



Mirror symmetrical transfer of perceptual learning by prism adaptation

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Abstract

Recent study of [Sugita, Y. (1996) Global plasticity in adult visual cortex following reversal of visual input. *Nature*, 380, 523–526.] demonstrated that prism adaptation to reversed retinal input generates the transfer of neuronal activities in monkey V1 to the opposite visual cortex. This raises the question if perceptual learning on one side of the visual field can transfer to the other side. We tested this in using the Gabor lateral masking paradigm. Before adaptation, long-range interaction was induced vertically on one side (i.e., the right) of the visual field with training (perceptual learning). Prism adaptation was achieved by wearing right-left reversing goggles. During adaptation period, perceptual learning transferred to a mirror symmetrical region across the vertical meridian. Results in the post adaptation period revealed that both learning and transfer persisted for over three months. These results provide direct evidence of transferred perceptual plasticity across the visual field, the underlying mechanism of which is supported by the mirror symmetrical connection between the right and left cortices.

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1. Introduction

Human observers who adapt their vision by wearing prism spectacles which optically inverts images are able to restore normal visual perception after a certain period. This is referred as the phenomenon of prism adaptation and it has been studied for over a century (Harris, 1965; Stratton, 1896; Von Helmholtz, 1962). The mechanism responsible for such a drastic change in perception has been of great interest to researchers. It has conventionally been argued that prism adaptation occurs at a relatively high-level processing stage such as that in visuomotor link (Held, 1961; Welch, 1978; Redding & Wallace, 1992), the mechanism for which was recently found in the parietal cortex (Andersen, 1997; Clower et al., 1996; Cunningham & Welch, 1994) and in the cerebellum (Imamizu et al.,

2000). Recent research by Sugita (1996) challenged this notion; his study demonstrated that the function of prism adaptation to reverse visual images occurs as early as in the primary visual cortex (V1). The neural activities in monkey V1 elicited on one side of the visual field (within a receptive field; Hubel & Wiesel, 1968) transferred to the other side at the mirror symmetrical location with adaptation to right-left reversed images (Sugita, 1996). This suggests that the process of prism adaptation already begins at an early stage of visual processing, contrary to the belief that the mechanism for adaptation lies in high-level visuomotor coordination. The involvement of early vision during adaptation was recently confirmed in humans using functional magnetic resonance imaging (fMRI) (Miyauchi et al., 2004).

However, the relationship between low-level neural activities during adaptation and their behavioural consequences remained unclear. One example that may demonstrate functional plasticity in low-level vision is perceptual learning. Perceptual learning is defined as

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improvement, with training, of visual (behavioural) performance such as visual detection or discrimination (Fiorenzini & Berardi, 1980; Karni & Sagi, 1991). Perceptual learning was also found in neurophysiology, demonstrated by enhanced neuronal activities in a particular receptive field in the monkey or cat V1, after training of orientation discrimination tasks (Ghose, Yang, & Maunsell, 2002; Kapadia, Ito, Gilvert, & Westheimer, 1995; Schoups, Vogels, Qian, & Orban, 2001). Similar enhancement in V1 was recently found with human brain imaging (Schoups et al., 2001; Shwartz, Maquet, & Frith, 2002). As learning has occurred at retinotopically specific locations, no transfer has been assumed at non-retinotopic locations. Yet, as described above, Sugita (1996) demonstrated the transfer of neuronal activities across the visual field from one side to the other side of the visual field with adaptation. Therefore, if we assume there is a causal link between neural plasticity and its behavioural consequences on perception, especially if we consider Sugita's (1996) results, it is possible to expect prism adaptation to induce the transformation of retinotopic perceptual learning in the other non-retinotopic side of the visual field.

The goal of this study was to explore the relationship between perceptual learning and prism adaptation. We assumed that the effect of perceptual learning on one side of the visual field could transfer to other side with adaptation. To test this, we set up the combined paradigm of perceptual learning and prism adaptation. First, perceptual learning of long-range interaction was rapidly induced on one side of the visual field by a technique which was recently developed, temporal cueing (Tanaka & Sagi, 2000b). This technique was applied to Gabor lateral interaction (Adini, Sagi, & Tsodyks, 1997; Polat & Sagi, 1993, 1994). Note this type of learning occurs rapidly within hours, significantly faster than previous slow learning which tasks weeks (Polat & Sagi, 1994). Then, we employed prism adaptation for a week (see Fig. 1). Effects of prism adaptation were tested everyday during the adaptation period measuring the contrast detection on each side of the visual field. Furthermore, persistence of prism adaptation was examined after adaptation. We found that prism adaptation produced the transfer of retinotopic perceptual learning from one side of visual field to the other. The effect persisted for months, demonstrating an involvement of visual plasticity.

2. Methods

2.1. Visual stimuli

Visual stimuli were generated as grey modulation on a 17-in. colour monitor (Sony Inc., Trinitron Multiscan 17se II, Tokyo, Japan). The video format was 60.0-Hz non-interlaced refresh rate (VSINC, HSINC = 48.3 kHz) with a resolution of 1024 × 768 pixels occupying a visual area of 17.8 (vertical) × 10.9 (horizontal) degrees. The stimulus generation was controlled by a graphic board (Radeon 7200, ATI technologies Inc. Ontario, Canada) with 10-bit luminance resolution, which was Gamma

corrected. The images were controlled by a conventional Pentium II processor (Intel, Co., Ltd, California USA). The stimuli consisted of Gabor patches defined as a spatial luminance distribution described by:

$$GS(x, y, t) = \cos[2\pi/\lambda\{(x - x_0) \cos \theta + (y - y_0) \sin \theta\}] \exp[-\{(x - x_0)^2 + (y - y_0)^2\}/\sigma^2] T(t - t_0, du). \quad (1)$$

The location of the GS is determined by x_0 and y_0 , the initial time presented $t_0 = 0$, its duration du , its orientation θ (in radius), and wavelength ω . The standard deviation of the Gaussian envelope is given by $\sigma = 1/\omega$, and $T(t)$ for the temporal square pulse function. The stimuli used in the experiment were $\omega = 5$ cycles per degree (cpd) and $\sigma = \lambda = 0.2$ degrees, which were kept constant. The luminance distribution of the three GSs is described by:

$$I(x, y, t) = I_0 + AtGS(x, y, t|x_0, y_0, t) + Af_1GS(x, y|x_0, y_0 + y_1, t) + Af_2GS(x, y|x_0, y_0 + y_2, t). \quad (2)$$

with At representing the target amplitude and $Af_{(1,2)}$ representing those of the two flankers. The flanker amplitudes $Af_{(1,2)}$ in all the experiments were 31% of the mean luminance ($0.31I_0$) and the background luminance $I_0 = 30$ cd/m². Under non-flanker conditions, $Af_{(1,2)} = 0$, only the target GS was presented. The target GS was presented on one side (left or right) of the visual field on the horizontal meridian with an eccentricity of 3.2 degrees. The flanker GSs were presented both above and below the target at an equal distance defined by λ . Both target and flanker orientations were vertical in the collinear configuration. The target orientation was vertical and the flanker orientation was horizontal in the orthogonal configuration. Four peripheral crosses (Fig. 1), which were presented at each quadrant at a diagonal direction of ± 45 deg at a distance of 7.2 degrees from the central spot (size: 0.46 by 0.46 deg, luminance: 60 cd/m²) served as the temporal cue. The local orientation of the peripheral crosses was randomized between 0 and 90 degrees on each trial to reduce possible spatial attention effects to fixed cues. Fixation was maintained on a central white circle throughout the trial (luminance: 60 cd/m² and diameter: 0.34 degrees). Each stimulus was viewed binocularly in a dark room. The observation distance was 100 cm. A chin-head rest (Eye Instruments, Handaya Co., Ltd., Tokyo, Japan) was used to minimize the subjects' head motion as well as misalignment of their head positions relative to the video display. This was particularly important to reduce the noise from visuomotor discordance during adaptation.

2.2. Goggles

The prism goggles were hand-made using two right-angled (dove) prisms made of acrylic resin. The prisms were attached to balsa wood carved to match the shape of each subject's nose and forehead. This was done to place the prism in front of each eye precisely and to obtain accurate reversed optical images for each subject. A rubber band was used to tightly fix the prisms and the balsa on each subject's head. A right-left reversed image was obtained with the right-left reversing goggles. The retinal images were reversed mirror symmetrically (from left to right and vice versa) across the vertical meridian. Upside-down reversing goggles were made of one dove prism that covered both the left and right eyes. The viewing angles extended 65 degrees vertically and 71 degrees horizontally for the right-left reversing goggles and 80 degrees vertically and 40 degrees horizontally for the upside-down reversing goggles.

2.3. Participants

Nine volunteers participated in the experiments. All subjects were free of pathology related to the senses or the nervous system, and had normal (KM, NO, YD, KI, HH, and MI) or corrected-to-normal (AS, TF, and YT) visual acuity with spectacles on a routine clinical ophthalmologic measure using an auto kerato-refractometer (KR-8100, Topcon, Japan). Subjects, except YT (the first author), were college students who were naïve in terms of the purpose of the experiment. Informed consent was acquired from all subjects following procedures in accordance with the

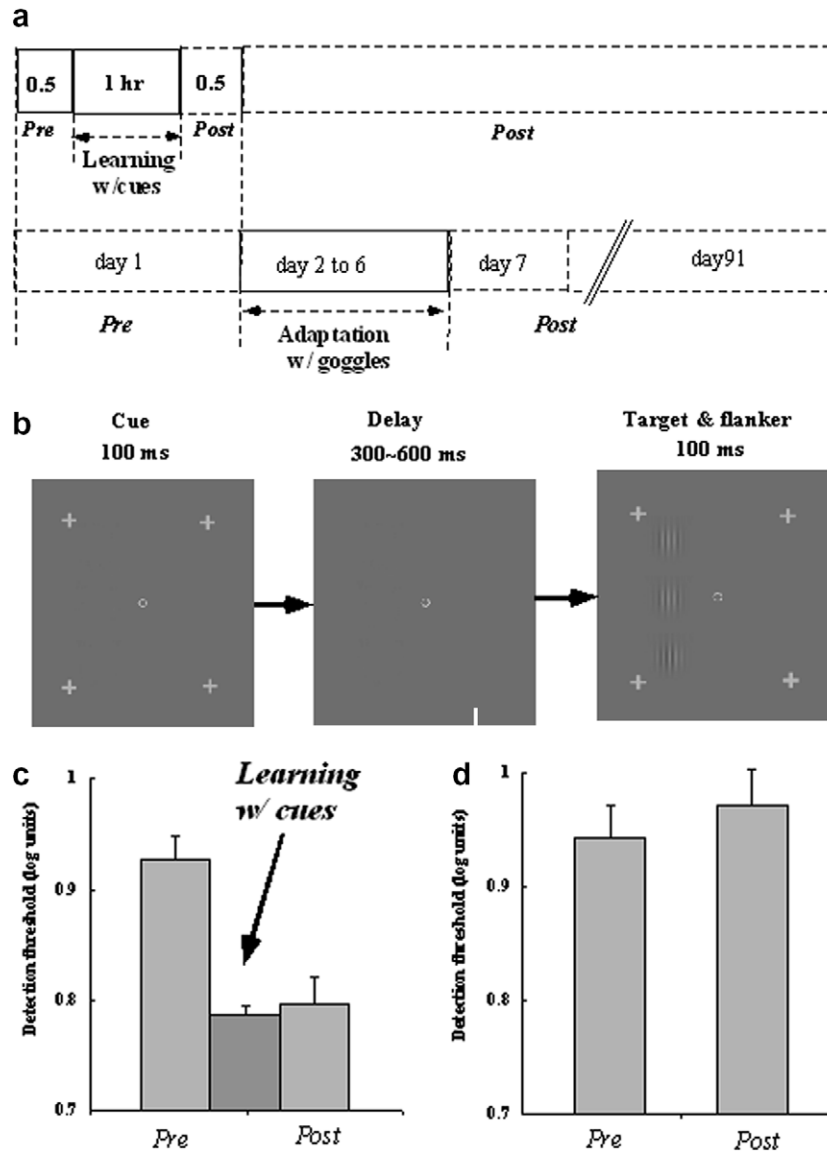


Fig. 1. (a) Time course of combined paradigm of learning and adaptation. The upper part shows the paradigm of learning and the lower part shows the paradigm of adaptation. Both went parallel from day 1 to day 91. In the pre-adaptation period (day 1), fast learning was induced by practice with temporal cues. Prism adaptation was employed with wearing the reversing goggles on days 2–6. Our assumption was that adaptation would produce the transfer of learning from one to the other side. To examine the effect of learning and adaptation, detection threshold was measured on each side of the visual field every day. In the post-adaptation period (days 7 and 91), the goggles were removed and the detection threshold was measured 1.5 h after as well as 3 months after adaptation. (b) Sequence of temporal cueing. A temporal cue (high-contrast peripheral crosses, eccentricity of 7.2 degrees) was presented for 100 ms in each quadrant, followed by a blank background (delay period), and target and flanker GSs presented simultaneously for 100 ms on one side of the visual field. Subjects fixated at the centre of the screen (fixation spot) throughout trials. SOA was defined by the difference between the onset of the cue and the onset of target presentation (Section 2). In the figure, σ and λ are not equal for demonstration purpose. Training with temporal cues was done to induce fast perceptual learning. (c and d) Detection sensitivity during pre-adaptation period. Data from seven subjects (KM, NO, YD, HH, MI, KI, and AS) were averaged and presented (c) for the trained and (d) untrained side of the visual field. The error bars indicate standard errors of the mean (SEM, this and succeeding graphs) derived from approximately 1400 trials of the temporal 2AFC task. (c) The threshold reduced with temporal cues (indicated by an arrow) on the trained side, which persisted after cueing (*Post*), thus learning effect was preserved. (d) No threshold reductions occurred on the untrained side without temporal cues.

1964 Declaration of Helsinki, which was approved by the Ethical Committee of the National Institute of Information and Communications Technology.

2.4. Procedures and task

Contrast sensitivity was determined by a standard two-alternative temporal forced choice (2AFC) procedure, in which the target GS was flashed for 100 ms at one of the stimulus intervals presented sequentially. A trial

began with a presentation of a small fixation circle (0.5 degrees in diameter) at the centre of the screen. By pressing a key, the subjects activated a trial sequence that followed (1) a non-stimulus interval (randomized within a range of 1000 ± 500 ms to reduce the timing effect), (2) a first stimulus interval, (3) a no stimulus interval (randomized within a range of 1000 ± 500 ms), and (4) a second stimulus interval. The presentation of the target GS was intermixed between the first and second stimulus intervals on each trial. In the temporal cueing task, both (5) cue intervals (100 ms) and (6) another non-stimulus interval (200–600 ms) were intro-

duced between (1) and (2) as well as (3) and (4). The difference in onset between the cue and target intervals was defined as stimulus onset asynchrony (SOA), and optimized for each subject (see below). After the trial sequence, subjects were asked to determine which stimulus intervals contained the target by pressing one of the keys. Auditory feedback by means of a keyboard bell was given immediately for erroneous responses. Using the staircase method, the target amplitude (A_t) was increased by 0.1 log units in trials following an erroneous response, and decreased by 0.1 log units following three consecutive correct responses. As each block consisted of approximately 50 trials, the staircase took approximately 5 min to complete. The staircase sequence was terminated after eight amplitude reversals (a block of trials) with the last six amplitudes averaged, yielding a threshold estimate. The threshold elevation was calculated relative to the detection threshold of the target GS in the absence of a cue GS (non-cue conditions). The amplitude of the target (A_t) was initially set at about 1.5 times the threshold contrast attempting to reduce such effects as the perceptual memory of low-contrast signals from previous trials or blocks (Tanaka & Sagi, 1998). Each threshold was estimated four to six times by averaging them as well as calculating the standard errors. Three experiments were employed in each experimental period of (1) *pre-adaptation*, (2) *adaptation*, and (3) *post-adaptation*. (1) *Pre-adaptation*: On day 1, perceptual learning was carried out during this period on one side of the visual hemifield, either left or right depending on the subjects, without them putting on the reversing goggles. The side was fixed to that of the subdominant eye for each subject. A fixed visual field was used to reduce spatial uncertainty about target detection in the parafovea (Pelli, Palomares, & Majaj, 2004). The learning sessions consisted of *pre-learning*, *learning*, and *post-learning* sessions. In the *pre-learning* session, thresholds were estimated for (a) a single GS target (non-flanker conditions) and (b) a GS target with two GS flankers (flanker conditions) located at a distance of 6λ on each side of the visual field at a target eccentricity of 3.2 deg for the collinear and orthogonal configurations. The temporal cueing paradigm was used in the learning session. The temporal cue preceded the GS target and collinear flankers (simultaneously presented for 100 ms) on one side of the visual field with a flanker distance of 9λ . Note that the flanker-target distance (9λ , 1.8 degrees) was set to be outside the critical range of crowding effects (Bouma, 1970). Previous studies have demonstrated that long-term learning can be rapidly acquired by repeating optimally primed temporal signals (Tanaka & Sagi, 2000a, 2000b). The cue-lead time (SOA) was determined for each subject where individual subjects exhibited a minimal detection threshold in detecting the target. Different magnitudes of SOA (200, 300, 450, and 600 ms) were tested. The SOA that gave the minimum detection threshold was chosen as the one for optimal temporal cueing for each subject and used for the practice session (Fig. 1b). Practice was carried out by repeating the temporal cueing task for approximately 30–60 min. Thresholds in the post-learning session were measured again for the flanker conditions with collinear and orthogonal configurations as well as non-flanker conditions without using temporal cues. (2) *Adaptation*: Prism adaptation started with subjects wearing the reversing goggles. Seven participants wore them (Fig. 1); four (KM, NO, HH, and MI) wore the right-left reversed goggles, and three (YD, KI, and AS) wore the upside-down reversed ones. Two participants (YT and TF) did the experiments without goggles. They continuously wore the goggles for either five (KM, NO, YD, YT, and TF) or six (HH, MI, KI, and AS) consecutive days except for the sleep period (blindfolded) and experimental sessions. Participants started to wear the goggles immediately after pre-adaptation, and spent several hours with them on before their first night's sleep. The experiment began the following morning (day 2). The subjects' hands were hidden behind a black box during the experiment in an attempt to minimize visuomotor discordance. The goggles were removed during the experimental session, which were worn again after the session terminated. The experiments were carried out every day throughout the adaptation period. (3) *Post adaptation*: On the last day (day 6), the goggles were taken off and prism adaptation was tested. This was done to evaluate the short-term after effects of adaptation. The thresholds were also measured three months (91 days) after the goggles were taken off to evaluate the long-term after effects of adaptation. Both flanker and non-flanker conditions were tested.

3. Results

One typical way of conducting an adaptation experiment is to compare performance during each period of adaptation. Behavioural modification using prism adaptation can provide an estimate of the transition of perceptual plasticity. Here, we set up three experimental periods: I. A pre-adaptation period in which perceptual learning was induced on one side of the visual field (conducted on the first day) II. An adaptation period in which subjects wore reversing goggles (one week) III. A post-adaptation period in which the subjects removed the goggles and the after-effects were tested (a) about 1 h, and (b) three months after adaptation (see Fig. 1a).

3.1. Pre-adaptation: perceptual learning of long-range interaction

The pre-adaptation period consisted of pre-training, training, and post-training sessions (upper part of Fig. 1a). Long-range interaction was tested in the pre-training session. This interaction is defined as detection threshold facilitation in Gabor lateral masking. It is well known that the detection threshold of the target decreases (i.e., facilitation) when there are two flanking Gabor signals that have identical orientation to the target (Polat & Sagi, 1993). The effect is limited within a certain range of space or flanker distance, usually within six times the wavelength or λ . Here, we examined whether detection facilitation occurred on one side of the visual field (i.e., right) with a target eccentricity of 3.2 degrees (parafovea). Fig. 1b illustrates the configuration: Gabor patches were positioned vertically. There was no facilitation at flanker distance 6λ (0.05 ± 0.03 log units, mean \pm standard error, n.s., paired *t*-test, seven subjects). This is consistent with some of previous results of lateral interaction in periphery (Giorgi, Soong, Woods, & Peli, 2004; Shnai & Sagi, 2005; see Section 4). We attempted long-range interaction to extend the vertical direction (upper and lower sides) with practice. Temporal cueing was used to induce fast learning of lateral interaction (Tanaka & Sagi, 2000b). With this technique, priming visual signals or temporal cues are given prior to the appearance of the target, which facilitates its detection with appropriate timing (Posner & Boies, 1971; Tanaka & Sagi, 1998, 2000a). The thresholds were measured for all subjects using temporal cues with SOA chosen from 300, 400, 500, or 600 ms. Maximal facilitation was found at an average SOA of 371 ± 15 ms (mean \pm SEM) from seven subjects, consistent with our previous study (Tanaka & Sagi, 2000a). Note that as SOAs effective for maximal facilitation differed across subjects, we used different SOAs depending on each subject (range: 300–500 ms). Assuming this temporal cueing would be effective for perceptual learning (Tanaka & Sagi, 2000b) we used this technique to induce perceptual learning on one side of the visual field (i.e., left). Under flanker conditions, training was done for the target with flankers. The flanker distance was set to 9λ

where no detection facilitation had been found before training. Practice with temporal cues produced perceptual learning of long-range interaction in periphery. The detection threshold decreased by 0.14 ± 0.01 log units on the trained side within an hour (seven subjects, $p < 0.0001$, paired t -test, Fig. 1c). Immediately after training, the interaction was tested at a flanker distance of 6λ without temporal cues. Facilitation was preserved on the trained side with a magnitude of 0.13 ± 0.02 log units (seven subjects, $p < 0.0001$, paired t -test, Fig. 1c) whereas no facilitation was found on the untrained side (0.03 ± 0.04 log units, n.s., paired t -test, Fig. 1d). There were no significant differences under the non-flanker conditions between pre- and post-training sessions (i.e., 0.02 ± 0.01 log units on the trained side, and 0.001 ± 0.01 log units on the untrained side, both n.s., paired t -test), ensuring that it was indeed lateral interaction, not the detection threshold, which had improved in training (Adini et al., 1997; Polat & Sagi, 1994). These results demonstrate that practice with temporal cueing produced an extension of long-range interaction in periphery, which is specific to the retinotopic visual field. This is in accordance with previous lateral masking studies in fovea (Adini et al., 1997, Adini, Sagi, & Tsodyks, 2002; Polat & Sagi, 1993, 1994; Tanaka & Sagi, 2000b). In the following period, we assumed no further learning because only one flanker distance (6λ) was used for the rest of the period. It is well known that testing various flanker distances is necessary to achieve learning of long-range interaction (Adini et al., 1997; Polat & Sagi, 1994). Therefore, the rest of the period can also be defined as the post learning period (Fig. 1a).

3.2. Adaptation: transfer of learning

The adaptation period was the next step. Subjects were exposed to a natural environment wearing the reversing prism goggles from days 2 to 7 (Lower part of Fig. 1a, see Section 2.4). During this period, the detection threshold of the Gabor target was measured every day with (flanker conditions) and without flankers (non-flanker conditions). Both trained and untrained visual fields were tested. Note the goggles were temporarily removed during the experimental session (see Section 2). The question was whether the retinotopic learning effect transferred to the other side with adaptation.

Fig. 2a and b illustrate the performance during pre-, during, and post-adaptation periods. The thresholds both on the trained and untrained sides are plotted against the experimental periods (days). Note that the data on days 0 and 1 indicate thresholds during pre- and post-training sessions, respectively. The threshold increased on days 2 to 4 due to noise from visuomotor discordance, possibly due to external noise from the vestibulo-ocular reflex (VOR, Gonshor & Melvill-Jones, 1976) in the initial adaptation phase. Indeed, three participants reported feelings of jitter and distortion in the visual field during this period. Despite that, the threshold decreased under

flanker conditions was maintained on the trained side (Fig. 2a). This means that perceptual learning persisted on the trained side during the initial stage of adaptation. Fig. 2b illustrates the untrained side. Threshold began to decrease on day 3 towards the end of adaptation while non-flanker (control) conditions yielded to maintain a relatively high threshold. To demonstrate net-facilitation, data were re-plotted in terms of threshold elevations. On day 2, the magnitude of facilitation was -0.12 ± 0.01 log units (threshold reduction: four subjects, $p < 0.0001$, paired t -test) on the trained side (Fig. 3a), while there was no facilitation (-0.01 ± 0.01 log units, n.s., paired t -test) on the untrained side. Facilitation on the trained side remained throughout the adaptation session. Facilitation on the untrained side started on day 3, and persisted throughout the adaptation period increasing with a magnitude of 0.13 ± 0.02 log units ($p < 0.001$, paired t -test, four subjects) from days 3 to 6 (Fig. 3b). These results demonstrate that the learning effect on the trained side was persistent, while it transferred to the untrained side during the course of adaptation. If there is traditional perceptual learning with repeating lateral interaction, threshold would reduce day by day. However, facilitation by mere repetition of task was not observed; no systematic threshold reduction was found with repeated tasks in this period. Threshold decreased, increased, or unchanged on days 2 and 3. Only on day 4 thresholds reduced in each visual field independent of goggle type, but the trend disappeared on the next day. Therefore, we consider no perceptual learning with repeating tasks.

One of the important characteristics of right-left reversed images is their spatial layout, i.e., symmetry. The right-left symmetrical structure across the vertical meridian is often referred to as mirror symmetry (Barlow & Reeves, 1979; Dakin & Watt, 1994). In previous studies, transfer was found by accident between the loci, which composed a mirror symmetrical layout across the vertical meridian (Sugita, 1996). Here, we tested whether the locus of transfer was mirror symmetrical between the left and right visual fields. First, perceptual learning was induced on one side (3.2 deg. eccentricity) and we tested whether it transferred to the opposite side at eccentricities of 2.6 deg, 3.2 deg (symmetrical locus), and 3.8 deg. Two subjects participated in this experiment. The learning effect (facilitation on day 1: -0.17 ± 0.03 log units, $p < 0.01$, paired t -test, two subjects) transferred to the mirror symmetrical locus at a 3.2 degree eccentricity (average facilitation from days 4 to 6: -0.12 ± 0.01 log units, $p < 0.001$, paired t -test, two subjects), while there was no transfer at the asymmetrical locus (average facilitation: -0.02 ± 0.01 log units, n.s. paired t -test) at an eccentricity of 2.6 degrees, and -0.04 ± 0.01 log units at an eccentricity of 3.8 degrees, respectively. These results indicate that the transfer was specific to the mirror symmetrical area within ± 0.6 degrees of the spatial zone across the vertical meridian.

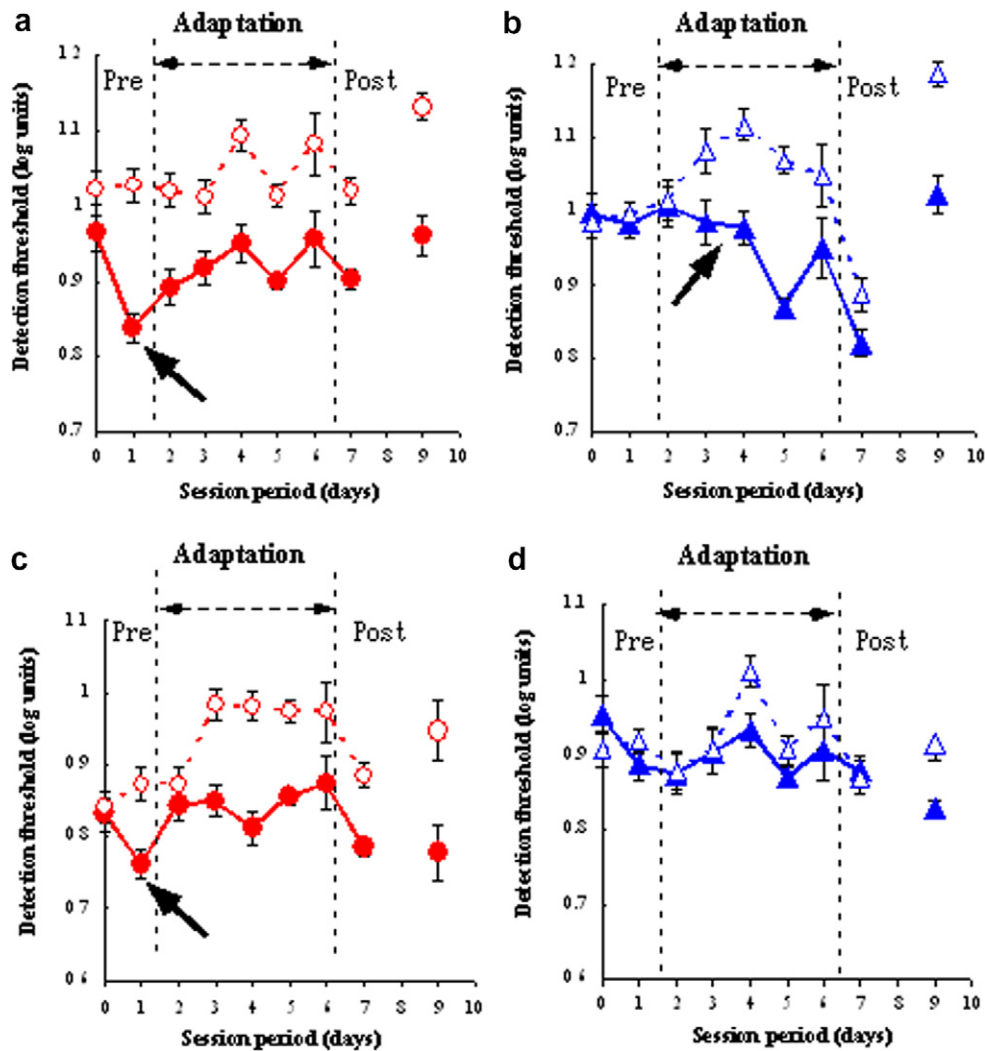


Fig. 2. Detection sensitivity in pre-, during, and post-adaptation periods using right-left reversing goggles. Days 0 and 1 specify the pre-adaptation period (indicated by “Pre”). Days 2 to 6 designate the adaptation period when the goggles were worn (note the goggles were taken off during the experimental session). The adaptation periods, in these and following graphs, are illustrated in the region between the two dotted lines (the area indicated by *Adaptation*). Days 7 and 9 indicate the post-adaptation period when the goggles were removed (indicated by “Post”). The data for day 9 were from the experiments employed three months (91 days) after adaptation. The thresholds under (i) flanker (bold line) and (ii) non-flanker conditions (dotted line) were plotted according to (a) the trained side and (b) the untrained side of the visual field. (c and d) The detection sensitivity (threshold) was plotted using the upside-down reversing goggles for the (c) trained and (d) untrained side. Each point has been averaged from approximately 600 to 800 trials. Arrows in (a and c) indicate perceptual learning. An arrow in (b) indicates the transfer of learning.

3.3. Post adaptation: learning persistence

To test the persistence of learning and its transfer during the post-adaptation period, the same type of experiment was repeated 1.5 h after the goggles were removed. The results on day 7 are plotted in Fig. 2a and b, in which facilitation was persistent on the trained side with a magnitude of 0.13 ± 0.08 log units ($p < 0.01$, paired *t*-test, four subjects). This indicates that learning was preserved after adaptation. Facilitation on the untrained side was also persistent with a magnitude of 0.12 ± 0.01 log units ($p < 0.001$, paired *t*-test, four subjects), indicating that transfer was preserved (Fig. 3a and b). We employed the same experiment three months after adaptation to examine the long-

term effects. Both learning and transfer existed three months after adaptation. Facilitation remained both on the trained and untrained sides with a magnitude of 0.18 ± 0.02 ($p < 0.0001$) and 0.16 ± 0.02 ($p < 0.0001$, both paired *t*-tests, four subjects) log units at a distance of 6λ . This demonstrates the consolidation of both learning and transfer effects with identical magnitude. We also tested other flanker distances ranging from 3 to 16λ . Facilitation was found up to 16λ on the trained side (0.11 ± 0.03 log units, $p < 0.01$, paired *t*-test, four subjects, Fig. 4a) as well as on the untrained side (0.10 ± 0.03 log units, $p < 0.01$, paired *t*-test, four subjects, Fig. 4b), ensuring that extended interaction was preserved both on the trained and the untrained sides.

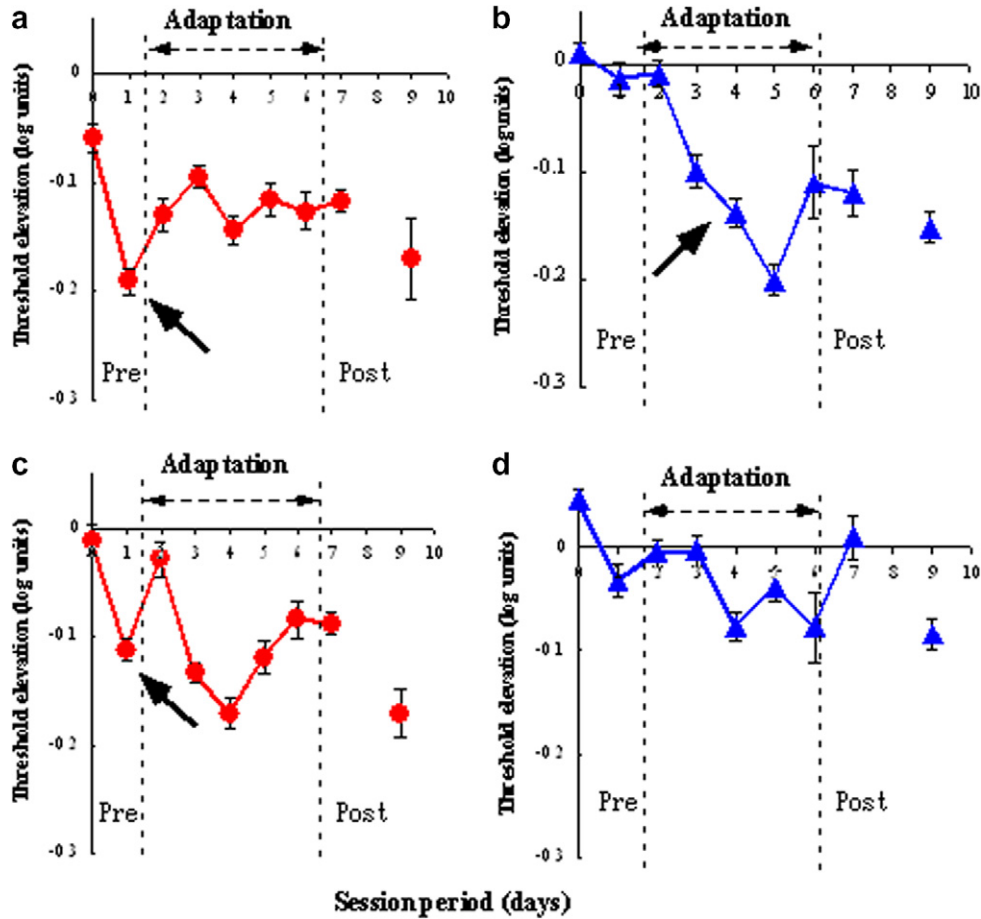


Fig. 3. Normalized threshold from Fig. 2(a–d) based on non-flanker conditions (threshold elevation). It is clear from (a) that facilitation persisted on the trained side during and after adaptation to right-left reversal, while (b) facilitation appeared on the opposite side after a few days of adaptation. Arrows in (a and c) indicate perceptual learning. An arrow in (b) indicates the transfer of learning.

3.4. Upside-down reversal, and no reversal without goggles

Up to this stage, we have demonstrated that perceptual learning indeed transferred with prism adaptation to right-left reversed images. One aspect of the spatial recognition of the visual world associated with our body is visual direction. Since our eyes are positioned in the upper part of the head, our visual world is not homogeneous between the upper and lower visual fields. We were interested in the vertical direction because environmental factors influence human vision and the body, such as sunlight and gravity. To test whether the right-left direction was critical for transfer, the same experiment was carried out by a second group who wore the upside-down reversing goggles (three subjects). A learning effect due to temporal cues was also found on the trained side in the pre-adaptation period, while there was no facilitation on the untrained side (both are in Fig. 1c and d; also see days 0 and 1 in Fig. 2c and d). Facilitation on the trained side was observed throughout the adaptation period with a magnitude of 0.13 ± 0.02 log units ($p < 0.01$, paired t -test, three subjects, see Fig. 3c) while there was no facilitation on the other untrained side (0.01 ± 0.02 log units, three subjects, n.s.;

paired t -test, see Fig. 3d). This indicates that right-left reversal, but not upside-down reversal, was the crucial factor in the mirror symmetrical transfer of learning. The learning effect was persistent on the trained side after several months with a magnitude of 0.12 ± 0.04 log units (three subjects, $p < 0.01$, paired t -test, Fig. 3c), while there was no effect on the untrained side (-0.04 ± 0.04 log units, n.s., paired t -test, three subjects, Fig. 3d). Manipulating the flanker-target distance also revealed extended long-range interaction at 6 to 16λ on the trained side (average 0.11 ± 0.05 log units, $p < 0.01$, paired t -test, three subjects, Fig. 4c) while there was no interaction at distances longer than 9λ on the untrained side (0.02 ± 0.05 log units, n.s., paired t -test, three subjects, Fig. 4d), ensuring that learning of long-range interaction was restricted in the retinotopic area without transfer. To examine the effect of adaptation, i.e., the effect of a restricted visual field with goggles, the same experiment was employed without goggles on two subjects (YT and TF). Rapid learning was only attained on the trained side (0.16 ± 0.03 log units, $p < 0.01$, paired t -test, two subjects). The learning effect persisted for 5 days without goggles (0.13 ± 0.02 log units, $p < 0.01$, paired t -test, two subjects) and survived after three months. There

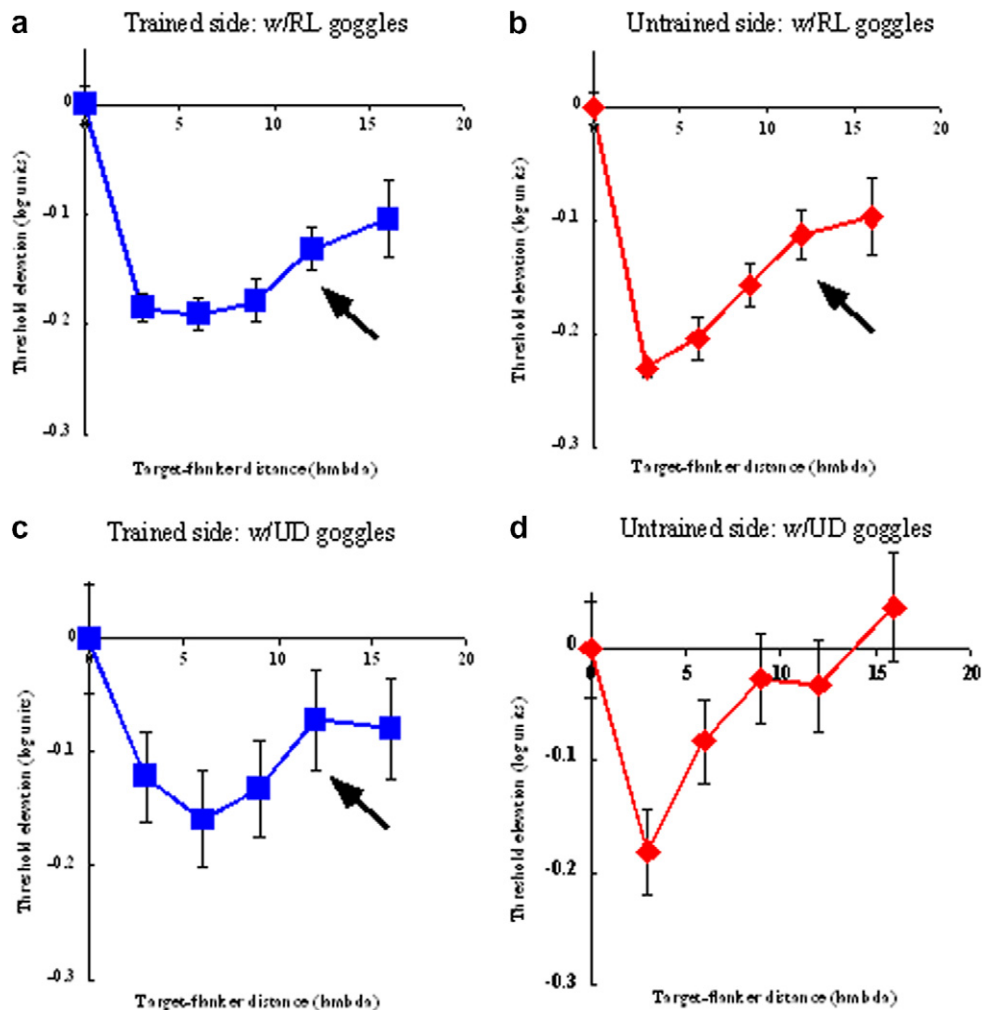


Fig. 4. The persistence of long-range interaction three months after prism adaptation. The threshold elevation was plotted against the target-flanker distance (in λ). The top two panels (a and b) reveal the results from the right-left reversed inputs and the bottom two panels (c and d) from the upside-down reversed images. Distance 0 denotes the control (non-flanker conditions). Extended facilitation was persistent both (a) on the trained and (b) untrained sides with adaptation to right-left reversal, indicating that the effects of learning and transfer spread to shorter distances than 3λ as well as longer distances up to 16λ . A similar extension was found with adaptation to upside-down reversal (c) on the trained side, but (d) not to longer distances on the untrained side. Note that learning with cueing was conducted with a flanker distance of 9λ . Arrows in (a) and (c) indicate perceptual learning. An arrow in (b) indicates the transfer of learning.

was no facilitation on the untrained side of the hemifield (0.03 ± 0.03 log units, n.s., paired *t*-test, two subjects) during practice or after prism adaptation, indicating there was no transfer of learning when the goggles were not used. Therefore, the results reveal the size of the visual field had no effect during adaptation.

The results demonstrated that perceptual learning occurred on the trained side irrespective of whether goggles were worn, whereas transfer only occurred across the visual field with adaptation to right-left image reversal. Right-left transfer did not occur with upside-down reversal or without image reversals. These results reject the hypothesis that simple repetition of the task during the adaptation period is the main factor responsible for transfer. Rather, the results point to the fact that adaptation to right-left reversal was indeed the critical factor to induce transfer.

3.5. Orientation selectivity

We next examined orientation specificity, which is known to be a basic feature achieved in the primary visual cortex of primates (Hubel & Wiesel, 1968) as well as humans (Fiorentini & Berardi, 1980). Lateral interaction was strongest with the collinear configuration where the local Gabor orientation and global axis direction were identical (Polat & Sagi, 1993). However, a previous adaptation study demonstrated that there was no orientation specificity after adaptation (Sugita, 1996). Here, we tested orientation specificity by comparing a collinear configuration with an orthogonal configuration (Polat & Sagi, 1993, 1994) where the orientation of the flanker GS was horizontal while the target orientation remained vertical. The results obtained from two participants (HH and MI)

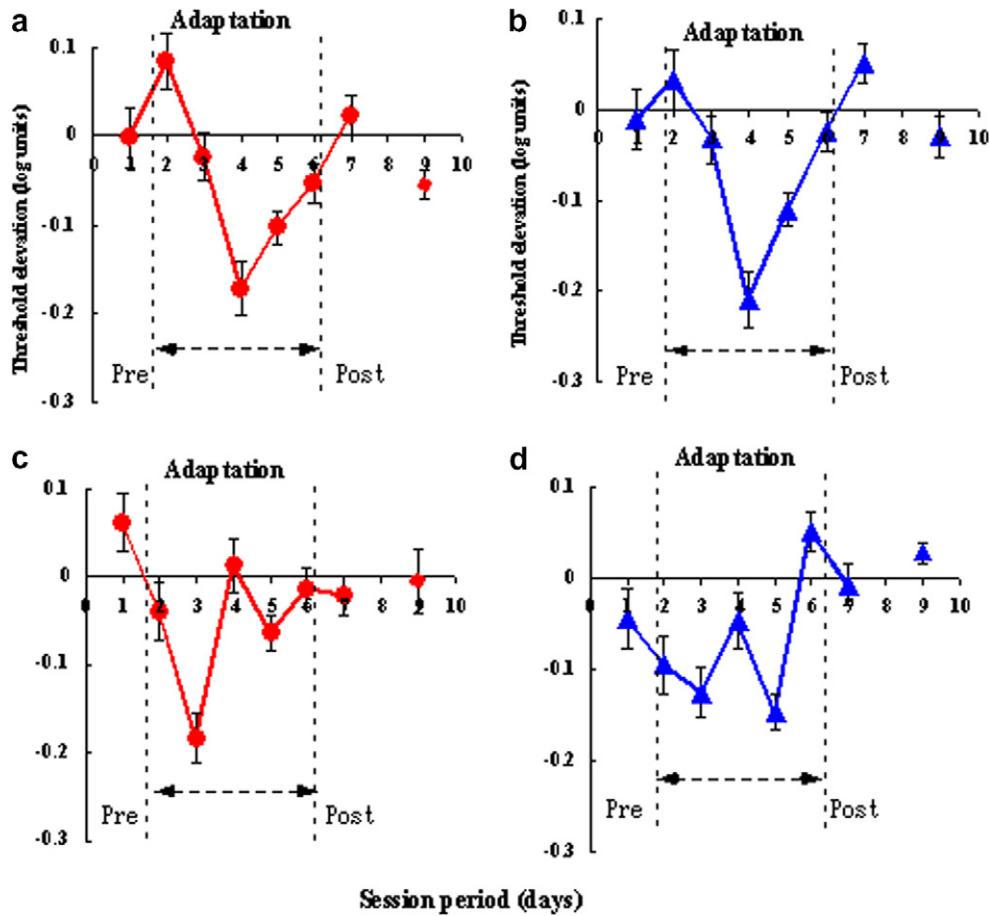


Fig. 5. Results for orthogonal configuration. The threshold elevation was plotted for the pre-, during, and post-adaptation periods. The results are for the trained and untrained sides, with the right-left reversing goggles (a and b) and the upside-down reversing goggles (c and d). There was no facilitation during the pre-adaptation period. Facilitation occurred after a few days of adaptation to right-left reversal, but disappeared in the post-adaptation period. Facilitation was found with adaptation to upside down reversal, but also disappeared after adaptation. The details are described in the text.

indicated that there was no facilitation after practice with temporal cues (see day 1 in Figs. 5a and b), demonstrating that orientation specificity was preserved for learning, in accordance with the previous studies (Polat & Sagi, 1994; Tanaka & Sagi, 2000b). During the adaptation period, the detection threshold increased by 0.09 ± 0.04 ($p < 0.05$, paired t -test) log units on day 2, and decreased significantly on days 4 and 5 both on trained (-0.17 ± 0.03 log units, $p < 0.001$, paired t -test, Fig. 5a) and untrained sides (-0.2 ± 0.02 log units, $p < 0.001$, paired t -test, Fig. 5b). Facilitation was thus found on both sides (Fig. 5c and d). There are two possible factors responsible for facilitation. The first is loss of orientation specificity in early visual processing. This suggests the involvement of high-level visual processing such as that in the parietal cortex during adaptation, i.e., feeding back to V1, as was discussed in Sugita (1996). The other factor could be visual motor discordance during adaptation. The misalignment of the direction of the head may have produced noise in terms of body direction, which could have caused disturbances in the visuomotor recalibration process during adaptation (Gonshor & Melvill-Jones, 1976). This can interfere with orientation

selectivity. For the moment, we cannot determine which one was a main factor. Nevertheless, facilitation disappeared after adaptation. This indicates that orientation selectivity recovered during the post-adaptation period after visual-motor coordination was restored, suggesting that perceptual learning at early stages of visual processing.

4. Discussion

The principal aim of our study was to find the causal link of perceptual learning and prism adaptation. For this, we devised the paradigm of combination of perceptual learning and adaptation. First, we used the novel technique of temporal cueing to achieve fast learning on one side of the visual field. Prism adaptation was employed using the reversing goggles. We found direct evidence that prism adaptation indeed changed the visual functional process. Perceptual learning, demonstrated by local contrast threshold improvements on one side of the visual field, transferred to the other side with adaptation to left-right reversed retinal images. Since Stratton (1896), numerous researchers have argued that human visual perception is

reversed with adaptation to reversed retinal images. However, these were mostly based on introspective reports by subjects or indirect cognitive tests, and there has been little evidence in relation to functional aspects of perception based on visual performance. In the current study, we demonstrated, for the first time, that improved visual contrast sensitivity, which is a typical psychophysical measurement, transferred across the visual field with prism adaptation. Our result points to the fact that a functional plastic process is indeed involved during the course of prism adaptation, indicating that perceptual functionality and neuronal plasticity are closely correlated (Sugita, 1996).

Second, this study extends the scope of perceptual learning beyond the field of retinotopy. Previous studies on perceptual learning had been limited by local visual fields, i.e., the receptive field (RF), which mostly occurs in V1 based on the effective range, if the commitment of high-level components such as attention or working memory is limited (Hochstein & Ahissar, 2002, review). The learning effect transferred across the visual field, demonstrating that the limitation with retinotopy was overcome by means of prism adaptation. The transferred distance was 6.4 degrees, much farther from the receptive field properties in V1. This is probably because the prism adaptation process activates a vast range of visual fields, i.e., through symmetrical interaction with reversed images, producing communication across visual fields. We will argue this further in the following discussion.

Another remarkable characteristic found in the current study was persistence. The effect of prism adaptation have been reported to disappear after a certain time, usually within minutes (e.g., Sugita, 1996 and Miyauchi et al., 2004), with one exception that demonstrated long-term persistence with neglect patients (Rossetti et al., 1998). Perceptual learning was rapidly induced within an hour, which was significantly faster than the time course of conventional perceptual learning (Adini et al., 1997; Polat & Sagi, 1994 etc.). Here, we assumed that learning occurred with temporal cues. Test was done without temporal cues during the adaptation period, therefore no learning should not be produced during this period. Learning persisted during the adaptation period. Moreover, both learning and transfer persisted in normal humans for as long as three months. Although long-term persistence has been often found in the literature on perceptual learning (Karni & Sagi, 1991; Polat & Sagi, 1994; Tanaka & Sagi, 2000b), it is surprising that the transfer of learning with adaptation persisted as much. The difference between the short-term and long-term characteristics of learning may lie in different processes concerning adaptation, the former being the visuomotor link (Andersen, 1997; Kitazawa, Kimura, & Uka, 1997; Sekiyama, Miyauchi, Imaruoka, Egusa, & Tashiro, 2000) and the latter being low-level visual processing (Adini et al., 2002; Karni & Sagi, 1991; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). This tendency is consistent with the previous findings by Sugita (1996) where the effects persisted for several months, suggesting some feed-

back process from higher cortical area to the lower areas for the transfer.

What is the possible mechanism underlying such transfer of learning? One aspect of our findings was that learning transferred to the mirror symmetrical region across the vertical meridian. This is in accordance with the fact that the early visual function is based on the symmetrical layout of the representation of space (Barlow & Reeves, 1979; Dakin & Watt, 1994). In our study, as in Sugita (1996), the eccentricity where learning and transfer took place was 3.2 degrees to the left or right of the vertical meridian, which consisted of a mirror symmetrical configuration. There was no transfer at the asymmetrical locus, which shifted more than one degree from the symmetrical locus. Since these symmetrical receptive fields in V1 with an eccentricity of 3.2 degrees revealed no anatomical commissural connections (Clarke & Miklosy, 1990; Horton & Hoyt, 1991), the results suggest that the transfer of perceptual learning is acquired by a neuronal connection that projects from the right to the left (or vice versa) visual cortices outside V1 (corpus callosum: Van Essen & Mauncell, 1983), probably through V2 or V3 (Abel, O'Brien, & Olavarria, 2000; Misaki, Miyauchi, Tanaka, & Hashimoto, 2005). This is consistent with the findings on fMRI activities during prism adaptation for reversed images in MT (Miyauchi et al., 2004) and V3 using mirror symmetrical images (Misaki et al., 2005; Tyler et al., 2005; Tanaka, Miyauchi, & Misaki, in press). The right-left symmetrical structure in early vision has previously been argued to contain information on "bi-orientedness" (Welch, 1978). Rollenhagen and Olson, 2000 found neural activation for mirror symmetrical images such as "b" and "d" although they found it at the high-level processing stage of the inferotemporal cortex. One model to explain our findings, therefore, would be that visual plasticity or memory traces of Gabor long-range interaction at one side of the visual field was produced at relatively high stages of visual processing, i.e., V3 or higher areas which have trans-cortical connection. The memory traces of long-range interaction achieved by learning might transfer across the opposite side of the visual field via prism adaptation to the mirror symmetrical regions. Since the long-lasting memory traces were orientation specific, there must be a feedback process from the higher areas to early visual areas such as V1. The finding that there is no transfer across the upside-down direction is in accordance with the previous findings of mirror symmetrical connection between the right and left cortices (Miyauchi et al., 2004). This is consistent with Linden, Kallenbach, Heinecke, Singer, and Goebel, 1999 where there was no change in the visual cortex with adaptation to 180 degrees of rotated vision.

Finally, we argue psychophysical lateral interaction in a non-fovea area. Lateral interaction in periphery was controversial in the literature. Long-range interaction in periphery was reported indeed (Polat & Sagi, 1994; Giorgi et al., 2004), however, sometimes subjects did not show facilitation (Giorgi et al., 2004; Shnai & Sagi, 2005), and

sometimes there was no facilitation at all (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). The range of facilitation differed between eccentricities of 2 to 6 degrees (Giorgi et al., 2004; Levi, Hariharan, & Klein, 2002; Polat & Sagi, 1994; Shnai & Sagi, 2005). The main reason for such inconsistency might be due to different attention manipulation across subjects, and across experimental designs, during task operation. It seems that using the temporal, but not spatial 2AFC task is necessary for peripheral facilitation (Giorgi et al., 2004; Zenger-Landolt & Koch, 2001). In our experiment, the temporal 2AFC paradigm was used. We took spatial care of manipulating attention, namely of its temporal factor. We used temporal cues to focus attention within a specific time window. Repeating the task with temporal cues produced facilitation, possibly via feedback from the high level attention (Tanaka & Sagi, 2000a). As for the spatial factor, we presented the four peripheral crosses at each quadrant in each target display (Fig. 1b). Target and flanker Gabor signals were always presented on one side of the visual field within sessions (similar to Giorgi et al., 2004). Both were done to fix the subject attention spatially. These manipulations successfully produced stable facilitation at the flanker distance of 6λ at an eccentricity of 3.2 degrees after learning. Note that facilitation was found at further distance up to 16λ as well as at nearer distances to 3λ (Fig. 4). It might be that temporal cues reduced the effect of crowding in periphery (Bouma, 1970; Levi et al., 2002; Pelli et al., 2004; Shnai & Sagi, 2005). [Considering the target eccentricity of 16λ (3.2 deg), crowding effect was expected within target-flanker distance 8λ , which is half eccentricity (Bouma, 1970).] These results are in accordance with previous results that attention is concerned in lateral interaction (Freeman, Sagi, & Driver, 2001; Giorgi et al., 2004; Shnai & Sagi, 2005; Tanaka & Sagi, 2000a) with a special emphasis of temporal factors (Giorgi et al., 2004; Tanaka & Sagi, 2000a).

In conclusion, we found the transfer of perceptual learning across mirror symmetrical regions with prism adaptation to right-left reversed visual images. Learning of long-range interaction occurred at relatively early level of visual processing, which is still orientation selective. The learning transferred to the mirror symmetrical visual areas with adaptation. This may occur via neuronal communication at higher stages such as in V3 through cortices. The detail functional mechanism of the transfer is yet to be determined, thus further research is necessary to elucidate the relationship between visual plasticity and prism adaptation.

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References

- Abel, P. L., O'Brien, B. J., & Olavarria, J. F. (2000). Organization of callosal linkages in visual area V2 of macaque monkey. *Journal of Comparative Neurology*, 428, 278–293.
- Adini, Y., Sagi, D., & Tsodyks, M. (1997). Excitatory-inhibitory network in the visual cortex: psychophysical evidence. *Proceedings of the National Academy of Sciences United States of America*, 94, 10426–10431.
- Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, 415, 790–793.
- Andersen, R. A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. *Philosophical Transactions of Royal Society B: Biological Science*, 352, 1421–1428.
- Barlow, H. B., & Reeves, B. C. (1979). The versatility and absolute efficiency of detecting mirror symmetry in random dot patterns. *Vision Research*, 19, 783–793.
- Bouma, H. (1970). Interaction effects in peripheral letter recognition. *Nature*, 226, 177–178.
- Clower, D. M., Hoffman, J. M., Votaw, J. R., Faber, T. L., Woods, R. P., & Alexander, G. E. (1996). Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature*, 383, 618–621.
- Clarke, S., & Miklossy, J. (1990). Occipital cortex in man: Organization of callosal connections, related myelo- and cytoarchitecture, and putative boundaries of functional visual areas. *Journal of Comparative Neurology*, 298, 188–214.
- Cunningham, H. A., & Welch, R. B. (1994). Multiple concurrent visual-motor mappings: implications for models of adaptation. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 987–999.
- Dakin, S. C., & Watt, R. J. (1994). Detection of bilateral symmetry using spatial filters. *Spatial Vision*, 8, 393–413.
- Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, 287, 43–44.
- Freeman, E., Sagi, D., & Driver, J. (2001). Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. *Nature Neuroscience*, 4, 1032–1036.
- Gonshor, A., & Melvill-Jones, G. (1976). Extreme vestibulo-ocular adaptation induced by prolonged optical reversal of vision. *Journal of Physiology*, 256, 381–414.
- Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, 87, 1867–1888.
- Giorgi, R. G., Soong, G. P., Woods, R. L., & Peli, E. (2004). Facilitation of contrast detection in near-peripheral vision. *Vision Research*, 44, 3193–3202.
- Harris, C. S. (1965). Perceptual adaptation to inverted, reversed, and displaced vision. *Psychological Review*, 72, 419–444.
- Held, R. (1961). Exposure-history as a factor in maintaining stability of perception and coordination. *Journal of Nervous and Mental Disease*, 132, 26–32.
- Horton, J. C., & Hoyt, W. F. (1991). The representation of the visual field in human striate cortex. *Archives of Ophthalmology*, 109, 816–824.
- Hochstein, S., & Ahissar, M. (2002). Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36, 791–804.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215–243.
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Putz, B., et al. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, 403, 192–195.
- Kapadia, M. K., Ito, M., Gilvert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron*, 15, 843–856.

- Karni, A., & Sagi, D. (1991). Where practice makes perfect. *Proceedings of the National Academy of Sciences United States of America*, 88, 4966–4970.
- Kitazawa, S., Kimura, T., & Uka, T. (1997). Prism adaptation of reaching movements: specificity for the velocity of reaching. *Journal of Neuroscience*, 17, 1481–1492.
- Linden, D. E., Kallenbach, U., Heinecke, A., Singer, W., & Goebel, R. (1999). The myth of upright vision A psychophysical and functional imaging study of adaptation to inverting spectacles. *Perception*, 28, 469–481.
- Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: peripheral crowding is neither size independent nor simple contrast masking. *Journal of Vision*, 2, 167–177.
- Misaki, M., Miyauchi, S., Tanaka, Y., Hashimoto, F., & Tashiro T. (2005). *Retinotopic analysis of visual cortex reorganization after adaptation to reversing spectacles*. 35th Annual meeting of Society for Neuroscience (abstract), Washington, DC, USA.
- Miyauchi, S., Egusa, H., Amagase, M., Sekiyama, K., Imaruoka, T., & Tashiro, T. (2004). Adaptation to left-right reversed vision rapidly activates ipsilateral visual cortex in humans. *Journal of Physiology (Paris)*, 98, 207–219.
- Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision*, 4, 1136–1169.
- Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature*, 391, 580–584.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33, 993–999.
- Polat, U., & Sagi, D. (1994). Spatial interactions in human vision: from near to far via experience-dependent cascades of connections. *Proceedings of the National Academy of Sciences United States of America*, 91, 1206–1209.
- Posner, M. I., & Boies, S. J. (1971). Components of attention. *Psychological Review*, 78, 391–408.
- Redding, G. M., & Wallace, B. (1992). Adaptive eye-hand coordination: Implications of prism adaptation for perceptual-motor organization. In L. Proteau & D. Elliott (Eds.), *Vision and motor control* (pp. 105–128). Amsterdam: Holland.
- Rollenhagen, J. E., & Olson, C. R. (2000). Mirror image confusion in single neurons of the macaque inferotemporal cortex. *Science*, 287, 1506–1508.
- Rossetti, Y., Rode, G., Pisella, L., Farnè, A., Li, L., Boisson, D., et al. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, 395, 166–169.
- Sekiyama, K., Miyauchi, S., Imaruoka, H., Egusa, H., & Tashiro, T. (2000). Body image as a visuomotor transformation device revealed in adaptation to reversed vision. *Nature*, 407, 374–377.
- Schoups, A., Vogels, R., Qian, N., & Orban, G. A. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412, 549–553.
- Shnai, R., & Sagi, D. (2005). Eccentricity effects on lateral interactions. *Vision Research*, 45, 2009–2024.
- Shwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: a function MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences United States of America*, 99, 17137–17142.
- Stratton, G. M. (1896). Some preliminary experiments on vision without inversion of the retinal image. *Psychological Review*, 3, 611–617.
- Sugita, Y. (1996). Global plasticity in adult visual cortex following reversal of visual input. *Nature*, 380, 523–526.
- Tanaka, Y., & Sagi, D. (1998). Perceptual memory for low contrast visual signals. *Proceedings of the National Academy of Sciences United States of America*, 95, 12729–12733.
- Tanaka, Y., & Sagi, D. (2000a). Attention and short-term memory in contrast detection. *Vision Research*, 40, 1089–1100.
- Tanaka, Y., & Sagi, D. (2000b). Fast learning of lateral interaction induced by temporal cueing. *Investigative Ophthalmology and Visual Science*, 41(4), 49, ARVO abstract.
- Tanaka, Y., Miyauchi, S., & Misaki, M. Bilateral long-range interaction across right and left visual hemifield. *Vision Research*, in press.
- Tyler, C. W., Baseler, H. A., Kontsevich, L., Likova, L. T., Wade, A. R., & Wandall, B. A. (2005). Predominantly extra-retinotopic cortical response to pattern symmetry. *NeuroImage*, 24, 306–314.
- Van Essen, D. C., & Maunell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neurosciences*, 6, 370–375.
- Von Helmholtz, H. (1962). In J. P. C. Southall (Ed.), *Helmholtz's treatise on physiological optics*, Vol. 3, Sect. 2. Translation from 3rd German Ed. pp. 242–270. New York, NY, Dover Press.
- Welch, R. B. (1978). *Perceptual modification: Adapting to altered sensory environments*. New York: Academic Press.
- Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America A Optics Image Science and Vision*, 15, 2046–2051.
- Zenger-Landolt, B., & Koch, C. (2001). Flanker effects in peripheral contrast discrimination-psychophysics and modelling. *Vision Research*, 41, 3663–3675.