment lasted roughly 1 h including an intermission (at least 15 s) between blocks. After each block, performance feedback informing subjects about the accuracy of the previous 40 trials was presented on a computer display.

2.1.3. Defining a basic learning tendency

In the genuine-feedback condition, subjects received genuine feedback (actual accuracy) after each block of trials. We defined a basic learning regression line for the time-course of the mean accuracy across subjects in this condition as a basic learning tendency. A basic learning regression line was obtained with a gradient $a = 0.0067$ and an intercept $b = 0.64$ (Fig. 1b). Fake feedback for the other group of subjects was generated on the basis of this regression line.

2.1.4. Fake-feedback conditions

Fake feedback was generated by manipulating the basic learning regression line obtained in the genuine-feedback condition, to produce five fake feedback conditions that were defined by three levels of gradient (same, larger, and smaller) and two levels of noise variance (same and smaller; Fig. 1c). Performance improvement in the same/different task was measured under each condition. Note that the same-gradient condition was tested with only the same noise variance. The fake feedback was generated with a gradient depending on the condition and the intercept b (0.64) with additional Gaussian noise with variance σ^2. For the same-gradient condition, the gradient was the same ($a = 0.0067$, Fig. 1c; a green line) as the basic learning regression line. For the larger-gradient conditions, the gradient was set larger ($a = 0.0097$, Fig. 1c; reddish lines), and for the smaller-gradient conditions, the gradient was set smaller ($a = 0.0037$, Fig. 1c; bluish lines) compared with the basic learning regression line. We also manipulated the noise variance (uncertainty). For the same-variance conditions, the noise variance was equalized to the mean squared error between individual accuracy time-course and its regression line across subjects/blocks in the genuine-feedback condition ($\sigma^2 = 0.0065$). For the smaller-variance conditions, the noise variance was halved ($\sigma^2 = 0.0065/2$). Across blocks, no significant autocorrelation was observed in the time-course of the squared error. To verify a proposed computational model, we also conducted a negative-gradient with same-variance condition ($a = -0.0067$, $b = 0.84$, $\sigma^2 = 0.0065$). Thus, with the addition of this negative-gradient condition, there were six fake-feedback conditions in total in the psychophysical experiments. In each fake-feedback condition, subjects received the predefined fake feedback regardless of their actual task performance (accuracies).

2.1.5. No-feedback conditions

In the no-feedback condition, subjects did not receive any feedback after each block. In the self-rating condition, subjects did not receive any feedback and were asked to guess their accuracies after each block using two buttons to adjust a number (ranging from 0% to 100%, step by 2.5%) presented at the center of a display.

2.1.6. Calculating sensitivity in the same/different task

In the same/different task, accuracy could vary based on subjects' perceptual sensitivity d' and a decision criterion λ. Because perceptual learning is regarded as a change in perceptual sensitivity rather than a change in the decision criterion (Karmarkar & Dan, 2006; Seitz & Dinse, 2007), we examined statistics of d' within and between the experimental conditions.

Signal detection theory (SDT) enables us to calculate the perceptual sensitivity d' and the decision criterion λ separately when subjects attempt to detect a signal in a noisy environment (Wickens, 2001). SDT assumes that the strength of sensory and cognitive inputs is a continuous variable, and generates an internal distribution of sensory responses. For the simplest case (e.g., a detection task), there are two distributions: one for noise and one for signal with noise. The hypothetical internal response distributions could follow a Gaussian distribution with means of 0 (noise) and d' (signal with noise), and equal variances. A subject could set the solution to divide the strength axis into two regions (e.g., "yes" vs. "no" detected) with a criterion λ. Errors arise when these two distributions overlap. This process corresponds to a log posterior ratio test when all stimuli are presented in equal probability.

In the case of the current same/different task, an sensory response could be replaced with a difference between two sensory responses evoked by two observations according to the 'differencing model' (Noreen, 1981). Underlying distributions in this model are three Gaussian distributions; the same distribution for $\langle g_1\ g_1 \rangle$ and $\langle g_2\ g_2 \rangle$, and the different distributions for $\langle g_1\ g_2 \rangle$ and $\langle g_2\ g_1 \rangle$ (g_1 is grating 1 and g_2 is grating 2) with means of 0, $-d'$, and d', respectively (supplementary Fig. 1a). The decision rule is to respond "different" whenever the observed difference is extreme, with a criterion λ, in either a positive or a negative direction. Using this model, λ is calculated by

$$\lambda = \phi^{-1}(p_{same}),$$

where p_{same} is the correct ratio for the "same" stimuli in one block and ϕ is a cumulative Gaussian distribution. d' is calculated by

$$d' = \lambda - \phi^{-1}(p_{different}),$$

where $p_{different}$ is the correct ratio for the "different" stimuli in one block (supplementary Fig. 1b) (Macmillian & Creelman, 1991).

2.2. Results

2.2.1. Learning results

Here, the effects of blocks, experimental conditions, and interactions between these factors on the mean d' across subjects were examined using statistical tests. In the genuine-feedback condition, the mean d' across subjects significantly improved in block 30 compared with block 1 (Fig. 2d; two-sample paired t-test, $P = 0.001$). Even when no feedback was given (no-feedback condition), the mean d' across subjects significantly improved in block 30 compared with block 1 (Fig. 2d; two-sample paired t-test, $P = 0.0018$). No significant difference was observed in the time-course of the mean d' across subjects between the genuine- and no-feedback conditions (two-way factorial ANOVA, $P = 0.0728$).

In the two larger-gradient conditions, we found that fake performance feedback has significant effects on learning. In the larger-gradient with same-variance condition, the time-course of the mean d' across subjects was significantly higher than that in the genuine-feedback condition (Fig. 2e; two-way factorial ANOVA, $P < 0.00001$). Further, the time-course of the mean d' across subjects improved in the larger-gradient with smaller-variance condition compared with the larger-gradient with same-variance condition (Fig. 2e; two-way factorial ANOVA, $P = 0.00005$). Indeed, the mean d' across subjects in block 30 was significantly different between the genuine-feedback, larger-gradient with same-variance, and larger-gradient with smaller-variance conditions (Fig. 2e; one-way factorial ANOVA, $P = 0.0318$). No interaction between factors of the three conditions and blocks was observed (two-way factorial ANOVA, $P > 0.52$).

In contrast, in the following three comparisons, we found no significant effects of fake performance feedback on learning. In the same-gradient with same-variance condition, the time-course of the mean d' across subjects was not significantly different from that in the genuine-feedback condition (Fig. 2d; two-way factorial ANOVA, $P = 0.7581$). This suggests that matching feedback to actual accuracy for each individual block is not important for learning. The gradient and noise variance of the feedback, however, did appear to have important effects on learning. Further, no significant difference was observed between the smaller-gradient with same-variance, the smaller-gradient with smaller-variance, and the genuine-feedback conditions (Fig. 2f; two-way factorial ANOVA, $P > 0.1898$). No interaction between factors of the three conditions and blocks was observed (two-way factorial ANOVA, $P > 0.96$) (see supplementary Figs. 2–7 for individual data in each feedback condition).

The mean d' across subjects in block 1 did not differ across all conditions (one-way factorial ANOVA, $P = 0.1717$). This confirms that the obtained conditional differences in the psychophysical experiments were not a result of initial differences in sensitivity between conditions.

2.2.2. Correlation between actual accuracy and feedback

To examine the relationship between actual accuracy and feedback, we calculated correlation coefficients between actual accuracy and performance feedback (see Fig. 3 for typical subject data and Table 1 for the group mean for each condition). In each panel of Fig. 3, each circle represents actual accuracy/feedback values for each block. For the five fake-feedback conditions, the mean correlation coefficient was 0.3095 ± 0.0312 (mean ± s.e. for 60 subjects). Note that if the fake feedback was similar to the real accuracy, the correlation coefficients should be close to 1.0. The results show that the fake feedback given to each subject was not closely related to the actual accuracy for each block, confirming that the fake feedback did not provide subjects with information about their actual accuracy.

2.2.3. Post-experiment interview

To determine whether subjects noticed the inaccuracy of the fake feedback, after the experiment, we asked the subjects in the conditions with the performance feedback the following questions: (1) did you notice anything about the experiment? (yes/no), and, if yes, (2) what did you notice? (free report). Seventeen out of 84 subjects answered "yes" to the first question. Further, 5 out of 17 subjects mentioned that they felt some discrepancies between the observed feedback and expected accuracies. However, two of these subjects were in the genuine-feedback condition, illustrating

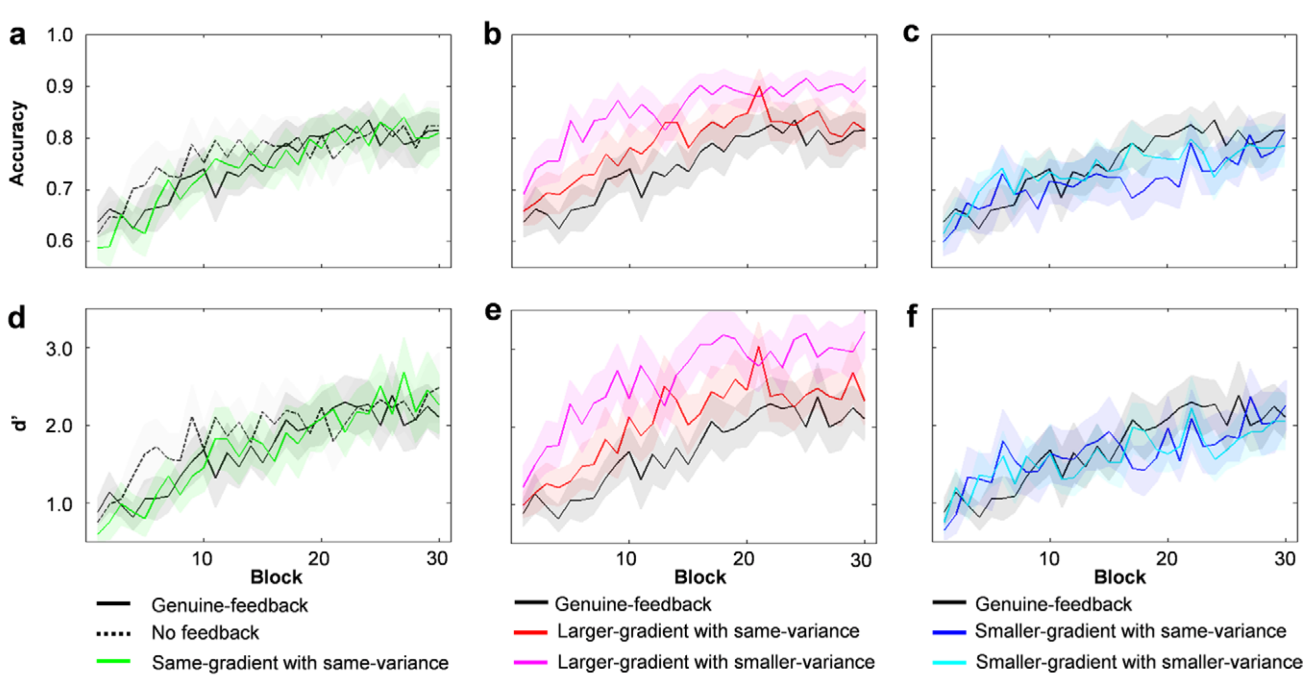

Fig. 2. Learning results in psychophysical experiments. Top panels show the accuracy results, and bottom panels show results of d'. (a) Time-courses of mean accuracy across 12 subjects in genuine-feedback, no-feedback, and same-gradient with same-variance conditions (colored shades reflect s.e.). (b) Time-courses of mean accuracy across 12 subjects in genuine-feedback, larger-gradient with same-variance and larger-gradient with smaller-variance conditions (colored shades reflect s.e.). (c) Time-courses of mean accuracy across 12 subjects in genuine-feedback, smaller-gradient with same-variance, and smaller-gradient with smaller-variance conditions (colored shades reflect s.e.). (d–f) Time-course of mean d' across 12 subjects in each condition (colored shades reflect s.e.).

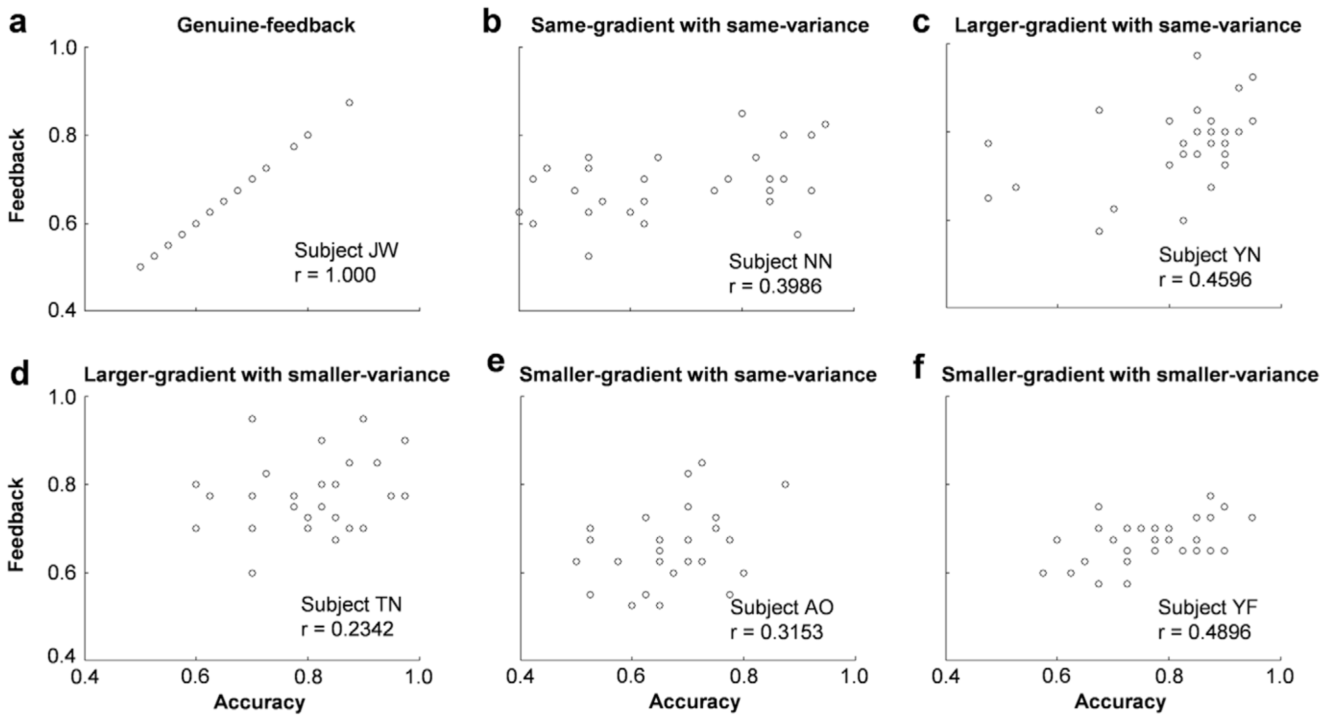

Fig. 3. Correlation between actual accuracies and fake feedback given to subjects. (a–f) Scatter plot for actual accuracy and fake feedback. Each point represents each block, and data are shown for 30 blocks for a representative subjects in each condition. Correlation coefficient (r) is presented in each panel.

Table 1
Correlation coefficient between actual accuracy and fake feedback in each condition.

Condition	Mean ± s.e.
Genuine-feedback	1 ± 0
Same-gradient with same-variance	0.3379 ± 0.0573
Larger-gradient with same-variance	0.3824 ± 0.0764
Larger-gradient with smaller-variance	0.4316 ± 0.0747
Smaller-gradient with same-variance	0.2206 ± 0,0428
Smaller-gradient with smaller-variance	0.1749 ± 0.0723

that a feeling of discrepancy was not specific to the subjects who received the fake feedback. Three subjects reported that they did not notice the fake feedback even after they were told that it was fake. This suggests that all subjects received the fake feedback in the same way as the real genuine feedback, and that the fake feedback affected learning implicitly rather than explicitly.

2.3. Summary and discussion

The psychophysical experiments revealed the following: first, learning occurred even without performance feedback (Fig. 2d). Second, the learning pattern in the genuine-feedback condition did not differ from that in the no-feedback condition (Fig. 2d). Third, when subjects received fake but larger-gradient feedback after each block, their learning was facilitated compared with the genuine-feedback condition (Fig. 2e). Fourth, even using the same larger-gradient, reducing noise variance of the fake feedback led to further improvement (Fig. 2e), suggesting that the feedback uncertainty also affected learning. Fifth, there was no evidence that subjects were aware of the inaccuracy of the fake feedback. Finally, smaller-gradient fake feedback led to similar learning compared with when genuine feedback was received (Fig. 2f).

One might argue that differences in subjects' initial attentional status or motivation between groups might lead to the differential learning patterns obtained in this study. Previous studies have reported cases in which subjects' performance was affected by the pre-existing expectations of the experimenters (Peters, 1971; Rosenthal & Jacobson, 1992). However, in this study, all subjects received the same instruction regardless of their conditions. In addition, the mean d' of the first block did not differ across conditions. These factors suggest that there was no initial difference in attentional status or motivation between groups. We believe that our results cannot be explained by the initial differences of subjects' psychological state between groups; rather, the predefined fake feedback for each experimental group implicitly led to differential learning patterns. We speculate that learning rate might be updated from block to block, and it fluctuates over time. In the next section, we constructed computational models to quantitatively test this hypothesis.

3. Simulation experiment

3.1. Computational model

The psychophysical results provided important clues about mechanisms underlying neural control of perceptual learning. First, significant learning was observed even in the no-feedback condition (Fig. 2d). One possible mechanism explaining this finding is that unsupervised learning was taking place in the visual system (Herzog & Fahle, 1998; Weiss, Edelman, & Fahle, 1993). Moreover, these learning processes may be modulated by the various types of fake feedback (Fig. 2d–f). If this is the case, it would be predicted that changing feedback information might lead to different patterns of learning. Therefore, in the current simulation experiments, we assumed that unsupervised learning in the visual system is affected by high-level cognitive processes (Herzog & Fahle, 1998; Seitz & Watanabe, 2005).

Two key observations regarding processes of control in perceptual learning emerged from the psychophysical experiments. One is that learning was dependent on both the gradient and the noise variance of the fake feedback. It has been proposed a computational model that describes how performance feedback guides perceptual learning (Herzog & Fahle, 1998), and possible boosting methods of learning with neural networks (Bishop, 1995; Vogl et al., 1988). In these neural network models, the learning rate is determined by the recent history of performance (performance gradient). That is, improving performance leads to high learning rates. This theoretical framework supports our psychophysical finding that learning was affected by the gradient of the fake feedback. However, it cannot explain why learning was also modulated by the noise variance of the fake feedback. In these neural network models, it is assumed that learners are able to determine actual performance gradients directly from the observed performance feedback. Because learner's performance fluctuates over time, and performance is measured over a limited number of trials, this cannot be the case. The performance feedback inherently contains uncertainty, and the performance gradient is necessarily estimated from the observed feedback, taking this uncertainty into account.

One simple and general model to embody this concept is the Kalman filter (online Bayesian estimation; Kalman, 1960). The Kalman filter estimates a distribution of the performance gradients (posterior) based on prediction of the performance gradient (prior) and observable feedback gradient (likelihood) in a Bayesian manner. When the noise variance of the observed performance feedback is small, the performance feedback becomes more dominant in the estimation of the performance gradient; when the noise variance is large, the prediction of the performance gradient becomes more dominant.

The other key finding from the psychophysical experiments is that there was no effect of the smaller-gradient feedback on learning. In the larger-gradient conditions, learning was facilitated compared with in the genuine-feedback condition (Fig. 2e). Smaller-gradient fake feedback, however, had no effect on learning (Fig. 2f). This suggests that learning control process may respond with an optimistic bias to the performance feedback, consistent with several psychological studies (Alloy & Abramson, 1979; Sedikides & Campbell, 1998). In general, these studies report that when feedback is better than subjects expect, they tend to attribute the discrepancy to their ability or effort. On the other hand, when feedback is worse than expected, they tend to blame the discrepancy on other people or task settings, and try to minimize effects of the feedback (self-serving bias). We contend that subjects in the smaller-gradient feedback conditions may believe the observed performance feedback was worse than expected and became insensitive to it.

3.2. Methods

3.2.1. Visual system

Our computational model consisted of three systems: visual, decision, and learning rate control systems (Fig. 4a). For the visual system, we used a modified version of the hyper basis function network (Weiss et al., 1993). The visual system has 16 basis functions, and each of these has different tuning for spatial frequencies (f = 0.5, 1.0, 1.5, and 2.0 cycles/deg) and orientations ($\theta = 0°$, 45°, 90°, and 135°). Neurons showing similar properties of these basis functions have been reported in the lower visual cortices of monkeys (De Valois, Albrecht, & Thorell, 1982) and cats (Issa, Trepel, & Stryker, 2000; Shapley & Lennie, 1985). The response of each basis function H_i was calculated by

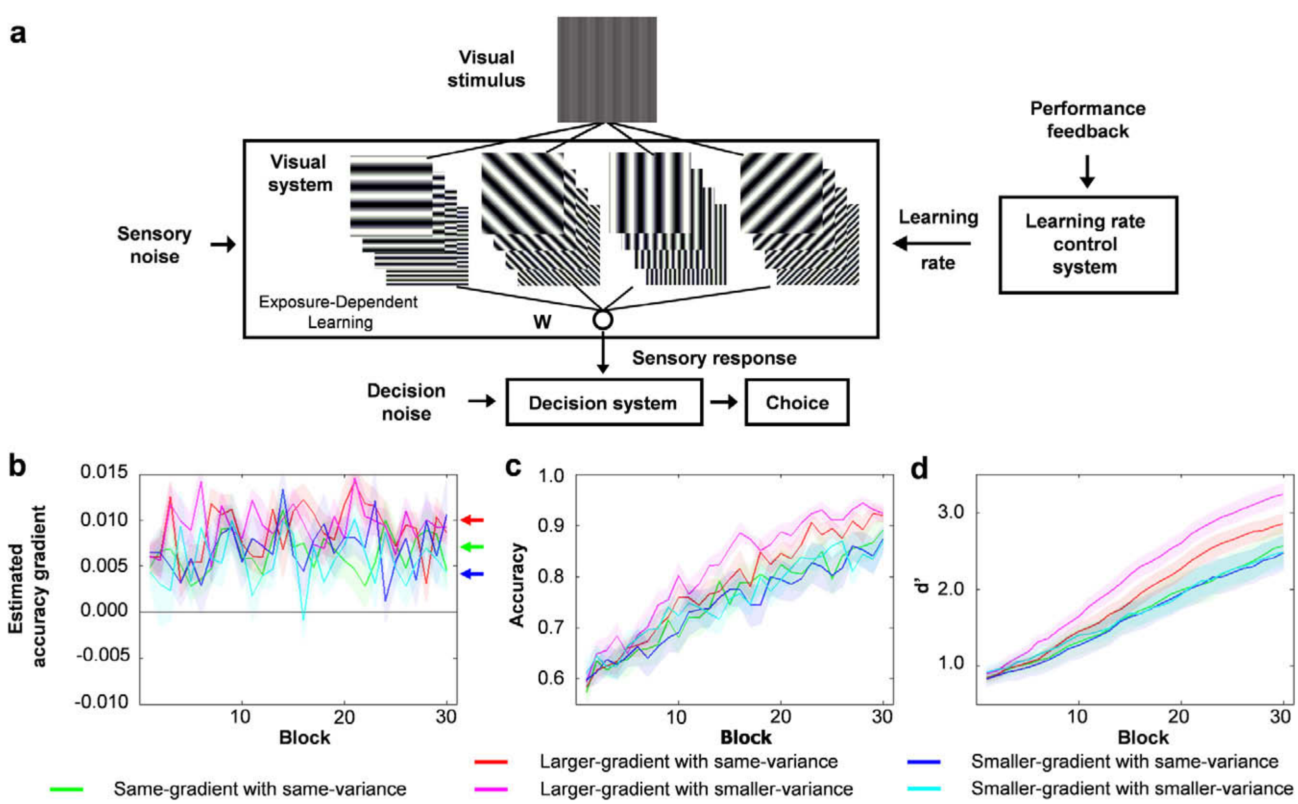

Fig. 4. Computational model and simulation results. (a) Model architecture. Visual system transforms visual stimuli (gratings) into sensory responses using basis functions. Weights between basis functions and output unit are updated based on unsupervised learning rule. Decision system performs same/different task based on sensory responses of visual system. Learning rate control system determines learning rate of visual system using performance feedback after each block (see text for more details). (b) Time-course of mean estimated accuracy gradient across 12 runs in each condition using a model with Kalman filter and self-serving bias. Red, green, and blue arrows show actual feedback gradient for larger-gradient (0.0097), same-gradient (0.0067), and smaller-gradient (0.0037) conditions, respectively (colored shades reflect s.e.). (c) Time-course of mean accuracy of decision system across 12 runs in each condition (colored shades reflect s.e.). (d) Time-course of mean d' of decision system across 12 runs in each condition (colored shades reflect s.e.).

$$H_i = \sum_{x,y} RF_i(x,y)I(x,y), \quad (1)$$

where RF_i represents the receptive field of ith basis function and I is the spatial contrast pattern of a presented grating. RF_i at each retinal position (x, y) was given by

$$RF_i(x,y) = \sin(fx\cos\theta + fx\sin\theta).$$

The output unit calculated a weighted sum of the responses of the basis functions. Thus, sensory response R of the visual system for one visual stimulus was calculated by

$$R = \sum_i \{w_i(H_i + \varepsilon_i)\}, \quad (2)$$

where w_i represents the weight between the output unit and ith basis function. ε_i is sensory noise in the basis function, reflecting spontaneous activity of neurons, and obeys a Gaussian distribution with a mean at zero and variance σ_s^2 (Weiss et al., 1993). We confirmed that similar simulation results were obtained when the sensory noise obeyed a Poisson distribution (signal-dependent noise). The weight w_i was updated according to the response of the basis function (exposure-dependent learning; Weiss et al., 1993) by

$$w_i = w_i + \alpha w_i \quad \text{if } H_i + \varepsilon_i > T, \quad (3)$$

where α is the learning rate of the visual system and T represents the learning threshold for the response of the basis function; α and T were common to all basis functions. Before learning, w_i is similar between all the basis functions. During learning, some of the basis functions tuned to the presented gratings generate strong sensory responses, and therefore, win the large weights. As a consequence, a limited number of the basis functions have larger weights while the others have small weights. This bias reduces noise from the basis function which is not tuned to the presented gratings, and therefore, leads to a stable sensitivity improvement of the visual system (Dosher & Lu, 1998). We confirmed that other unsupervised learning rules led to similar learning results. For example, similar results were obtained from

$$w_i = w_i + \alpha w_i \quad \text{if } H_i + \varepsilon_i > T, \text{ otherwise } w_i = w_i - \alpha w_i.$$

3.2.2. Decision system

The decision system performed the same/different task for two successive grating presentations. The system works on the difference Y between two sensory responses, R_1 and R_2, evoked by the first and second grating presentations, respectively. Y was calculated by

$$Y = R_2 - R_1 + \zeta, \quad (4)$$

where ζ represents noise in the decision system reflecting spontaneous activity of a neuron and obeys a Gaussian distribution with a mean at zero and variance $\sigma^2_{decision}$ (Weiss et al., 1993). The system compares the decision criterion λ and the absolute value of Y, and responds "different" when the absolute value of Y is larger than λ. This process is the same as SDT described in the Section 2.1.6. Combining Eqs. (1)–(4), perceptual sensitivity d' of the decision system was calculated by

$$d' = \frac{|\sum_i w_i \sum_{x,y} RF_i(I_2 - I_1)|}{\sqrt{\sigma^2_{decision} + \sum_i w_i^2 \sigma_s^2}}.$$

3.2.3. Learning rate control system

The learning rate control system determined the learning rate of the visual system based on the estimation of the performance gradient. As mentioned earlier, the performance feedback in this study inherently contains uncertainty. To deal with this uncertainty, we used the Kalman filter (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006; Kalman, 1960). Using the Kalman filter, we estimated the performance gradient by considering mechanisms underlying changes in the performance gradient over time (model for state transition process) and how the performance feedback contains the noise (model for observation process). We assumed that the learning rate of the visual system is proportional to this estimated performance gradient (Bishop, 1995). According to the current task settings, the observation (accuracy feedback) was given after each block of 40 trials. Thus, the learning rate of the visual system is updated after each block. However, this system can update the learning rate at arbitrary times (e.g., after each trial) when performance feedback is given.

In our Kalman filter model, the state transition process was defined by

$$s_{t+1} = s_t + \xi_t,$$

where s_t represents the prediction of accuracy gradient between block $t-1$ and t, and ξ_t represents system noise obeying a Gaussian distribution with a mean at zero and variance σ_d^2. The observation process was defined by,

$$x_t = s_t + \eta_t$$

where x_t represents the change in observed accuracy feedback between block $t-1$ and t, and η_t represents observation noise obeying a Gaussian distribution with a mean at zero and variance σ_d^2. After the accuracy feedback, estimated accuracy gradient μ and its variance ρ^2 were calculated by

$$\mu_t^{post} = \mu_t^{pre} + K_t(x_t - \mu_t^{pre}),$$

$$\rho_t^{post2} = (1 - K_t)\rho_t^{pre2}.$$

The heart of this procedure is an error-driven learning rule that is the same as the temporal-difference or other delta-rule methods: the difference is the additional tracking of uncertainty ρ^2, which determines the time-dependent coefficient K (Kalman gain), given by

$$K_t = \frac{\rho_t^{pre2}}{\rho_t^{pre2} + \sigma_o^2}.$$

When the noise variance of the feedback σ_o^2 is small, Kalman gain gets close to one. The learning rate control system then emphasizes the observed accuracy gradient in the estimation. The prediction of μ and ρ^2 in the next block was given by

$$\mu_{t+1}^{pre} = \mu_t^{post},$$

$$\rho_{t+1}^{pre2} = \rho_t^{post2} + \sigma_d^2.$$

To reproduce the psychophysical results in the two smaller-gradient conditions (Fig. 2f), we assumed a lower bound κ for the estimated accuracy gradient (self-serving bias). The learning rate basically increases linearly as a function of the estimated accuracy gradient. However, when the estimated accuracy gradient μ_t^{post} is smaller than κ, the learning rate control system temporally regards the observation noise σ_o^2 as large and replaces μ_t^{post} with the lower bound κ. This bias weakens the effect of the smaller-gradient fake feedback on the learning rate of the visual system. Thus, the learning rate is constant when the estimated accuracy gradient is smaller than the lower bound, and once the estimated accuracy gradient exceeds the bound, the learning rate increases linearly. The self-serving bias can also be defined in a different fashion. Using the difference between the predicted accuracy gradient and the observed accuracy gradient, taking proportional decrease of the effect of performance feedback (K_t) is one example. Even in this case, the basic arguments of the model do not change.

Learning rate α of the visual system in the next block was determined as proportional to the estimated accuracy gradient:

$$\alpha_t = c\mu_t^{pre}. \tag{5}$$

3.2.4. Simulation settings

Using the computational models outlined above, we ran simulations with similar settings to our psychophysical experiments with a total of 30 blocks. Each block comprised 40 trials. For each condition, the simulation was repeated 12 times (30 blocks $\times$ 12 runs) with different initial parameter settings. The fake feedback used in the simulations was identical to that in the psychophysical experiments.

A summary of the model parameters is shown in Table 2. The following model parameters were determined based on the results of the psychophysical experiment: the initial w_i was generated by adding Gaussian noise with a mean at one and variance 0.1 to reproduce the mean (0.81) and variance (0.04) of d' in block 1 of the no-feedback condition. σ_o^2 was equalized to the variance of the feedback gradient in the fake-feedback conditions (0.0134 for the same-variance conditions and 0.0067 for the smaller-variance conditions). σ_d^2 (0.00013) was determined to reproduce the time-course of the mean d' across subjects in the same-gradient with same-variance condition (Fig. 2d). κ (-0.006) was determined to reproduce the time-course of the mean d' across subjects in the two smaller-gradient conditions (Fig. 2f). Initial μ followed a Gaussian distribution whose mean and variance were equalized to the mean accuracy gradient (0.00517) and its variance (0.0000188) in the no-feedback condition, assuming that initial ρ^2 was large enough. c (4.5), the coefficient of μ in Eq. (5), was determined to reproduce the time-course of the mean d' across subjects in the no-feedback condition. The decision criterion λ of the decision system was determined based on the time-course of the mean λ across subjects in the no-feedback condition. σ_s^2 (50) and $\sigma_{decision}^2$ (150) were determined to reproduce the mean d' in block 1 of the no-feedback condition (0.81) with initial w_i T was a free parameter and set to 500. We confirmed that the simulation results barely changed as T ranged from 200 to 600.

Although our model contains the 12 parameters, they were determined using the subset of the psychophysical experiments: namely, the no-feedback condition, same-gradient with same-variance condition, and two smaller-gradient conditions. We did not use the results of two larger-gradient conditions and the negative-gradient condition for the parameter fitting. Thus, in these conditions, the simulation results were predicted rather than explained by the proposed computational model.

In the psychophysical experiments, in the genuine-feedback condition, the time-course of the mean accuracy across subjects over blocks 1–30 was well fitted by a linear regression (Fig. 1b; coefficient of determination = 0.849). For this reason, we used a simple linear equation for the state transition model of the Kalman filter. It is also possible to introduce nonlinearity into the model by considering ceiling effects of learning. This makes the shape of learning curve in the simulation experiments more similar to that in the psychophysical experiments. Even in this case, we can apply the same logic as in case of linear models by making the observation process nonlinear. This would change the arguments of the model only minimally.

3.3. Results

The simulation results showed that the time-course of the mean d' across simulation runs were significantly improved in the two larger-gradient fake-feedback conditions than in the other three conditions: same-gradient with same-variance, smaller-gradient with same-variance, and smaller-gradient with smaller-variance conditions (Fig. 4d; two-way factorial ANOVA, $P < 0.00001$). No significant difference was found among the three other conditions (Fig. 4d; $P > 0.2606$). Further, the mean d' improvement in the larger-gradient with smaller-variance condition was significantly higher than that in the larger-gradient with same-variance condition (Fig. 4d; $P < 0.00001$). Moreover, the results in the genuine- and no-feedback conditions were not significantly different because the genuine feedback, on average, did not affect the estimated accuracy gradient (results not shown). These simulation results showed close agreement with the psychophysical results (compare Fig. 2d–f and Fig. 4d).

3.4. Testing alternative models

We assumed two computational processes in the learning rate control system: the Kalman filter and the self-serving bias (see Sec-

Table 2
Model parameters used in simulation experiments.

	Parameter name	Role	Value	How to determine
Visual system	Mean of initial w_{i}	Initial weights between basis functions and output unit	1	Reproduce mean d' in block 1 of no-feedback condition
	Variance of initial w_{i}	Initial weights between basis functions and output unit	0.1	Reproduce variance of d' in block 1 of no-feedback condition
	σ_s^2	Variance of Gaussian noise of basis function	50	Reproduce mean d' in block 1 of no-feedback condition under initial w_{i}
	T	Learning threshold of basis function	500	Free parameter
Decision system	λ	Decision criterion in each block	Not shown here	Time-course of mean decision criterion in no-feedback condition
	$\sigma_{decision}^2$	Variance of Gaussian noise of decision unit	150	Reproduce mean d' in block 1 of no-feedback condition under initial w_{i}
Learning rate control system	σ_o^2	Variance of Gaussian noise in state transition process	0.00013	Reproduce time-course of mean d' in same-gradient with same-variance condition
	σ_o^2	Variance of Gaussian noise of observation process	0 0134 or 00067	Variance of Gaussian noise in same- or smaller-variance conditions, respectively
	κ	Lower bound of estimated accuracy gradient (self-serving bias)	-0.006	Reproduce two smaller-gradient conditions
	Mean of initial μ	Mean of initial estimated accuracy gradient	0.00517	Mean accuracy gradient in no-feedback condition
	Variance of initial μ	Variance of initial estimated accuracy gradient	0.0000133	Variance of accuracy gradient in no-feedback condition
	c	Coefficient of estimated accuracy gradient to determine learning rate of visual system in next block	4.5	Reproduce time-course of mean d' in no-feedback condition

tion 3.1 and 3.2.3). To evaluate the plausibility of these assumptions, we tested two further alternative models for the learning rate control system: (1) with the Kalman filter and without the self-serving bias, and (2) with neither the Kalman filter nor the self-serving bias.

In the model with the Kalman filter and without the self-serving bias, there was no lower bound of the estimated accuracy gradient ($\kappa = -\infty$). That is, the system did not reduce the effect of the fake feedback even when the estimated accuracy gradient was smaller than the expectation of the system. The simulation results showed that, inconsistent with the psychophysical results, the mean d' improvement in the two smaller-gradient conditions was significantly lower than those in the same-gradient with same-variance condition (Fig. 5c; two-way factorial ANOVA, $P < 0.00001$). This result was due to the estimated accuracy gradient (i.e., learning rate) in the two smaller-gradient conditions being generally smaller than in the same-gradient with same-variance condition (Fig. 5a).

For the model with neither the Kalman filter nor the self-serving bias, there are two alternative processes that may occur instead. First, the learning rate could be constant and not modulated by feedback. In this model, only the prediction of the accuracy gradient affects the learning rate of the visual system. Due to the significant d' improvement in the no-feedback condition, the learning rate should be positive even without performance feedback. This model is identical to the Kalman filter with infinite σ_o^2. However, this model cannot explain the conditional differences in the psychophysical results, because it ignores feedback. Second, the learning rate could be determined only by the feedback. In this model, only the observed accuracy gradient informed by the performance feedback determines the learning rate. Crucially, the Kalman filter requires the prediction of the accuracy gradient, but this model does not. This model is identical to the Kalman filter with infinite σ_d^2. However, no significant difference was observed in the results between the larger-gradient with same-variance and with smaller-variance conditions (Fig. 5f; two-way factorial ANOVA, $P = 0.912$), indicating that this model cannot reproduce the dependency of learning on the noise variance found in the psychophysical results.

These results support the following features of our proposed model: first, the internal evaluation of the feedback uncertainty is necessary to explain the effects of the noise variance on learning. Second, the assumption of the optimistic bias (i.e., a self-serving bias) is necessary to reproduce the lack of effect of the smaller-gradient feedback.

3.5. Model verification

3.5.1. Self-rating condition

Assuming that subjects use a Bayesian strategy in learning, they must have information about their accuracy (a prior distribution) in order to estimate their accuracy gradients. To test this, we conducted an additional psychophysical experiment involving a self-rating condition. In this experiment, after each block of trials, no feedback was given to the subjects, and they were asked to guess their accuracy. Fig. 6 shows the self-rating scores against the actual accuracy for six subjects. The mean correlation coefficient between the self-rating score and the actual accuracy across all subjects ($n = 12$) was significantly higher than zero ($r = 0.2658 \pm 0.0774$, one-sample t-test, $P = 0.0056$). In addition, when all data points were combined ($n = 360$), a significant correlation was obtained ($r = 0.256$, $P < 0.0001$). These results suggest that, at least at the conscious level, subjects are able to predict their accuracy with some degree of uncertainty. This ability may enable subjects to calculate the prior distribution of their accuracy gradient.

3.5.2. Negative-gradient condition

To generalize our proposed model, we conducted additional experiments using fake feedback that was not used in the main experiments, namely negative-gradient fake feedback. The psychophysical results were compared with the model predictions with-

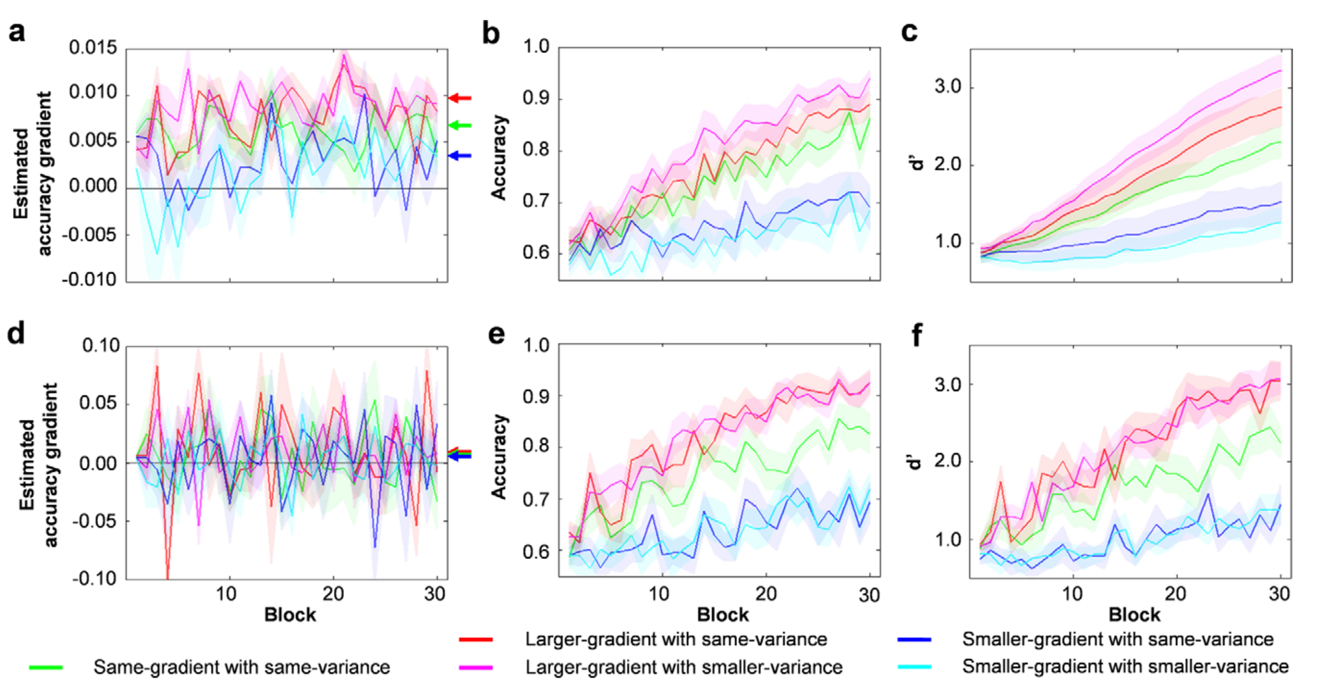

Fig. 5. Simulation results using two alternative models of learning rate control system. Top panels show results with a model including Kalman filter and without self-serving bias, and bottom panels show results with a model that determines learning rate of visual system only by accuracy feedback. (a and d) Time-course of mean estimated accuracy gradient across 12 runs in each condition. Data are shown for five conditions, and red, green, and blue arrows indicate actual feedback gradient for larger-gradient (0.0097), same-gradient (0.0067), and smaller-gradient (0.0037) conditions, respectively (colored shades reflect s.e.). (b and e) Time-course of mean accuracy of decision system across 12 runs in each condition (colored shades reflect s.e.). (c and f) Time-course of mean d' of decision system across 12 runs in each condition (colored shades reflect s.e.).

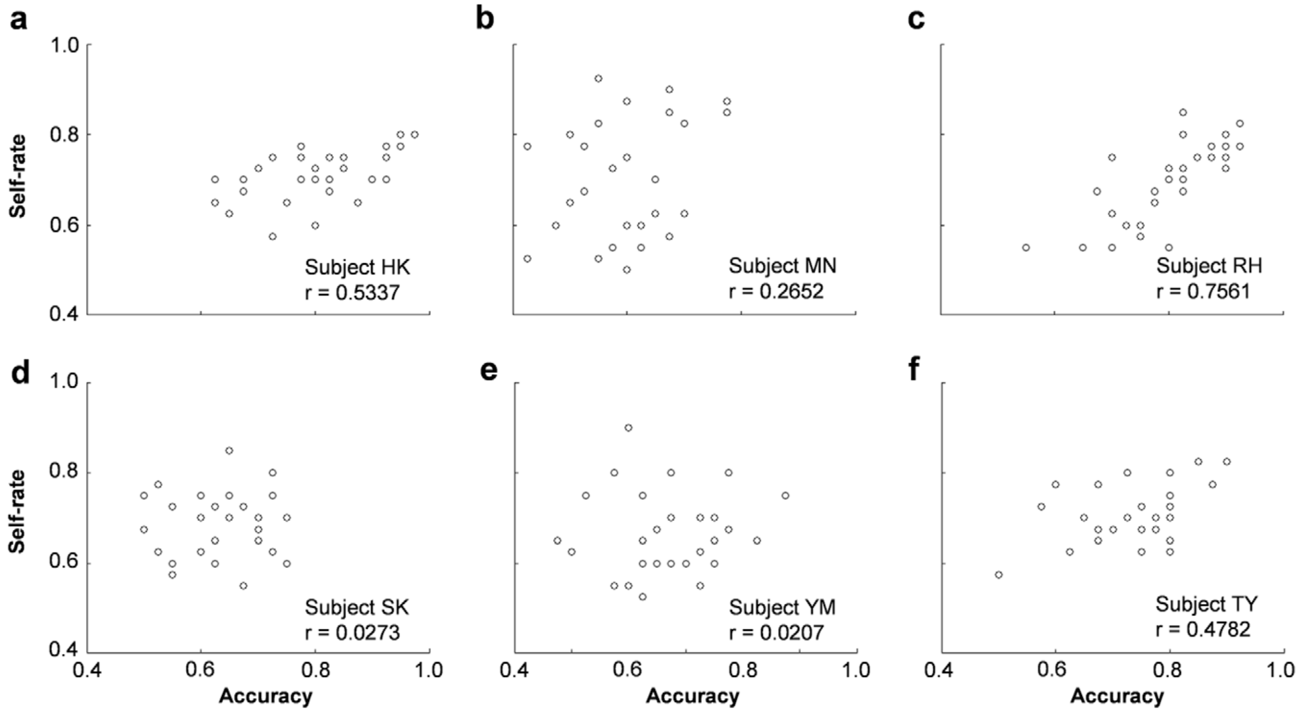

Fig. 6. Correlation between actual accuracies and self-rating scores. (a–f) A scatter plot for self-rating score and actual accuracy. Each point represents each block, and data are shown for 30 blocks for six subjects in self-rating condition. Correlation coefficient (r) is shown in each panel.

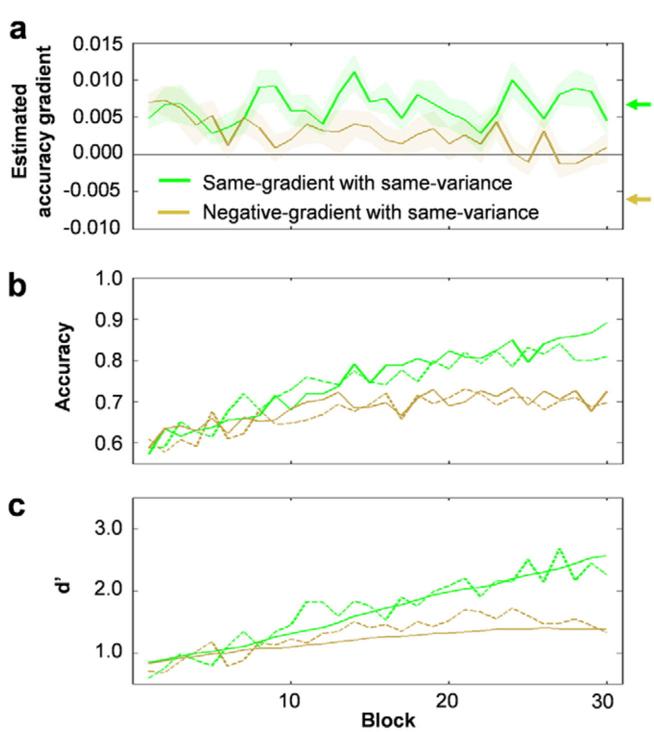

Fig. 7. Comparison between model prediction and psychophysical results. (a) Time-courses of mean estimated accuracy gradient across 12 runs in same-gradient with same-variance (green) and negative-gradient with same-variance (brown) conditions using the model with Kalman filter and self-serving bias (colored shades reflect s.e.). Green and brown arrows show actual feedback gradient used in the experiment for same-gradient with same-variance (0.0067) and negative-gradient with same-variance (−0.0067) conditions, respectively. (b) Time-courses of mean accuracy of decision system across 12 runs in the simulation (solid lines), and time-course of mean accuracy obtained in the psychophysical experiments (broken lines) for two conditions. (c) Time-course of mean d' across 12 runs in the simulation (solid lines), and time-course of mean d' obtained in the psychophysical experiments (broken lines) for two conditions.

out any additional parameter fittings. The self-serving bias weakens the effect of the smaller-gradient feedback, and therefore, no feedback effect on learning was found in the smaller-gradient conditions. On the other hand, the model predicts a significant effect of the performance feedback if the gradient is set to negative because although the self-serving bias weakens the effect, it does not ignore it entirely.

We applied the gradually decreasing feedback (negative-gradient with same-variance condition) to the model with the Kalman filter and the self-serving bias. The simulation results showed that the time-course of the mean d' across simulation runs was significantly lower than in the same-gradient with same-variance condition (Fig. 7c, solid lines; two-way factorial ANOVA, $P < 0.00001$). The estimated accuracy gradient (i.e., the learning rate) was positive in several initial blocks because the initial prediction of the accuracy gradient was positive. However, the learning rate gradually decreased and finally became zero as a result of the negative-gradient feedback (Fig. 7a; brown). Consistent with the model prediction, the results of the psychophysical experiment showed that the time-course of the mean d' across subjects in the negative-gradient with same-variance condition was significantly lower than that in the same-gradient with same-variance condition (Fig. 7c, broken lines; two-way factorial ANOVA, $P < 0.001$). In addition, no significant difference in the time-course of the mean d' across subjects/runs was observed between the model predictions and the psychophysical results (two-way factorial ANOVA, $P = 0.1186$). Moreover, these two time-courses of mean d' were quantitatively similar in the negative-gradient condition (Fig. 7c; coefficient of determination = 0.8341). This additional study shows our model's capability to make predictions in novel conditions, and that the predictions of the model were in agreement with the psychophysical results.

4. General discussion

In this study, we reported four main findings. First, giving fake performance feedback with a larger performance gradient facilitated learning compared with giving genuine feedback. Second, the variance of fake feedback also modulated learning. Third, fake feedback with a smaller performance gradient did not modulate learning. Forth, all subjects were not aware of the inaccuracy of the fake feedback. We speculate that the fake feedback in the larger-gradient conditions might have acted as a form of praise that implicitly facilitated visual perceptual learning. The importance of variance found here implies that feedback uncertainty may be evaluated and utilized in learning. Subjects might have discounted feedback information in the smaller-gradient conditions because it was worse than expected (i.e., a self-serving bias). Simulation results using a computational model supported these conclusions; the results of the simulation and psychophysical experiments studies closely agreed. The current results suggest that perceptual learning in the visual cortex might be controlled by internal evaluation of feedback uncertainty, and affected by an optimistic bias.

A theory of error-driven learning rules such as reinforcement learning and supervised learning cannot account for the psychophysical results observed in this study. These learning theories predict that fake feedback deteriorates learning regardless of the type of fake feedback because this method updates the system's response to minimize an error or maximize a reward (i.e., performance feedback). These predictions are not supported by our results, which found that larger-gradient fake feedback significantly facilitated learning compared with genuine feedback. We proposed a model that uses the performance feedback as a signal to control unsupervised learning in the visual system, not as a direct error or reward signal to the decision system. This model predicts learning facilitation by fake feedback observed in the current psychophysical experiments, suggesting that unsupervised learning mechanisms underlie perceptual learning (Barlow, 1989).

Previous studies in perceptual learning have found fake feedback to alter the decision criterion rather than affecting sensory plasticity (Herzog & Fahle, 1997; Herzog et al., 2006). In their studies, however, the gradient of the fake feedback was not manipulated. Instead, a constant gradient of zero was used for the fake performance feedback. The computational model in our study predicts no effect of the fake feedback under these conditions. Thus, our results are consistent with previous studies.

In accord with previous models (Herzog & Fahle, 1998; Seitz & Watanabe, 2005), in our computational model, plasticity in the visual system is controlled by the cognitive process (i.e., learning rate control system based on the estimated accuracy gradient). Which brain areas are involved in these processes? One possibility is that the locus of both learning and learning control processes is in the visual cortex. A recent physiological study reported that V1 neurons could predict reward timing after repetitive exposure to a stimulus-reward paring (Shuler & Bear, 2006). This result suggests the existence of a reinforcement learning system in the visual cortex. This kind of error-driven learning system could enable neurons in the visual cortex to learn optimal responses to sensory stimuli, minimizing error and/or maximizing reward. However, as discussed before, error-driven learning rules including reinforcement learning cannot explain the fact that the fake feedback facilitated learning compared with the genuine feedback. Thus, a reinforcement learning system in the visual cortex is not an adequate explanation for the current results.

Another possibility is that a locus of learning is in the visual cortex but is controlled by distant cortical areas such as the frontal cortex and basal ganglia. Previous physiological studies have reported that the frontal cortex is involved in a variety of cognitive processes including the calculation of expectation error (Matsumoto, Matsumoto, Abe, & Tanaka, 2007), uncertainty evaluation (Behrens, Woolrich, Walton, & Rushworth, 2007), and self-monitoring (Beer, 2007) including optimistic biases (Sharot, Riccardi, Raio, & Phelps, 2007). In addition, it has been suggested that neuromodulatory projections from the basal ganglia and forebrain influence plasticity in the sensory cortex (Fournier, Semba, & Rasmusson, 2004; Seol et al., 2007). Taken together, these findings suggest that estimation of the performance gradient may involve the frontal cortex, and the basal ganglia and forebrain may subsequently use this information to control the learning rate of the visual cortex.

What is the advantage of manipulating the learning rate based on the recent performance gradient? As mentioned earlier, previous theoretical studies using neural networks have proposed efficient learning methods based on the performance gradient (Bishop, 1995; Vogl et al., 1988). We extended this idea using a probabilistic approach to deal with uncertainty in learner's performance and performance feedback. The learning rate of the visual system, in our model, varies based on both the performance gradient and uncertainty of the performance feedback using Bayesian estimation. Based on research into conditioning in animals, a model has previously been proposed in which the learning rate changes based on the uncertainty of rewards (Dayan, Kakade, & Montague, 2000). This reinforcement learning model resembles our model in many ways, indicating that the Bayesian learning rate control might be a basic and efficient mechanism of both reinforcement and perceptual learning (sensory plasticity) in the brain.

In our proposed model, we assumed that the learning rate control system uses an optimistic bias (i.e., a self-serving bias) to deal with decreases in learning rate. Learning increases the adaptability of neural systems to the environment (Doya, 1999), and Bayesian learning rate control could provide an effective learning framework. However, in a situation with a very low learning rate, Bayesian estimation alone may not be the optimal solution for future survival because it leads near-termination of learning. Therefore, it is unsurprising that the learning rate control system incorporates a self-serving bias in such a situation.

In our computational framework, it seems that a higher learning rate always facilitates learning in the visual system. This raises a question: why does not the learning control system set a maximum learning rate from the beginning of learning? One possible reason is that a very high learning rate prevents the convergence of learning. A second potential reason is that the system may simultaneously control the learning rate of multiple learning systems in the brain. If this is the case, the effects of setting a maximum learning rate might not be optimal for other systems. For these reasons, setting a maximum learning rate before observing the performance gradient may not be an efficient strategy.

Our findings have important implications regarding the mechanisms controlling sensory plasticity in the brain. Our results suggest that an adaptive control mechanism based on performance feedback might be involved. We propose that, using our computational framework, it may be possible to design or manipulate performance feedback to maximize or boost perceptual learning. We believe that the proposed model can be extended to other learning frameworks such as motor and rule learning.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2009.06.009.

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