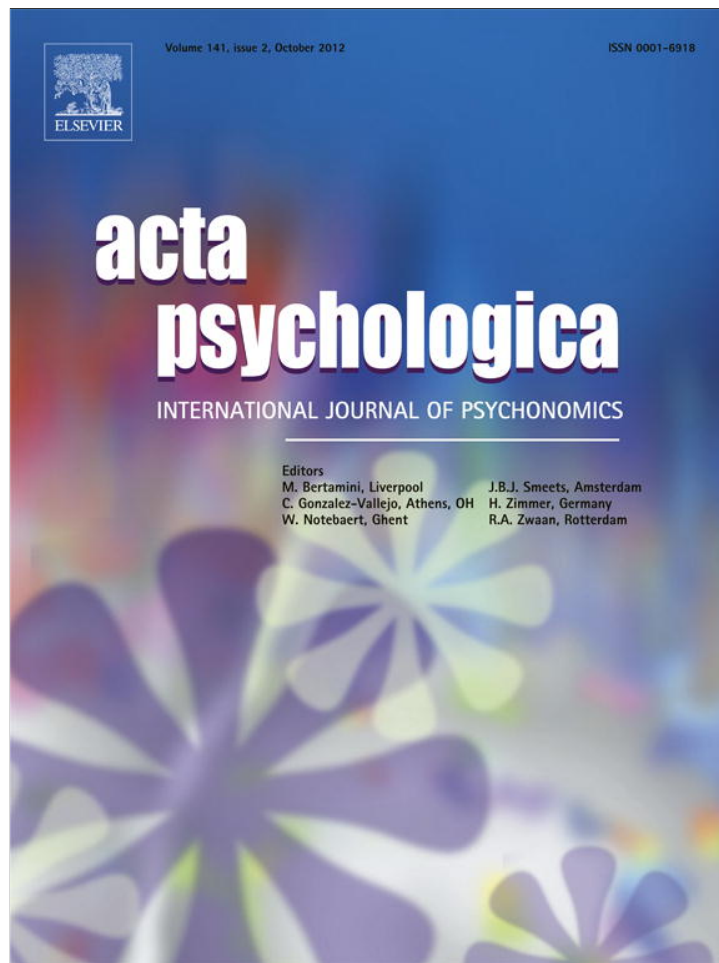


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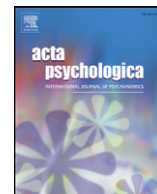
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Visuo-somatosensory reorganization in perceptual adaptation to reversed vision

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ABSTRACT

Humans can adapt to reversal of the visual field after long-term wear of reversing prism spectacles. Among various aspects of adaptation to reversed vision, adjustment of visually-guided behavior has been consistently found. On the other hand, there is relatively little quantitative evidence for 'perceptual adaptation', for example, restoration of perceptual harmony between the visual and tactile world. To elucidate perceptual adaptation to reversed vision, we conducted long-term experiments with continuous wear of reversing spectacles. Four human adult participants wore left–right reversing spectacles for 37 or 32 days. Perceptual adaptation was examined by spatial left–right judgment tasks for visual, auditory, and somatosensory stimuli. In the visuo-motor (VM) and somato-visual (SV) tasks, correct responses disappeared completely at the beginning of prism wearing, but gradually restored, first in the VM task, and subsequently in the SV task. Moreover, the VM and SV tasks revealed aftereffects (incorrect responses) upon removal of the reversing prisms after the long adaptation period. In the auditory-motor (AM) task, responses were mostly correct irrespective of the reversed vision, but incorrect responses transiently appeared approximately when the adaptive change was first observed in the SV task. Moreover, starting from the period when these changes in the SV and AM tasks emerged, an adaptive sign of interhemispheric interaction was revealed by functional Magnetic Resonance Imaging. These results indicate that perceptual adaptation to reversed vision does occur, and that it proceeds to visuo-somatosensory reorganization, which seems to transiently accompany global cross-modal interactions.

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1. Introduction

Retinal images are inverted with respect to the visual field in both the up-down and left–right dimensions, but our perceived visual world is not inverted/reversed: Spatial orientations of visible objects are in harmony with orientations of tangible objects and of the proprioceptive self. This fact indicates that our perceived orientation of the visual world is not directly associated with the retinal coordinates.

Stratton's classical psychological study suggested that human space coding is not associated with the orientation of the retinal image, but the relationship between visual and somatosensory orientations that can be newly acquired (Stratton, 1896, 1897). His conclusion is based on his experience of 'perceptual adaptation' after long-term wear of inverting lenses (3 days for the first time, and another 8 days after a 5-month break, with both up-down and left–right dimensions reversed). Similarly, perceptual adaptation was also reported for left–right reversal

of the visual field (Kohler, 1964, the adaptation period was 24 or 37 days). As immediate effects of reversing/inverting spectacles, they reported severe disruption in visually-guided behavior, as well as a perceptual discrepancy between apparent visible locations and tangible locations of objects. However, following continuous exposure to a reversed/inverted visual field, not only adjustment of visually-guided behavior, but also perceptual adaptation, emerged in which visual-tactile harmony was restored (Kohler, 1964; Stratton, 1897). The perceptual adaptation, that is, the restoration of visual-tactile harmony points to plasticity of the body-accounted reference frames, but the underlying processes of perceptual adaptation to reversed vision are largely unclear. Moreover, the perceptual adaptation to reversed vision was controversial until recent years (Ewert, 1930; Michel, Pisella, Prablanc, Rode, & Rossetti, 2007; Welch, 1986) partly because the above classical studies (Kohler, 1964; Stratton, 1897) present only introspective/qualitative descriptions. To date, quantitative studies on adaptation to reversed vision have consistently found *adjustment (error reduction) in visually-guided behavior* (Ewert, 1930; Linden, Kallenbach, Heinecke, Singer, & Goebel, 1999; Richter et al., 2002; Sekiyama, Miyauchi, Imaruoka, Egusa, & Tashiro, 2000; Snyder & Pronko, 1952) or *eye movements* (Gonshor & Melvill Jones, 1976), but *perceptual adaptation* has been reported only in limited studies (Sekiyama et al., 2000).

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On the other hand, in the case of wedge prism experiments, 'perceptual adaptation' to a horizontally displaced visual field has been well documented and the underlying processes have been relatively well delineated (e.g., Harris, 1963; Held & Hein, 1958; Helmholtz, 1925; Kaufman, 1974; Redding & Wallace, 1997; Redding, Rossetti, & Wallace, 2005; Welch, 1986). Thus, the theoretical framework for adaptation processes for displaced vision may be useful to clarify perceptual adaptation to reversed vision. For example, a recent view of two adaptation processes, that is, recalibration and realignment (Redding et al., 2005) seems to be helpful to understand the sharp differences between consistently-reported behavioral adjustment and controversial perceptual adaptation for reversed vision.

Wedge prism studies typically use prisms that shift the visual field laterally about 10-deg to the left or right (thus, relatively little optical transformation compared with reversed vision). Immediately after wearing such wedge prisms, participants tend to make spatial errors in pointing to a visual target without seeing the movement paths (errors are in the direction of the visual displacement), but the errors are reduced in a few minutes while repeating the pointing behavior with visual feedback at the end point of the movement. Moreover, aftereffects are observed when the prisms are removed. The aftereffects, that is, errors opposite the prism displacement, are observed in pointing to a visual target, in pointing straight ahead without vision, and even in non-manual (verbal) production of visual straight ahead. Compared with the rapid error reduction process, however, the aftereffects increase more slowly. Based on these phenomena, Redding et al. (2005) proposed that there are at least two adaptation processes: recalibration and realignment.

Recalibration (or strategic control) refers to adaptive modifications of feedforward movement plans through associative learning with movement-specific error feedback information. The magnitude of aftereffects due to recalibration is larger depending on the similarity of training and test conditions. Realignment (or true adaptation) refers to realignment of different spatial maps (e.g., visual-motor coordinates and proprioceptive-motor coordinates) for misalignment caused when the prisms displace the visual-motor reference frame. Realignment generalizes to the entire coordinates of a reference frame, extracting a constant parameter from repeatedly given error feedback information during recalibration. Whereas recalibration is thought to be a high-level (largely intentional) rapidly progressing process, realignment is thought to be low-level slowly developing process.

Returning to adaptation to reversed vision, 'behavioral adjustment' and 'perceptual adaptation' may roughly correspond to recalibration and realignment, respectively, although the time scale necessary for adaptation is much longer for reversed vision. If such an analogy is made, the current status is that the literature on adaptation to reversed vision shows relatively little evidence for slow realignment and a lot of evidence for rapid recalibration. For example, some recent quantitative reversing studies failed to show realignment, but showed recalibration in about 10 days of up-down reversal (Linden et al., 1999) or 180-deg rotation (Richter et al., 2002). On the other hand, positive realignment was behaviorally found in a 5-week left-right reversing experiment with a task to manually respond to the side (left or right) of a visual target without seeing the hands (Sekiyama et al., 2000). Thus, it seems that sufficient adaptation time will also generate a slow realignment process for reversed vision. The purpose of the present study was to show further evidence of perceptual adaptation to reversed vision analogous to realignment in adaptation to displaced vision.

To make an analogy with realignment, we should ensure that *perceptual harmony* as a result of perceptual adaptation is distinct from *visual capture*. In wedge prism experiments, immediate effects of wearing the prism include visual capture, that is, a stationary hand tends to be felt as if it is located near its displaced optical position (Hay, Pick, & Ikeda, 1965). Visual capture does not produce reliable aftereffects (Welch, 1978, 1986), so it is thought of as immediate weighting of visual over somatosensory input (Welch, 1978,

1986), perhaps analogous to the ventriloquism effect for auditory-visual mismatch. In short, visual capture or visual dominance is based on a process different from realignment. To examine perceptual adaptation distinct from immediate visual capture, the present study took criteria of perceptual adaptation as follows: 1) behavioral changes tested in cross-modal spatial judgment tasks without seeing one's own body, 2) behavioral changes that are not observed immediately after wearing prisms, but are slowly developed as a function of wearing time, and 3) aftereffects are produced. If observed behavioral changes meet all these criteria, the underlying process is certainly different from visual capture and more similar to realignment.

In light of the first criterion, cross-modal spatial judgment tasks were prepared such that the subject's own body was not seen during the tasks. Four kinds of cross-modal tasks were used: visuo-motor (VM), somato-visual (SV), auditory-motor (AM), and somato-motor (SM) tasks. The main focus of perceptual adaptation was on the VM and SV tasks, in which visual reversal produces misalignment with the other modality. The VM task was the same as in our previous study (Sekiyama et al., 2000) in which behavioral changes were observed in a few weeks. If such behavioral changes are based on visuo-somatomotor reorganization, then we should also observe behavioral changes in perceiving a somatosensory target stimulus in relation to visual reference points (SV task). However, if our previously found behavioral changes in the VM task are based on visuo-motor reorganization rather than visuo-somatosensory reorganization, responses to the SV task may not change because motor aspects are virtually eliminated in the SV task. Thus, the SV task was to examine the occurrence of inter-sensory reorganization between visual and somatosensory modalities. This task may be analogous to the visual straight ahead test in wedge prism studies (Craske & Crawshaw, 1978; Hatada, Miall, & Rossetti, 2006; Redding & Wallace, 1990; Uhlarik & Cannon, 1971) in which spatial matching between a visual point and proprioceptive position is verbally made.

In addition, the AM and SM tasks were introduced to investigate generalization of visuo-somatomotor reorganization to auditory-motor and somato-motor reference frames. In short-term wedge prism studies, such generalization has been consistently observed in pointing to a sound source (Harris, 1963; Hay & Pick, 1966; Michel et al., 2007) or pointing straight ahead (Harris, 1963; Hatada et al., 2006; Hay & Pick, 1966; Redding & Wallace, 2009). However, some rare long-term wedge prism experiments revealed that the erroneous behavioral shifts in these tasks are transient, limited to the early period of adaptation with a peak of 12 h of exposure to displaced vision (Hay & Pick, 1966, Experiment 1 and 2; exposure period was 42 days or 6 days, respectively). It was also found that the behavioral shift in pointing to a sound source diminishes by seeing one's whole body rather than just a hand during a 15-min exposure (Hay & Pick, 1966, Experiment 3). Therefore, in our long-term exposure to reversed vision in which participants see their whole body to manage their daily lives, the AM and SM tasks may not show errors. On the other hand, if such generalization to other reference frames is observed, it points to a general aspect of realignment.

Besides the perceptual tests, behavioral tasks also included a reaching task to measure behavioral adjustment. A more rapid change was anticipated compared with the perceptual tests.

In addition to behavioral tasks, we explored neural correlates of perceptual adaptation. In the case of wedge prism studies, several brain regions have been implicated for adaptation by using a pointing task in one-day measurement (Chapman et al., 2010; Clower et al., 1996; Danckert, Ferber, & Goodale, 2008; Kurata & Hoshi, 1999; Luauté et al., 2009; Pisella et al., 2005). However, it is not clear what kind of tasks are useful to investigate neural correlates of perceptual adaptation to reversed vision that needs much longer time to occur. In the literature on reversed vision, there is a monkey study showing neural changes in the primary visual cortex (V1) after wearing left-right reversing spectacles for 1.5 months (Sugita,

1996). In the adapted monkeys, some V1 cells began to respond to visual stimuli presented not only to the contralateral visual field, but also to the ipsilateral field. This bilateral receptive field, or an interhemispheric interaction, indicates plasticity that may be related to perceptual adaptation to left–right reversed vision, although the neural–perceptual correlation is not yet known. We used functional Magnetic Resonance Imaging (fMRI) to measure V1 responses to a hemi-visual field stimulus and examined whether or not such bilateralization of the V1 receptive field is related to perceptual adaptation in spatial judgment tasks.

2. Material and methods

2.1. Participants

This study involved four healthy human volunteers. One was the first author, a 46-year-old female (KS), and the other three were 20-year-old students at Future University Hakodate (one female and two males). They provided written informed consent as indicated by an approved protocol at the National Institute of Advanced Industrial Science and Technology. They were all right-handed and had normal hearing and normal or corrected-to-normal visual acuity. The student participants were paid 6000 JPY per day.

2.2. Overview of the experiment

The experimental tasks described below were given in three major experimental periods repeatedly: pre-adaptation, adaptation, and post-adaptation periods. During the adaptation period, the participants wore left–right reversing spectacles for more than one month continuously except when they slept (KS wore them for 32 days and the three students 37 days). The data collection in the pre-adaptation period was to measure the baseline of each task, measurement in the adaptation period was to examine the progress of adaption, and measurement in the post-adaptation period was to test aftereffects of adaptation which were supposed to last for a certain period.

The reversing spectacles were made in our laboratory to fit each participant's face (Supplementary Figure S1a). The visual field of the spectacles was approximately 40-deg wide and 35-deg high. We tried to fill the participants' days with exercises and recreational activities including a few trips to mountain regions (Supplementary Figure S1c). During the adaptation period, caretakers watched the participants' behaviors to avoid danger.

In the adaptation period, behavioral tasks were given every 2 to 4 days depending on the speed of adaptation anticipated from our pilot experiments. In addition, functional Magnetic Resonance Imaging (fMRI) was conducted on a weekly basis. During the adaptation period, the participants were tested while wearing reversing spectacles. In the pre- and post-adaptation periods, the participants were tested with a pair of empty spectacle frames to match the size of the visual field. In order to examine lasting aftereffects of adaptation, the post-adaptation period consisted of two measurement days for behavioral tasks, one was the day of removal of the reversing spectacles (Post 1 or Ps1) and the other was the next day (Post 2 or Ps2). In the behavioral tasks described below, a chin rest was used to stabilize the participant's head. In all the tasks, the participants observed stimuli monocularly with the right eye (the left prism was occluded). This was to avoid double images which were often induced by binocular reversing prism spectacles when the wearers looked at nearby objects.

The experiment was repeated over three years, testing one or two participants at a time on summer vacations. Thus, the testing days were not always identical for the four participants due to miscellaneous things in each experiment.

2.3. Behavioral tasks

2.3.1. Reaching task

The participant was instructed to reach each target as quickly and accurately as possible with the right index finger. The participant sat in front of a 17-in touch monitor (Touch Panel Systems, Yokohama, Japan, model ET17) at a 45-cm viewing distance. A trial began when the participant was ready by touching a metal plate on the table with the right hand without seeing the hand (Fig. 1). A fixation point (red circle, 1.5 mm in diameter) was presented at the center of the monitor against a black background and the participant held the starting position and looked at the fixation point for 2000 ms. Then, a visual target appeared as a small white circle (3 mm in diameter) at one of eight locations along a virtual circle surrounding the fixation point with a radius of 5 cm. The visual target disappeared when the participant released his/her hand from the starting position. Latency (from the onset of the visual target to the release of the hand), movement time (time for the hand to move from the starting position to the touch monitor), and error distance (distance between the reached point and the target) were measured by a computer with in-house software. The participant was given forty continuous trials as 5 × 8 trial blocks on each measurement day. In a block, the order of the eight locations was randomized.

2.3.2. Visuo-motor (VM) task

The participant was instructed to report his/her first impression on which hand side of the fixation point they perceived a visual stimulus (white dot), by pressing a left or right button with their hands invisible. The participant sat in front of a 17-in monitor on which a black background was displayed. He (she) was holding a game controller with both hands without seeing them. After a fixation point (red dot, 0.2° in diameter) was presented at the center of the monitor for 1500 ms, a white dot (0.7° in diameter) was presented as target stimulus for 200 ms at the left or right of the fixation point (2.4° off from the fixation point). The participant was told to press a left button by the left hand or a right button by the right hand while looking at the monitor to indicate the perceived location of the white dot. The response was input to a computer with in-house software and the left–right response and response time were recorded. Twenty trials were conducted in random order, resulting in 10 repetitions for each stimulus location on each day.

2.3.3. Somato-visual (SV) task

Spatial judgment as to the left–right location was requested for a cutaneous air-puff stimulus in relation to visual reference points. We used verbal responses to measure changes in a visuo-somatosensory reference frame which was separable from those in a visuo-motor reference frame possibly involved in the above VM task. For the verbal responses, we avoided the words 'left' and 'right' because our pilot experiments revealed that these words are ambiguous in left–right reversing experiments: Sometimes participants use the word 'right' to indicate the side of their somatosensory right shoulder, and sometimes to indicate the right side of the visual field which corresponds to the left side of the tangible world (Sekiyama, 1997, Pp.162–165). Thus, we presented two visual reference points (one was red and the other blue) and the location of a somatosensory stimulus was to be matched verbally (red or blue) to one of the two visual references. Air-puff stimulation was generated by using a cylinder of compressed air, a decompressor, and six electromagnetic valves (Takasago Electric, Nagoya, Japan, Model MTV-2-M6) that were integrated into a circuit controlled by a computer with in-house software. The air output from each valve was delivered to the participant's skin via Teflon tube (2-mm inner diameter). To mask auditory cues that the air-puff emits, white noise was presented through headphones. The participant sat in front of a 17-in monitor on which a black background was displayed. Following a warning signal for 500 ms, a trial began with the

presentation of a fixation point (red dot, 0.2° in diameter) for 300 ms. Then, two visual reference points were additionally presented for 1200 ms: one reference point was red and the other blue, and one was on the left of a fixation point and the other on the right (each reference point was 1.4° in diameter, and 4.2° off from the fixation point). The locations of the red and blue dots were randomly assigned to either the left or right in each trial. After 1500 ms from the onset of the reference points, an air-puff stimulus (150-ms duration, 0.2 MPa) was delivered to the skin surface of one of six invisible body locations (the left or right side of the head, bottom of the neck, or hands; see Fig. 2b). The participant was asked to report on which side of the body the air-puff stimulus was perceived by naming the color of the visual reference point located on the same side. The instruction emphasized that the first impression should be reported. The verbal response (red and blue, 'a-ka' and 'a-o' in Japanese) and response time were recorded in each trial via a microphone connected to the computer. Forty-two trials were given continuously as 7×6 trial blocks on each day. In each block, the presentation order of the six locations was randomized.

2.3.4. Auditory-motor (AM) task

Participants were instructed to judge the left–right location of an auditory stimulus by a manual response with invisible hands. The stimulus was a speech sound 'pa' pronounced by a Japanese female talker. The participant sat in front of a 17-in CRT monitor while holding a game controller with both hands without seeing them. After a fixation point (red dot, 0.2° in diameter) was presented at the center of the monitor against a black background for 1500 ms, an auditory stimulus was presented either from a left or right loud speaker for about 200 ms at approximately 58 dB at the participant's head position. The two loud speakers were placed on the left or right of the monitor (Fig. 3b). The participant was asked to respond with invisible hands as in the VM task. The left–right response and response time were recorded in each trial as in the VM task. Twenty trials were conducted in random order, resulting in 10 repetitions for each stimulus location on each day.

2.3.5. Somato-motor (SM) task

Participants were instructed to judge the left–right location of a somatosensory stimulus by manual response of invisible hands. The stimuli were identical to those in the SV task, that is, the air-puff stimulation to six different body locations. The response mode was button pressing as in the VM and AM tasks. The participants were instructed to report the left–right location of each air-puff stimulus by pressing one of the two buttons without looking at the hands.

2.4. Functional Magnetic Resonance Imaging (fMRI)

Data were obtained from the three student participants. No fMRI data were available for participant KS.

2.4.1. Stimulus (visual hemi-field stimulation)

The visual stimulus was a flickering checkerboard pattern presented in the periphery of the right visual field (thus, visual hemi-field stimulation). The edge of the checker board was away from the center of the gaze by 4° . The elements of the checkerboard were squares ($1.3^\circ \times 1.3^\circ$), each of which appeared in black or white alternately every 200 ms against a black background. The stimulus was monocularly presented to the participant's right eye. The participant's task was to gaze a fixation point throughout the fMRI scanning period for 3 min and 30 s. During the scanning period, a 30-s stimulation period and a 30-s rest period (only the fixation point was presented) alternated three times following a 30-s dummy scanning.

2.4.2. fMRI measurement

Data were acquired on a 3-T GE Signa LX MRI scanner (General Electric, Milwaukee, WI, USA) with a standard head coil. The

participant was positioned in the scanner with the head immobilized by support belts and cushions. Functional images were obtained using gradient echo planar imaging (EPI) with the following parameters: repetition time = 2000 ms, echo time = 70 ms, flip angle = 90° , field of view = 20 cm, matrix size = 64×64 , 3.14-mm inplane resolution. Eighteen axial noncontiguous 6-mm-thick slices (with 1-mm interslice gaps) were obtained in one volume, and 90 sequential volumes were collected during one run. After fMRI scanning, high-resolution T2 anatomical images were collected at the same slice as the EPI sequence (repetition time = 24 ms, echo time = 5 ms, field of view = 20 cm, matrix size = 256×192 , flip angle = 90°). On one of the measurement days, each participant's whole-brain anatomy images (matrix size = 256×256 , 1.2-mm slice thickness) were acquired.

All the fMRI data were analyzed by SPM2 (Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm/>). Functional images were first realigned for motion correction. The anatomical image was coregistered to the mean functional image that was created during motion correction. Realigned functional images were then spatially normalized based on parameters determined by normalizing the anatomical image to the T2 Montreal Neurological Institute (MNI) template. Spatial smoothing was not done in order to preserve spatial accuracy.

The preprocessed functional images were then analyzed individually using a general linear model. We did not conduct group analyses due to large individual differences in the time course of adaptation during the adaptation period. The blocks of stimulation and rest periods were modeled using the boxcar function convolved with the hemodynamic response function. We performed a planned subtraction between stimulation and rest. Significance of results for activated regions in paired *t* tests was set at $P < 0.05$ (Familywise-Error corrected for multiple comparisons).

3. Results and discussion

The participants went through severe disruption of visually-guided behavior at the beginning of the reversing period, but their behaviors were markedly improved during the first week, as confirmed by the reaching task. More complex movements based on coordination of several body parts took more time to restore. All the participants could ride a bicycle with reversing spectacles after one month adaptation (Supplementary Figure S1b). Results for each task are described below.

3.1. Reaching task performance

Replicating the previous results (Sekiyama et al., 2000), restoring reaching behavior was relatively rapid. The results were very similar among the four participants, so group data are shown (Fig. 1). ANOVAs with day as a within-subjects factor were conducted for error distance, latency, and movement time, respectively. The main effect of day was significant for movement time [$F(16, 48) = 18.39, P < 0.001$] and latency [$F(16, 48) = 4.35, P < 0.001$], but not for error distance. Subsequent multiple comparisons (Ryan's method, $P < 0.05$) on movement time revealed that movement time significantly increased on day 1 and 3 compared with the pre-adaptation measurement, but it was restored to the pre-adaptation level on day 5. In the post-adaptation period, a significant aftereffect (increase in movement time) versus pre-adaptation was confirmed on the day of removal (Post 1), but not on the next day (Post 2). Concerning latency, multiple comparisons revealed a significant increase only on day 1 versus pre-adaptation. These results indicate that the disturbance caused by the reversing spectacles was mainly in movement time, at the beginning of both the adaptation and post-adaptation periods. Latency was increased only on day 1. Error distance was constant even after the reversing spectacles were put on.

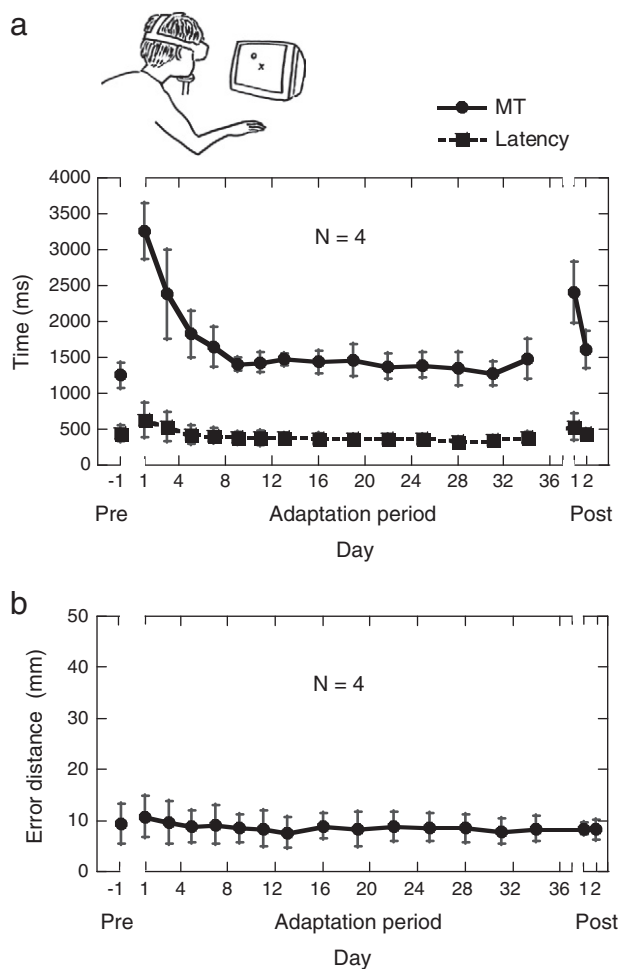


Fig. 1. Performance of the reaching task with regard to (a) time and (b) accuracy. Averages across participants are shown. Disturbance due to reversing spectacles was mainly on movement time (MT: time while the hand was moved until it touched the monitor) on day 1, 3, and Post 1, and there were small or no changes in latency (time from the target onset to the hand release) and error distance (distance between the target and the touched position). Bars indicate standard deviation.

These relationships indicate that the participants took time for error correction in reaching trajectory by using real-time visual feedback in the novel visuo-motor arrangement. Overall, the adaptation for the reaching task was attained within a week (about 5 days), and an aftereffect was observed only on the day of removal.

3.2. Behavioral tests of perceptual adaptation

Unlike the uniform results in the reaching task, perceptual tasks showed large individual differences in the adaptation and post-adaptation periods. Thus, individual results were examined. Despite the large individual differences, each participant showed a consistency among tasks. From the data obtained, only percent correct response is shown below as a function of day. Preliminary analyses found no significant correlations between percent correct response and response time in any tasks in any individuals, indicating the absence of a speed-accuracy trade-off.

3.2.1. Late changes in the VM and SV tasks

In the VM and SV tasks, correct responses disappeared early in the adaptation period, but correct responses gradually reappeared (Fig. 2). Aftereffects were observed in the post-adaptation period as incorrect responses when reversing prisms were taken off after a 5-

week adaptation. To statistically test restoration of correct responses, frequencies of correct and incorrect responses were tested by chi-square test between day 2 and each of the other adaptation days in each participant ($df=1$, with Yate's correction). Similarly, aftereffects were examined by chi-square test between the pre- and post-adaptation periods.

In the VM task (Fig. 2a), KS restored statistically significant correct responses on day 5 ($\chi^2=6.23, P<0.05$), day 18, and thereafter (χ^2 's $> 29.19, P<0.01$), F1 on day 10 ($\chi^2=20.9, P<0.01$), day 17 and thereafter (χ^2 's $> 23.43, P<0.01$), M1 on day 13 and thereafter (χ^2 's $> 32.48, P<0.01$), and M2 on day 36 ($\chi^2=16.2, P<0.01$). The dates with significant performance changes are indicated by asterisks in each panel in Fig. 2a. These results indicate that the restoration of correct responses in the VM task was achieved in about 2 weeks for three participants (KS, F1, and M1), while participant M2 was slower in adaptive change. Aftereffects were statistically significant on Post 1 and Post 2 for both KS (χ^2 's $> 20.91, P<0.01$) and F1 (χ^2 's $> 21.60, P<0.01$), but only on Post 1 for M1 ($\chi^2=17.91, P<0.01$), and no aftereffect was found for M2. The dates with significant aftereffects are indicated by plus (+) symbols in each panel in Fig. 2a. The persistence of aftereffects seems to be correlated with how early the first instance of adaptive change appeared.

In the SV task (Fig. 2b), KS restored statistically significant correct responses on day 18 and thereafter (χ^2 's $> 14.99, P<0.01$), F1 on day 13 and thereafter (χ^2 's $> 10.36, P<0.01$), M1 on day 21 and thereafter (χ^2 's $> 15.38, P<0.01$), and M2 on day 36 ($\chi^2=4.62, P<0.05$). Aftereffects were statistically significant on Post 1 and Post 2 for both KS (χ^2 's $> 18.08, P<0.01$) and F1 (χ^2 's $> 42.92, P<0.01$), only on Post 1 for M1 ($\chi^2=8.72, P<0.01$), while no aftereffect was found for M2. These results for the SV task were basically similar to those for the VM task, but the adaptive changes appeared about a week later compared with the VM task. It seems that the aftereffects decayed more rapidly in the SV task than in the VM task, at least for KS and F1.

Concerning body parts, one participant (M1) showed correct responses primarily for the hands and he showed an aftereffect only for the hands. In other participants, there was also a 'hand precedence' (F1) or 'dominant hand precedence' (KS) at earlier adaptive changes, but these two participants later showed generalization among most body parts tested.

Overall, the results for the VM and SV tasks similarly showed much slower changes than that in the reaching task. These late changes together with aftereffects meet our criteria of perceptual adaptation. In the two tasks, the VM task showed slightly faster adaptation (in about 2 weeks on average) than the SV task (in about 3 weeks on average). It seems that the initial stage of perceptual adaptation is led by visuo-motor, rather than visuo-somatosensory, reorganization, but eventually visuo-somatosensory reorganization also takes place.

As for individual differences, KS and F1 were the fastest in terms of adaptation and had robust aftereffects on both Post 1 and Post 2, M1 was intermediate in the speed of adaptation and had an aftereffect only on Post 1, while M2 was the slowest in adaptation and had no aftereffects. Based on our criterion for aftereffect, participant M2 did not achieve perceptual adaptation. These large individual differences were very different from the uniform results in the reaching task.

3.2.2. No/transient changes in the SM and AM tasks

The performance of the SM task was accurate throughout the experiment (Fig. 3a, post-adaptation data are missing for participants F1 and M1). To statistically test the influence of the reversed vision, frequencies of correct and incorrect responses were tested by chi-square test between pre-adaptation and each of the other days in each participant ($df=1$, with Yate's correction). No significant difference was found in any of these tests. These results indicate that the manual responses to somatosensory stimuli were not affected by reversed vision at all.

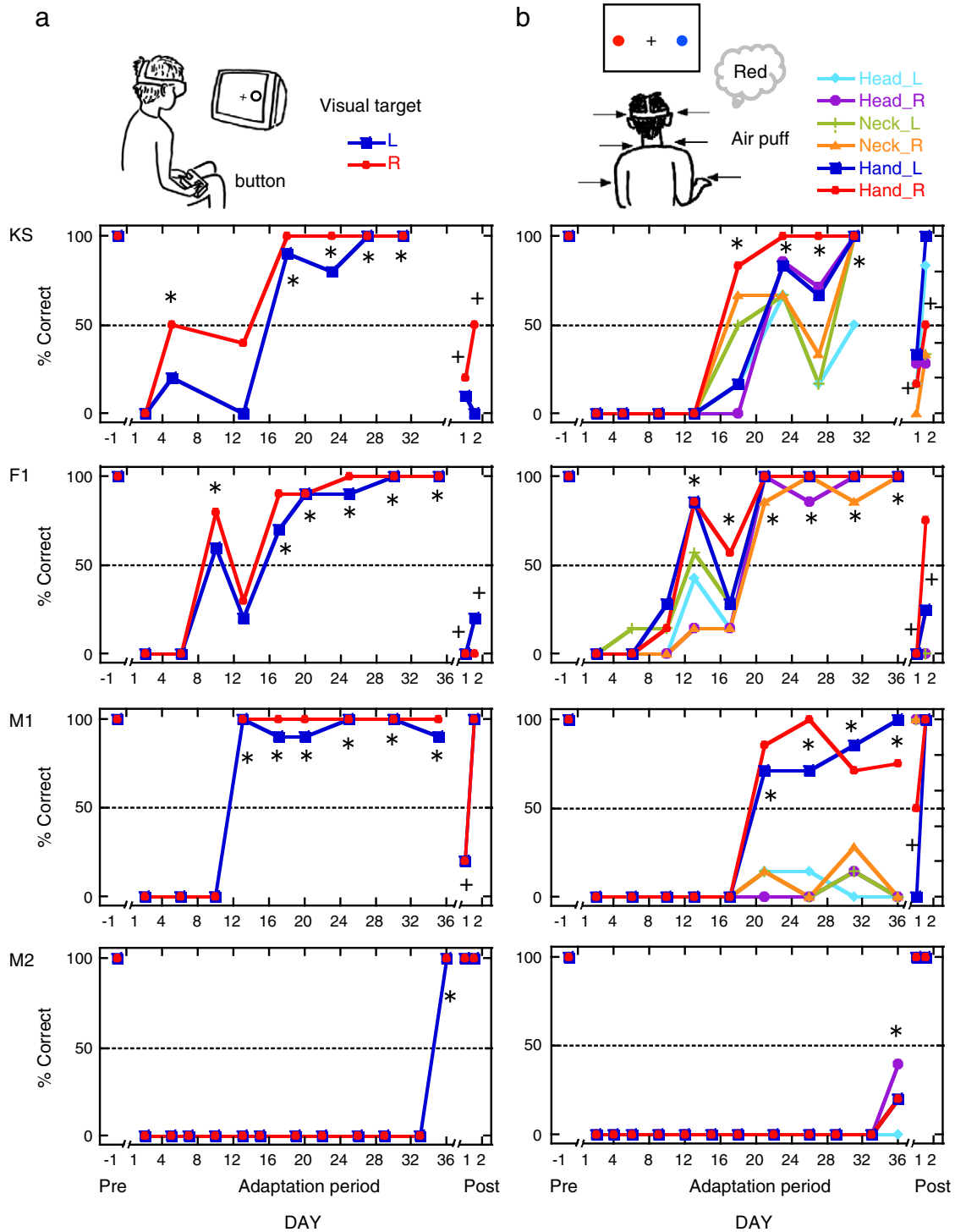


Fig. 2. Percent correct responses in the (a) VM and (b) SV tasks for each participant. In the VM task, the participant manually reported the left–right location of a visual target without seeing the hands. In the SV task, the participant reported the left–right location of a somatosensory stimulus by naming the color of one of the visual reference points. Correct responses were restored approximately in two weeks in the VM task, and in three weeks in the SV task, although the timing varied across participants. Aftereffects (incorrect responses) were observed immediately after the adaptation period (at least on Post 1) except for one participant (M2). Asterisks indicate dates on which a statistically significant performance change was found compared with Day 2. Plus (+) symbols indicate dates on which statistically significant aftereffects were found compared with the pre-adaptation period.

In the AM task, responses were mostly correct irrespective of reversed vision, but incorrect responses transiently appeared during the adaptation period (Fig. 3b). The appearance of incorrect responses was tested by chi-square test between day 2 and each of the adaptation days ($df = 1$, with Yate's correction). F1 showed statistically significant incorrect responses only on day 10 ($\chi^2 = 7.65, P < 0.01$), M1 on day 25 ($\chi^2 = 29.19, P < 0.01$), M2 on day 36 ($\chi^2 = 14.55,$

$P < 0.01$), and KS on day 18 and thereafter (χ^2 's $> 5.95, P < 0.05$ on day 27, $P < 0.01$ for days 18, 23, and 31). Although the incorrect responses lasted longer for KS compared with the other three, her incorrect responses also seemed to be transient because there were some correct responses in the later period. The reason for her exceptionally slow transition is not clear, but it could be related to age. More importantly, the onset of incorrect responses in the AM task approximately coincided

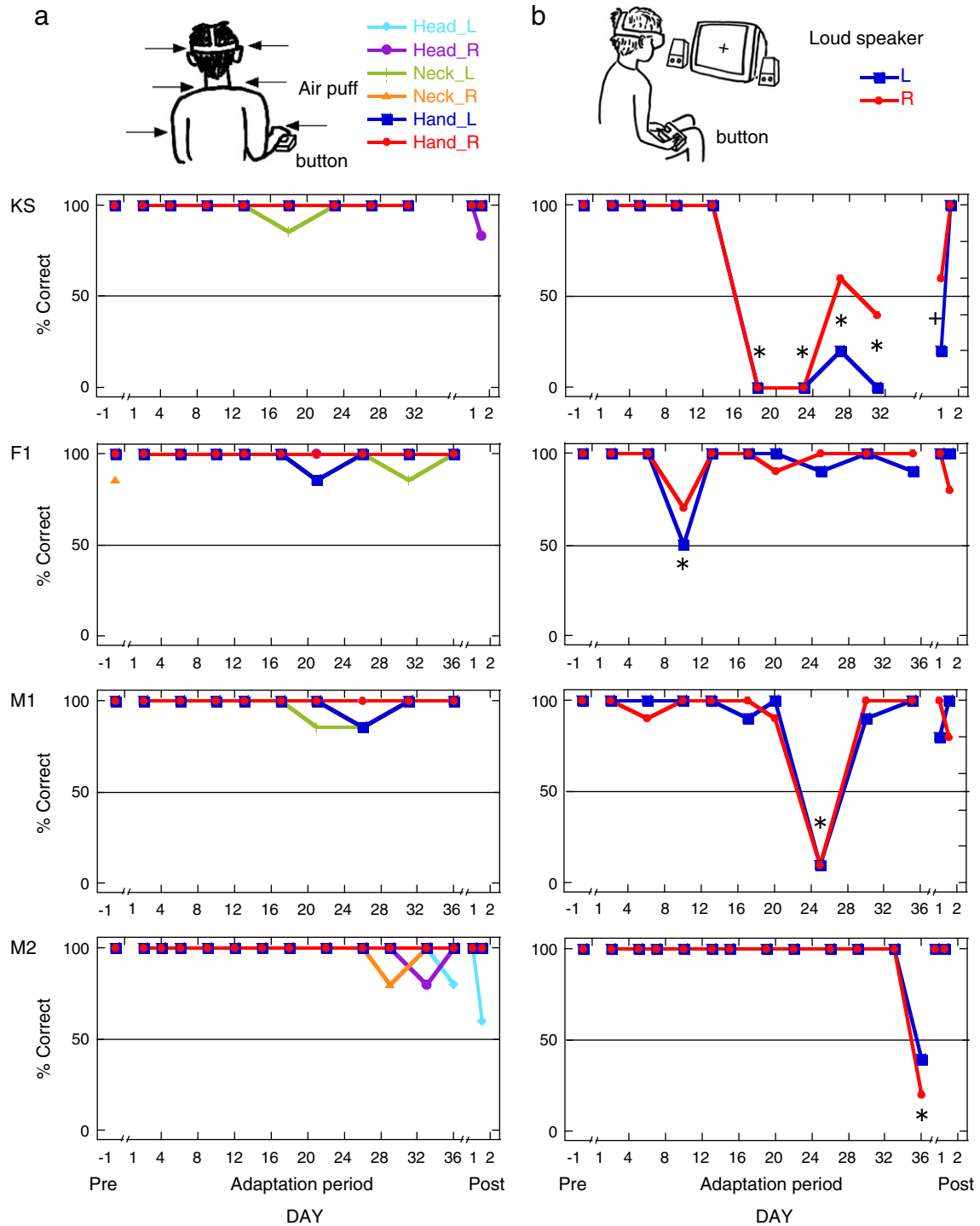


Fig. 3. Percent correct responses in the (a) SM task and (b) AM task for each participant. In the SM task, the participant manually reported the left–right location of a somatosensory stimulus without seeing the hands. In the AM task, the participant manually reported the left–right location of an auditory stimulus without seeing the hands. In the SM task, responses were correct throughout the experiment, showing no influence due to the reversing spectacles. In the AM task, responses were mostly correct, but incorrect responses appeared transiently, approximately synchronizing with the onset of adaptive correct responses in the SV task. Participant KS showed exceptionally prolonged errors in the AM task. Unlike the VM and SV tasks, aftereffects were absent/weak in the SM and AM tasks. Asterisks and plus (+) symbols are used as in Fig. 2.

with the onset of adaptive correct responses in the SV task in each participant (day 18 for KS, day 10 for F1, day 25 for M2, and day 36 for M2). Therefore, these transient incorrect responses in the AM task likely represent an early aspect of perceptual adaptation.

Aftereffects in the AM task were tested by chi-square test between pre-adaptation and each of post-adaptation days. The three student participants were almost perfectly correct in post-adaptation, with no statistically significant aftereffects at all. KS showed substantial

incorrect responses on Post 1, with a significant difference compared with pre-adaptation ($\chi^2 = 5.95, P < 0.05$), perhaps related to her substantial incorrect responses in the last stage of the adaptation period. On Post 2, KS's correct responses were restored to the pre-adaptation level. These results indicate absence/weakness of aftereffects, clearly different from the results in the VM and SV tasks.

In summary, the results for the SM and AM tasks were similar with regard to the absence/weakness of aftereffects, indicating a negative

sign of perceptual adaptation in these tasks. On the other hand, the two tasks differed in that the only AM task showed transient errors during the adaptation period. The reason for this sharp difference is not clear, but it may be attributable to the spatial layout of the task. The auditory stimuli were located in the exocentric space, similar to the visual stimuli, but the somatosensory stimuli were on the skin, and thus in the ego-centric space. The similarity in the exocentric nature between the AM and VM tasks may cause a transient generalization of visuo-motor reorganization to an auditory-motor reference frame.

3.3. Bilateral V1 activation in fMRI

The V1 activation to the hemi-field visual stimulus was unilateral in the pre-adaptation and early to middle adaptation periods for all three participants measured. The anticipated bilateral V1 activation emerged after a certain period of adaptation, approximately synchronizing with the onset of perceptual adaptation captured by the SV task. The bilateral activation was first observed on Day 18 for F1, Day 25 for M1, and Day 37 for M2 (Fig. 4). Once the bilateral V1 activation emerged, it seemed to last for about a week (observed on Day 18 and 25 for F1, Day 25 and 33 for M2) and then the activation again became unilateral for the rest of the adaptation period (Day 33 and 37 for F1, Day 37 for M1). In post-adaptation measurements (on the day

of removal of the reversing spectacles), all three participants again showed bilateral activation, indicating an aftereffect.

These results indicate that some kind of neural reorganization involving the other hemisphere took place transiently when perceptual adaptation was first observed in the SV task, as well as when re-adaptation to the normal visual world was progressing.

3.4. The relationship among perceptual tasks and fMRI responses

To make a comparison among the perceptual tasks for one participant, mean percent correct responses (across left–right and body parts) are shown as a function of day for the VM, SV, and AM tasks (Fig. 5). Each asterisk indicates the date on which the first instance of significant restoration appeared in the perceptual task. For simplicity, the SM task is not included here because no influence of reversing spectacles was observed for it. In addition to the perceptual tasks, Fig. 5 illustrates the periods in which the reaching performance (movement time) improved (shaded in beige, up to Day 5), as well as the dates on which fMRI revealed bilateral activation to the hemi-field visual stimulus (white numbers in black labels).

Combining these results, it is clear that changes in the reaching task are different from those in the other tasks. The movement time reduction in the reaching task was rapid and in the same manner

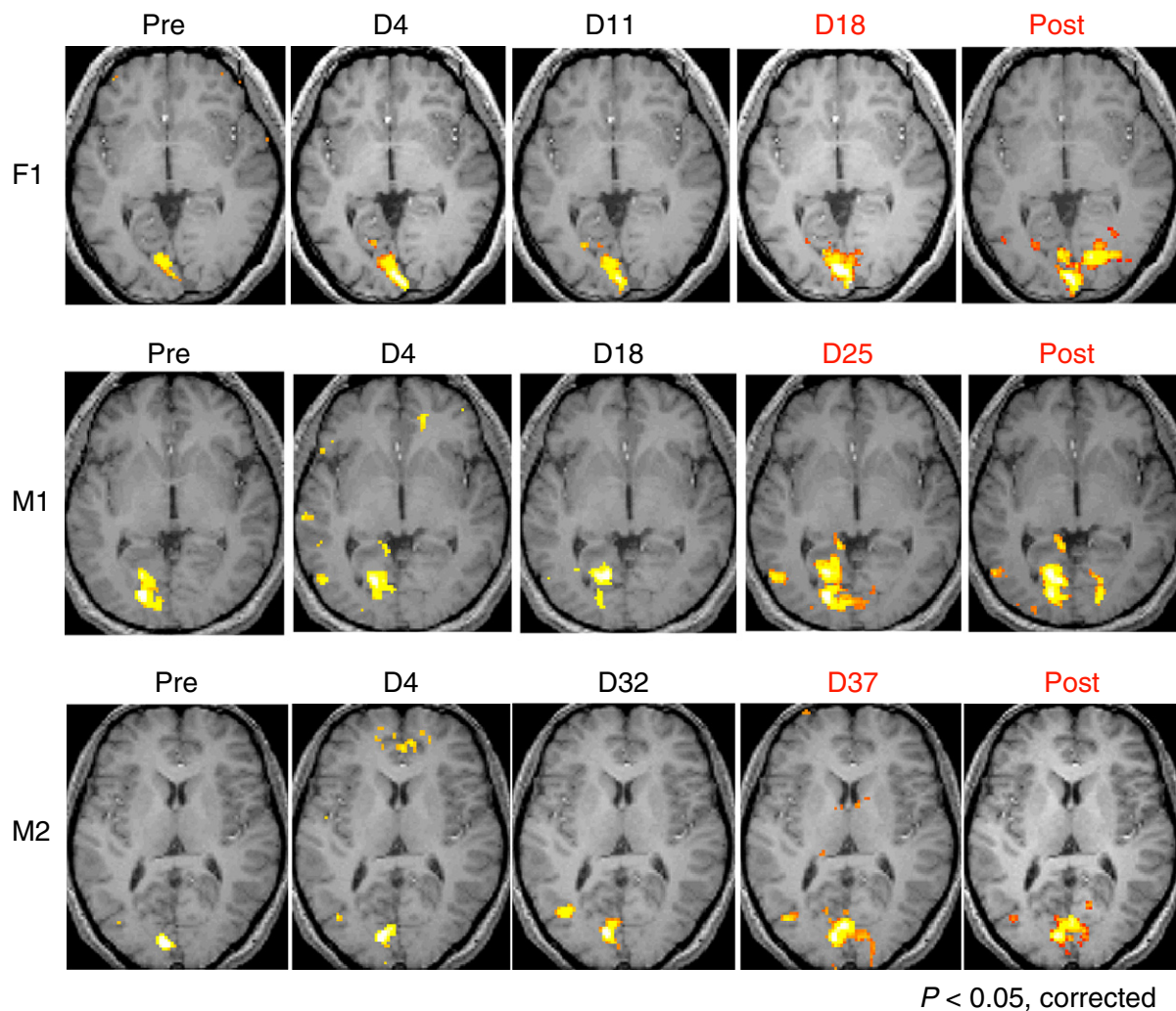


Fig. 4. Activation of the primary visual cortex in response to the hemi-field visual stimulus to the right visual field (after passing through the reversing spectacles during the adaptation period). In the pre-adaptation measurement (Pre), the unilateral (contralateral) activation was confirmed in each participant and it was maintained throughout the early to middle adaptation period. The anticipated bilateral activation was observed starting from the third week of adaptation, approximately synchronizing with the restoration of correct responses in the SV task in each individual. The onset of the bilateral activation was Day 18 for F1, Day 25 for M1, and Day 37 for M2. In the post-adaptation measurement (Post, on the day of removal of the reversing spectacles), the bilateral activation was again observed for all the participants, indicating an aftereffect.

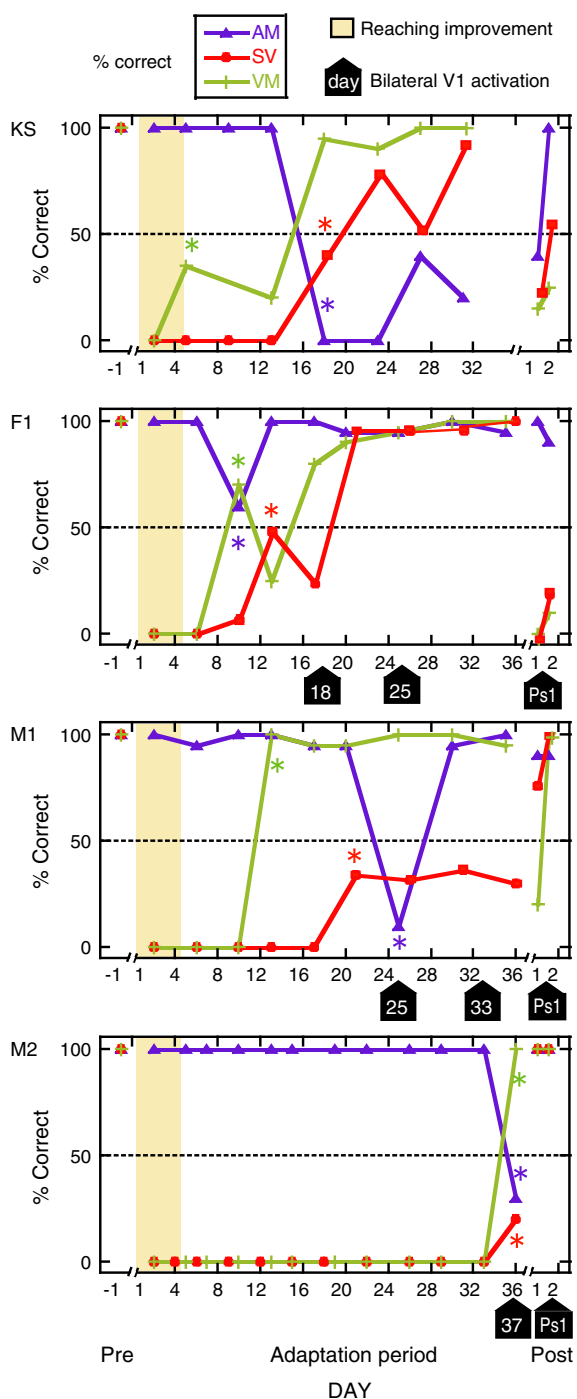


Fig. 5. The relationship of response changes among tasks in each participant (excluding the SM task). Lines show mean percent correct responses as a function of adaptation day for the AM, SV, and VM tasks. Each asterisk in green, red, and purple indicates the day when the performance of each of the three tasks significantly changed from that of Day 2 for the first time (based on chi-square tests, see the text of Section 3.3). The colored periods in beige indicate that the reaching performance (movement time) improved and was restored to the pre-adaptation level during the periods. The white numbers in black labels indicate the days on which fMRI revealed bilateral V1 activation to the hemi-field visual stimulus (fMRI data are not available for participant KS). On one hand, the adaptation in the reaching task was rapid and observed in the same fashion for all the participants. On the other hand, the perceptual tasks took a much longer time for changes to occur and the time varied depending on the individual. Most importantly, there was a rough synchronization of changes among the responses in the SV task (red asterisk), AM task (purple asterisk), and the neural response pattern to the hemi-field visual stimulus.

for all the participants. On the other hand, the three perceptual tasks took more time for performance changes and the time varied depending on the individual. More importantly, in spite of the large

individual differences, each participant showed among-task consistency in the perceptual tasks. Correct responses increased for the VM and SV tasks as a function of adaptation day, and the VM task showed a slightly faster adaptation than the SV task. In the AM task, incorrect responses transiently appeared approximately when the correct responses in the SV task first appeared; compare the red and purple asterisks indicating the first day of statistically significant performance change during the adaptation period. In addition, these changes in the SV and AM tasks roughly synchronized with the emergence of the bilateral V1 activation measured by using fMRI (Day 18 for F1, Day 25 for M1, and Day 37 for M2). Note that fMRI measurements were conducted only on a weekly basis.

The results are schematically summarized in Table 1 for changes in behavioral and neural responses during three periods: early adaptation period (possibly analogous to recalibration), late adaptation period (possibly analogous to realignment), and post-adaptation period (aftereffects). While the reaching task showed changes in the early adaptation period, the other tasks did not. All the perceptual tasks except the SM task (VM, SV, and AM tasks) showed changes in the late adaptation period. Aftereffects were found in three behavioral tasks in which visuo-somatomotor correlations were involved (Reaching, VM, and SV tasks). Virtually no aftereffects were found in the AM and SM tasks. In fMRI measurements, the anticipated bilateral activation was observed both as a late change and aftereffect. These results indicate that the two behavioral tasks (VM and SV) and the fMRI measurement meet our criteria of perceptual adaptation, that is, late changes and aftereffects.

4. General discussion

The present study aimed to collect quantitative evidence for perceptual adaptation to reversed vision. To do so, we adopted a sufficient adaptation time of more than one month, used several behavioral tasks to examine changes concerning cross-modal relationships, and investigated neural correlates of perceptual adaptation. In an analogy with two adaptation processes (recalibration and realignment) proposed for displaced vision (Redding et al., 2005), we set criteria for perceptual adaptation analogous to realignment as follows: 1) behavioral changes observed in cross-modal spatial judgment tasks in which one's own body is not seen, 2) behavioral changes emerged in relatively late adaptation period, and 3) aftereffects are produced.

It seems that a five-week adaptation period was not sufficient for one participant (M2), but for the other three participants, the results indicated evidence of perceptual adaptation based on the above criteria. As shown in Table 1, the response pattern for the VM and SV tasks provides evidence for perceptual adaptation in our criteria. In these tasks, the three participants showed restoration of correct responses in the second to third week, as well as aftereffects immediately after the adaptation period. In addition, the robustness of the aftereffects was related to how early significant adaptation (error reduction) was achieved during the adaptation period. These results are an indication of slowly developed perceptual adaptation analogous to realignment. Moreover, to borrow the word realignment, the results indicate that realignment occurs not only for the visuo-motor reference frame, but also for the visuo-somatosensory reference frame, as observed in the SV task.

The fMRI data revealed anticipated bilateralization of the V1 receptive field starting from the third week of adaptation. This late change is consistent with the neurophysiological changes in monkeys observed well after reaching behavior was restored (Sugita, 1996). Because the monkeys did not have prior knowledge of the nature of the reversing spectacles unlike human participants, the consistency with monkey results indicates that the bilateralization of the V1 receptive field is not due to intentional processes. Notably, this type of neural change appeared to approximately synchronize with the behavioral change in the SV task in our participants. The present data based on the passive observation task are not enough to clarify what kind of global network is involved with the bilateral V1 responses.

Table 1
Observed changes in the adaptation period (early or late changes) and post-adaptation period (aftereffect) in each task (++ indicates a continuous change, + indicates a transient change or aftereffect, - indicates no change, and NA indicates that the data are not available).

Participant	Early changes in adaptation				Late changes in adaptation				Aftereffects			
	KS	F1	M1	M2	KS	F1	M1	M2	KS	F1	M1	M2
Task												
reaching	++	++	++	++	-	-	-	-	+	+	+	+
VM	-	-	-	-	++	++	++	+	+	+	+	-
SV	-	-	-	-	++	++	++	+	+	+	+	-
AM	-	-	-	-	+	+	+	+	?	-	-	-
SM	-	-	-	-	-	-	-	-	-	(-)	(-)	-
fMRI	NA	-	-	-	NA	+	+	+	NA	+	+	+

Note: The post-adaptation measurement for the SM task was missing for F1 and M1, but it is natural to estimate that the aftereffect was absent as there were no changes of performances in the adaptation period (Fig. 3a).

However, the synchrony between the emergence of the bilateral V1 responses and the error reduction in the SV task suggests that an inter-hemispheric interaction is somehow related to visuo-somatosensory reorganization for left–right reversed vision. The bilateral V1 responses were maintained only for one or two weeks during the adaptation period, indicating its transient role in reorganization. It may be that when reorganization is completed, the newly formed visuo-somatosensory relationship is represented in other brain regions.

The observed aftereffect in the present fMRI data suggests that switching back to the old reference frame is not an automatic, effortless process but requires some kind of neural and behavioral practice. It should be noted that participant M2 also showed an aftereffect in the fMRI data, although he did not exhibit behavioral aftereffects in the VM and SV tasks. The neural aftereffect suggests that behavioral aftereffects would also occur for him if a longer adaptation period was given.

Is the visuo-somatomotor reorganization generalized to other reference frames? In fact, the AM task showed a transient generalization, eliciting errors in synchrony with the emergence of the adaptive correct responses in the SV task. Thus, the visuo-somatomotor reorganization was initially (and erroneously) generalized to the auditory-motor relationship, but such a generalization disappeared later. This transient error in the AM task is consistent with the previous results for long-term wedge prism experiments, namely, transient errors in pointing a sound source (Hay & Pick, 1966, Experiment 1 and 2). In wedge prism studies, short-term experiments have generally observed such errors in pointing to a sound source and pointing straight ahead (Harris, 1963; Hatada et al., 2006; Hay & Pick, 1966; Michel et al., 2007; Redding & Wallace, 2009) and those errors have been assumed to represent a proprioceptive change of the pointing arm, namely, a shift of the felt arm position toward the prism displacement. In the case of reversed vision, it is unlikely that a right hand is felt as if located at the position of a left hand when the hand is not seen, because our results for the SM task did not show any response changes. As mentioned earlier, we proposed a distinction between the exocentric (auditory) and egocentric (somatosensory) layout of the target to explain the presence/absence of the transient change. It may be that early perceptual adaptation occurs for the exocentric space irrespective of sensory modality. However, the perceptual adaptation would further proceed such that the error-eliciting auditory-motor reorganization is corrected back for the purpose of adaptive behavior. If not, one cannot avoid a collision with an approaching car that is only heard. Eventually, only adaptive visuo-somatomotor reorganization will be enhanced. According to this view, 'proprioceptive change,' if any, is not a change by itself, but in relation to the exocentric space. Therefore, it may represent generalization of visuo-motor reorganization to non-visual exocentric spatial targets. Wedge prism studies often use sound sources and straight ahead (an extended plane of the body midline) as pointing targets without vision. It is also worth pointing out that both of these targets have a non-visual exocentric nature. A recent study

showed that cortical somatosensory suppression transiently occurs at an early stage of adaptation in tracing with mirror-reversed vision (Bernier, Burle, Vidal, Hasbroucq, & Blouin, 2009). It is possible that 'proprioceptive change' in prism adaptation is also based on such cortical somatosensory suppression in relation to the exocentric space. The present results suggest that early perceptual adaptation contains generalization of visuo-moto reorganization to the non-visual exocentric space, and at an advanced stage, perceptual adaptation attains differentiation between prism-relevant visuo-somatomotor and the other cross-modal relationships. Such a time course, generalization first and differentiation next, is consistent with results for long-term adaptation to displaced vision (Hay & Pick, 1966, Experiment 2) in which early errors in pointing to a sound source and pointing straight ahead almost disappeared in about 3 days after peaking at 12 h. Of course, the time scale is very different between the two optical transformations (12 h in displaced vision versus 3 weeks in reversed vision), but the exocentric space may be a useful concept to understand the transient increase in errors in the non-visual domain during adaptation.

The exocentric versus egocentric distinction is also useful to understand the spatial layout of the tasks in the present study. In the four perceptual tasks, we used three stimulus modalities (visual, auditory, and somatosensory) and two response modes (manual or verbal). While the visual and auditory stimuli were exocentric, the somatosensory stimuli were egocentric. For the response mode, the manual response was egocentric, but the verbal response concerned exocentric visual reference points. Hence, the spatial layout of the SV task requested 'egocentric–exocentric' sensory-sensory matching, and that of the SM task 'egocentric–egocentric' sensory-motor matching. With this framework, the present results for the four perceptual tasks indicate that an 'exocentric–egocentric' relationship (VM, SV, and AM) is newly acquired in adaptation to reversed vision, either stably or transiently. The 'egocentric–egocentric' somato-motor relationship is not altered, presumably due to the close connection between the somatosensory and motor systems.

To observe perceptual adaptation with our criteria took rather a long time (a few weeks or more). While participants develop a representation for the new (reversed) visuo-somatomotor relationship during the adaptation period, the conflicting old representation presumably still exists as suggested qualitatively (Kohler, 1964; Stratton, 1897) and quantitatively (Sekiyama et al., 2000) in previous research. The present results confirmed that it is not until a few weeks into the adaptation period that the new representation can dominate the old one.

Adaptive performance modulation occurred slightly earlier for the VM task compared with the SV task. This is probably because the stimulus–response relationship in the VM task was similar to that learned in daily life in the adaptation period; thus, visuo-motor habits were more easily transferred in the task. In this sense, the VM task may include an aspect of recalibration. In contrast, to attain correct responses in the SV task, in which matching between a somatosensory

stimulus and visual reference points was requested, a more established representation for the new visuo-somatosensory relationship should be acquired. In this sense, the SV task was primarily perceptual, and visuo-somatosensory reorganization is analogous to realignment. Thus, we could measure perceptual adaptation to reversed vision analogous to 'realignment' following an approximately three-week adaptation period. The aftereffect for the SV task suggests that the new visuo-somatosensory relationship can dominate the old one until the day after removal of reversing spectacles unless visual feedback is present in the task.

Concerning the visuo-somatosensory reorganization, one participant (M1) showed behavioral changes in the SV task only for stimuli presented on the hands, but not for the head or trunk (bottom of the neck). Others showed a 'hand precedence' in that the hands preceded the other body parts in restoring correct responses, with subsequent generalization to the head and trunk. These results raise a possibility of multiple visuo-somatosensory reference frames for different body parts. In fact, a long-term wedge prism experiment by Hay and Pick (1966, Experiment 2) showed that early components of adaptation are concerned with a hand-related reference frame (they called this 'proprioceptive adaptation'), including transient errors in pointing to a sound source or pointing straight ahead, but later components are concerned with a head-related reference frame (they called this 'visual adaptation'). How such multiple visuo-somatosensory reference frames differentially contribute to space perception deserves future research (also see Howard, 1982; Redding & Wallace, 1997).

Overall, the present results share important aspects with those of the long-term wedge prism study by Hay and Pick (1966). The primary similarity was found in the transient errors in the AM task, and these could be explained by the 'generalization first, differentiation next' principle for exocentric space. Another similarity can be pointed out in the roles of hand-related and head-related reference frames at different stages. Of course, there were some differences between the two optical transformations. The most obvious difference was in the time scale for adaptation (3 weeks for the reversed vision was equivalent to 12 h for displaced vision), perhaps due to the difference in the amount of optical transformation. Another difference was the large individual differences in our participants, which was not the case for displaced vision. The reasons for the large individual differences are not clear, but it is suggested that some higher-order processes could be involved in perceptual adaptation to reversed vision in which initial cross-modal conflict is very obvious and confusing. The interhemispheric interaction observed in the fMRI data may also indicate the involvement of higher-order processes, but due to the limited scope of the data, this remains a question for further research.

Did Stratton (1897) attain perceptual adaptation in terms of our criteria? It is difficult to infer his adaptation for rotated vision (reversed in both left–right and up–down dimensions) from our left–right reversal data. If his description of 'the harmonization of the new experience' on the last day of adaptation was not due to visual capture (although we do not know), we can speculate that he was at the beginning of perceptual adaptation when correct responses in the VM task can be observed. Concerning aftereffects, his introspection indicates no aftereffects for upright vision ('It was hardly the feeling that things were upside down', p. 470), but possible aftereffects for left–right localization ('I found myself more than once at a loss which hand I ought to use to grasp the door-handle at my side', p. 470). Thus, left–right reversal may more easily cause realignment than up–down reversal. The neural aftereffects in the bilateral V1 receptive field in our participants suggest that the left–right symmetrical structure of the brain hemispheres plays a role in the adaptation to left–right reversed vision.

5. Conclusion

The present study showed the time course of human adaptation to reversed vision over more than one month of adaptation. After rapid

behavioral adjustment in the reaching task within five days, perceptual adaptation took place as late changes and also as aftereffects upon removal of reversing prisms. The perceptual adaptation initially occurred as visuo-motor reorganization in about two weeks, and it was stably generalized to visuo-somatosensory reference frames within about three weeks of adaptation. The generalization of visuo-motor reorganization also transiently took place for an auditory-motor reference frame, but it disappeared later. The fMRI data showed a neural change in synchrony with the visuo-somatosensory reorganization, suggesting the role of interhemispheric interaction in perceptual adaptation to left–right reversed vision. These results show that perceptual adaptation as realignment of different spatial coordinates does occur for left–right reversed vision in about three weeks, transiently accompanying global cross-modal interactions.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.actpsy.2012.05.011>.

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