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RESEARCH NOTE

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Long-lasting aftereffects of prism adaptation in the monkey

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Abstract The errors in target-reaching that are produced by laterally displacing vision with wedge prisms decrease with trials (prism adaptation). When the prisms are removed, errors in the opposite direction are observed (aftereffect). We investigated the size of the aftereffect 24 h and 72 h after a monkey had adapted to a visual displacement (30 mm), with rapid reaching movements. The aftereffect more than half of the size of the displacement was observed when the effect was tested immediately after the monkey had been exposed to the displacement for 50 trials. In contrast, the aftereffect was not observed at 24 h even when the monkey had been exposed to the displacement for 250 trials. However, when the monkey had been exposed for 500 trials, significant aftereffects more than half of the size of the displacement were observed at 24 h and 72 h. When both arms were adapted to opposite prism displacements, the long-lasting aftereffect was further shown to be specific for the arm used during the exposure. The results indicate that the aftereffects of prism adaptation last for at least 3 days, though more than 200 trials of additional repetition are required to consolidate the short-term effects into long-lasting ones.

Keywords Reaching · Arm movements · Motor learning · Bimanual transfer · Consolidation · Monkey

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Introduction

The ability to accurately reach towards a visual target is disturbed after the visual field is displaced by wedge prisms. However, this ability recovers with practice (prism adaptation; for review, see Welch 1978). When the prisms are removed, the subjects err by reaching in the direction opposite the prism displacement (aftereffect). The aftereffect persists for 24 h (Lackner and Lobovits 1977) or even more (Klapp et al. 1974) in human subjects, suggesting that a brief exposure to prismatic displacement elicits long-lasting changes in the nervous system. In this study, we examined the duration of the aftereffect in the monkey.

Materials and methods

One monkey (*Macaca fuscata*, 7.5 kg) was used. The experiments were approved by the Institutional Committee on Animal Experimentation, and followed the *Guiding Principles for the Care and Use of Animals* approved by the Council of the Physiological Society of Japan. The monkey was trained to make rapid reaching movements toward a visual target that appeared on a concave cylindrical screen (r=200 mm) located 200 mm from the eyes. The monkey reached from a button positioned 200 mm below the eyes in the midsagittal plane. The cylindrical screen was positioned so that its axis passed vertically through the midpoint of the two eyes. A trial began when the monkey pressed the button. A target then appeared in a square target zone (40 mm×40 mm) in the straight-ahead direction on the screen after a random delay (800–1,200 ms). One target was chosen randomly from nine targets that were positioned three by three, with an even space of 20 mm in the square target zone. The monkey had to release the button within 240 ms of the appearance of the target and touch the screen within 300 ms of releasing the button. The peak velocities of movements averaged around 2 m/s. The monkey's view of its hand and of the target was blocked at the release of the button by liquid-crystal shutters in front of the eyes. The shutters opened again when the screen was touched, allowing the monkey to see the target and the final position of its hand for 300 ms. The touch and the touch position were detected with a touch sensor (Nihon-Binary, custom made) that covered the surface of the cylindrical screen. The monkey had to hold the final position of its hand for 1,200 ms until given a reward. The size of the reward was inversely proportional to the magnitude of the error, to

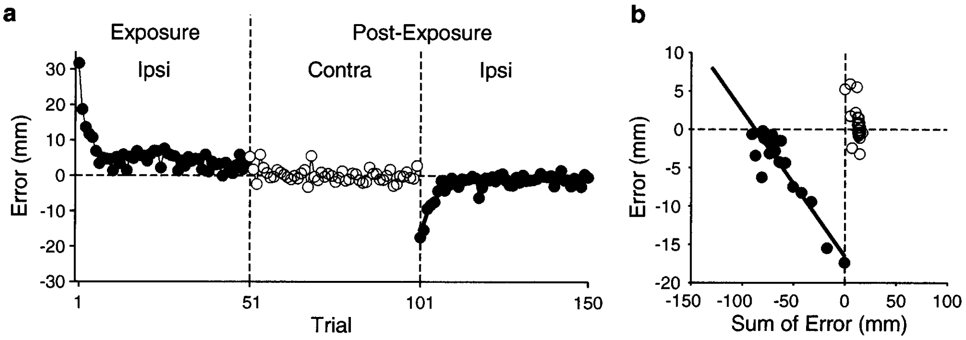


Fig. 1a, b Aftereffects of prism adaptation immediately after the exposure. **a** Mean horizontal errors (*ordinates*) from eight experiments plotted against trial sequence (*abscissa*). Errors in the direction of prism displacement (right or left) are indicated as positive. *Black dots* show mean errors with the arm used during the exposure (*Ipsi*), and *white dots* show mean errors with the contralateral arm (*Contra*). Note the little transfer of adaptation from one arm to the other. **b** Horizontal errors in the postexposure period, plotted against the cumulative sum of errors (See Materials and methods). Errors in the initial 20 trials are plotted for the contralateral (*white dots*) and ipsilateral (*black dots*) arms. The regression line for the ipsilateral arm is superimposed

encourage accurate reaching (Kitazawa et al. 1998). It took 3–4 s to complete one trial.

Two pairs of motor-driven wedge prisms were placed behind the shutters, just in front of the eyes. The device is designed to achieve a desired displacement of 0–30 D (0–16.7°) in any direction with a command from a PC (NEC, Xa16). In this study, one of two lateral displacements, 15 D (8.5°) to the right or 15 D to the left, was used during the prism-exposure period, and zero displacement was used in the pre- and postexposure periods. A cylindrical screen was chosen so that the prismatic displacement caused little, if any, changes (e.g., tilt) in the visual scene experienced by the monkey. The position of the target zone on the screen was displaced to compensate for the prismatic displacement (Kitazawa et al. 1995).

Immediate aftereffects

To see the size of aftereffects immediately after the exposure, and to examine the size of bimanual transfer of adaptation from one arm to the other, the monkey was exposed to rightward or leftward displacement (15 D, 30 mm) for 50 trials with either of the two arms (experiment 1). The monkey was immediately tested for the aftereffects under zero-displacement with the arm contralateral to the one used during the exposure (50 trials), and then tested with the arm used during the exposure (50 trials). Each of four types of experiments (two directions by two arms) was repeated twice in a pseudo-random order.

Long-term aftereffects

Before the visual field was displaced, the monkey made 500 reaching trials under zero displacement (preexposure). The mean horizontal error relative to the target was less than 2 mm in all preexposure periods. On day 1, the monkey was exposed to a prism displacement of 15 D (30 mm) for 250 trials (experiment 2) or 500 trials (experiment 3). It took about 15 min and 30 min to complete the 250 trials and 500 trials, respectively. The monkey was then returned to its cage for 24 h. During this period after being exposed to the displacement, the monkey showed no apparent difficulty in retrieving food or playing with toys. The next day (day 2), 24 h later, the monkey was tested for aftereffects under zero-displacement. Each type of experiment was repeated twice, once for each arm, and once for each direction of displacement.

In experiment 4, the monkey was exposed to the two opposite displacements, one for each arm (Prablanc et al. 1975). It was exposed to rightward displacement with its left arm (500 trials) and then exposed to leftward displacement with its right arm (500 trials) on the same day (day 1). The monkey was tested about 72 h later (day 4), under zero displacement, first with its left arm (100 trials) and then with its right arm (100 trials).

Data analysis

Errors in the postexposure period were analysed using a discrete model (Kitazawa et al. 1995) formulated as:

$$h(n) = h(n-1) - k\,h(n-1) \tag{1}$$

where $h(n)$ and k denote the horizontal error in the nth trial and a constant rate at which the error is assumed to decrease, respectively. The model defines a learning algorithm, in which the error decreases by an amount proportional to the error in the preceding trial. Equation 1 can then be transformed into

$$h(n) = h(1) - k\sum_{i=1}^{n-1} h(i) \tag{2}$$

which predicts that the error in the nth trial is linearly related to the summation of errors from the first to the (n-1)th trials. The horizontal error $h(n)$ was then plotted against the summation of errors (error-summation scattergram) to test whether the model could explain the data (Figs. 1b, 2b, 3b). The slope of the regression line gives an estimate of k, termed the “correction rate”, in the model equation. The intercept of the ordinate gives an estimate of the initial error $h(1)$, namely the size of the aftereffect. We judged that the aftereffect was significant when the linear regression was significant (F-test) and that the estimate of the initial error was in the direction opposite to that of the visual displacement during exposure. Initial 20 errors in the postexposure period were used for the quantitative analysis.

Results

Immediate aftereffects

Before the exposure, the horizontal error distributed around zero (0.3±5.4 mm, mean ± SD). During the exposure period, the monkey initially made errors in the direction of displacement of about the size of displacement (30 mm), and the error decreased with trials (Fig. 1a, trials 1–50). When the monkey was tested with the contralateral arm immediately after the exposure (Fig. 1a, white dots), no significant aftereffect was observed. The monkey, however, misreached by 17 mm on average, when it was tested again with the arm used during the exposure (Fig. 1a, trial 101). The results show that 50 trials of exposure to the

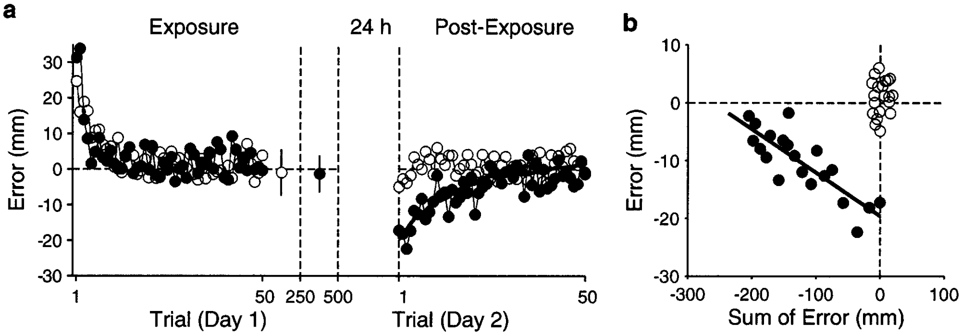


Fig. 2a, b Aftereffects of prism adaptation at 24 h. **a** Horizontal errors (*ordinates*) plotted against trial sequence (*abscissa*). Errors in the direction of prism displacement (right or left) are indicated as positive. *White dots* show mean errors from two experiments in which the monkey was exposed for 250 trials (experiment 2). *Black dots* show mean errors from two experiments in which the monkey was exposed for 500 trials (experiment 3). The mean error in the exposure period from trial 51 to 250 in experiment 2 (*white dot*) and those from trial 51 to 500 in experiment 3 (*black dot*) are shown, respectively, with *error bars* (± SD). Note the apparent aftereffect and subsequent decrease of error after 500 trials of exposure (*black dots* in postexposure). The *thick line* shows the model prediction using Eq. 1 in Materials and methods. **b** Error-summation scattergram in the postexposure period. Data from the initial 20 trials for each arm are plotted. The regression line for the data in experiment 3 is superimposed

visual displacement were sufficient to produce significant aftereffects ($F_{1,19}$=101.3, $P<10^{-8}$, r=0.85) more than half of the size of the displacement (16.5 mm, y-intercept in Fig. 1b), when the effect was tested immediately after the exposure, and that the aftereffect was specific to the arm used during the exposure. These results agree well with those of human subjects (Kitazawa et al. 1997).

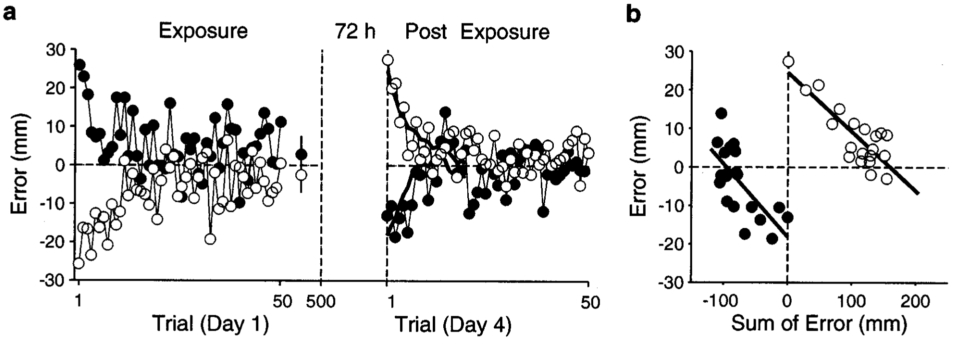
Aftereffects at 24 h

During the exposure period, the monkey was exposed to the displacement for 250 trials in two experiments (white dots in Fig. 2a) and for 500 trials in two others (black dots) to evaluate the effect of the number of trials during the exposure. The aftereffect was tested 24 h later. The aftereffect was apparent (about 20 mm) after 500 trials, whereas it was negligible after 250 trials. The difference became more apparent when the error was plotted against the cumulative sum of error (Fig. 2b): the linear regression was significant ($F_{1,19}$=40.0, $P<10^{-5}$; r=0.69) after 500 trials but was not ($F_{1,19}$=0.27, $P>0.6$, r=0.01) after 250 trials. The y-intercept of the regression line (Fig. 2b), an estimate of the size of the aftereffect, was 19.6 mm, more than 60% of the prismatic displacement (30 mm).

Aftereffects at 72 h

The aftereffect at 72 h was tested in another experiment. In this experiment, the left arm was exposed to rightward displacement (black dots, Fig. 3a) and the right arm to leftward displacement (white dots), to test whether the aftereffect is arm-specific. Based on the results at 24 h, the monkey was exposed to the displacement for 500 trials with each arm. Seventy-two hours later, the left arm misreached to the left (black dots in Fig. 3a), and the right arm to the right (white dots), that is, in opposite directions. The estimated size of the aftereffect was 18 mm for the left arm (a regression line on black dots in Fig. 3b) and 25 mm for the right arm (white dots in Fig. 3b). The aftereffect was significant for both the left arm ($F_{1,19}$=16.5, P=0.0007, r=0.48) and the right arm ($F_{1,19}$=40.4, $P<10^{-5}$, r=0.69). The results clearly show that the adaptation for one arm was acquired independently of the other, and that the aftereffects lasted for at least 3 days.

Fig. 3a, b Aftereffects at 72 h. **a** Horizontal errors in reaching with the right arm (*white dots*; trials 1–500 on day 1 and 1–50 on day 4) and the left arm (*black dots*; trials 501–1,000 on day 1 and 101–150 on day 4) are plotted against the trial sequence. Rightward errors are indicated as positive. *Thick lines* in the postexposure period show the model prediction using Eq. 1. **b** Error-summation scattergram in the postexposure period. Data from the initial 20 trials for each arm are plotted. Regression lines are superimposed



Discussion

This study shows that the aftereffect of prism adaptation persisted for at least 3 days in a monkey that was exposed to prismatic displacement for 500 trials lasting about 30 min. It is worth noting that the aftereffect at 24 h was not apparent with 250 trials of exposure (Fig. 2a, white dots), whereas the immediate aftereffect was apparent with only 50 trials of exposure (Fig. 1a, black dots). The results clearly show that the exposure up to 250 trials had only transient effects on the nervous system, fading within 24 h, whereas some kind of consolidation process is triggered during the additional repetition of 250 trials. This is surprising because the error during the exposure period had already decreased to a nil asymptote by the 250th trial (Fig. 2a). It is the additional repetition of reaching with approximately zero errors that was crucial for triggering the consolidation. Because the size of the aftereffect at 72 h (18 mm and 25 mm; Fig. 3) was comparable with the size of the aftereffect at 24 h (20 mm, an estimate from the two experiments shown in Fig. 2), the decay of the aftereffect might be very slow, possibly persisting for weeks once it is consolidated.

The size of the long-lasting aftereffect in this study (4–6° to the 8.5° of displacement) was much larger than the size of the aftereffects at 24 h reported in previous human studies: a mean aftereffect of 1.2° to an 8° displacement in the study by Klapp et al. (1974), and a mean aftereffect of 2.6° to a 11.5° displacement in the study by Lackner and Lobovits (1977). The larger size of aftereffects in the present study might have resulted from the larger number of arm movements (500 trials) during the exposure (around 30 min) than those in the previous studies; arm thrusts were repeated for a total of 15 min in the study by Klapp et al. (1974), and only 200 of arm movements were repeated in the study by Lackner and Lobovits (1977) in 10 min. Other experimental conditions specific to our study such as the exposure with rapid reaching, complete terminal exposure at the end of the movement, and the elimination of changes in the visual scene (Kitazawa et al. 1995) might have additionally contributed to the larger aftereffects.

In agreement with a comparable human study (Kitazawa et al. 1997), the adaptation in the present study was shown to be specific at least for the arm not only in the short term (Fig. 1) but also in the long term (Fig. 3). In addition, we infer that the adaptation was velocity specific as was shown in the human study (Kitazawa et al. 1997). Without the velocity specificity, aftereffects must have dissipated during the stay in the cage owing to much slower but frequent arm movements, such as reaching for foods and toys.

The arm specificity in the adaptation precludes a possibility that the adaptation was a change in visual coordinates (Harris 1965; Welch 1978) that must affect both arms. Assuming in addition that the long-term adaptation in this study was specific for the type of motor skill as well as for the velocity (Baily 1972; Martin et al. 1996; Kitazawa et al. 1997), the adaptation would not have been a change in the felt hand position (Harris 1965; Welch 1978) but rather a motor-response learning (Harris 1965). The paradigm of adaptation with long-term aftereffects may thus provide a useful animal model for studying how independent motor skills are acquired, consolidated, and stored in the brain, a topic of intense debate (Wolpert and Kawato 1998). Target regions of study may include the cerebellum (Baizer et al. 1999), the premotor cortex (Kurata and Hoshi 1999), and the intraparietal area (Clower et al. 1996), which have been reported to be involved in prism adaptation.

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