Exp Brain Res (2002) 144:258–261
DOI 10.1007/s00221-002-1089-6

RESEARCH NOTE

Shigeru Kitazawa · Ping-Bo Yin

Prism adaptation with delayed visual error signals in the monkey

Received: 27 November 2001 / Accepted: 3 March 2002 / Published online: 10 April 2002

Abstract Errors in reaching produced by displacing the visual field with wedge prisms decrease with trials, even when the error is not revealed until the completion of the movement. To examine how much additional delay in visual feed-back the monkey can compensate for, the effects of delaying the visual error signals were studied by presenting the terminal visual images after one of five delays, ranging from 0 to 500 ms. Adaptation was fastest when the delay was 0 or 10 ms, decreased significantly with a delay as small as 50 ms and approached zero when the delay was 500 ms. The size of the after-effect decreased with the delay accordingly. The results indicate that prism adaptation in the monkey critically depends on the availability of visual information within 50 ms of completion of the movement. Comparing the results with those for humans, we suggest that monkey and human share a mechanism of adaptation with a short time window of 50 ms, but the monkey lacks another mechanism of adaptation that allows a visual delay of 500 ms or more in humans.

Keywords Prism adaptation · Reaching · Arm movements · Motor learning · Visual delay · Error signals · Monkey

S. Kitazawa (✉) · P.-B. Yin
Neuroscience Research Institute,
National Institute of Advanced Industrial Science and Technology,
1-1-1 Umezono, Tsukuba 305-8568, Japan
e-mail: kitazawa-s@aist.go.jp
Tel.: +81-298-615176, Fax: +81-298-615849

S. Kitazawa
PRESTO, JST, 1-1-1 Umezono, Tsukuba 305-8568, Japan

P.-B. Yin
CREST, JST, 1-1-1 Umezono, Tsukuba 305-8568, Japan

Present address:
P.-B. Yin, Laboratory of Neuropsychology, NIMH,
NIH, Bldg. 49, Rm 1B80, Bethesda, MD 20892, USA

Introduction

The ability to accurately reach towards a visual target is disturbed if the visual field is displaced by wedge prisms. This ability recovers with practice (prism adaptation; for reviews see Harris 1965; Welch 1978). When the prisms are removed, subjects err by reaching in the direction opposite to the prism displacement (after-effect). Adaptation occurs not only when vision is concurrent with the movement (concurrent exposure), but also when the error is revealed at completion of the movement (terminal exposure). With terminal exposure, the visual images of the target and the hand at the end of reaching provide information on the error that has resulted from the movement. In a previous study (Kitazawa et al. 1995), the effects of delaying the terminal visual error information were studied in human subjects. A delay as short as 50 ms reduced both the rate and the amount of prism adaptation by 30–40% compared to zero delay. This indicates that a considerable part of the adaptation in the human requires the association of motor outputs with visual error signals given within a brief time window. To further elucidate the underlying neural mechanisms, it is desirable to develop an animal model of the phenomena observed in the human. In this study, we examined the effects of visual delay on prism adaptation in a 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 apparatus was as described elsewhere (Yin and Kitazawa 2001). The monkey was trained to make rapid reaching movements towards a visual target that appeared on a concave cylindrical screen (radius=200 mm) located 200 mm from its eyes. The monkey reached from a button positioned 200 mm below its eyes in the midsagittal plane. A trial began when the monkey pressed the button and, after a random delay (800–1,200 ms), a target appeared in a square target zone

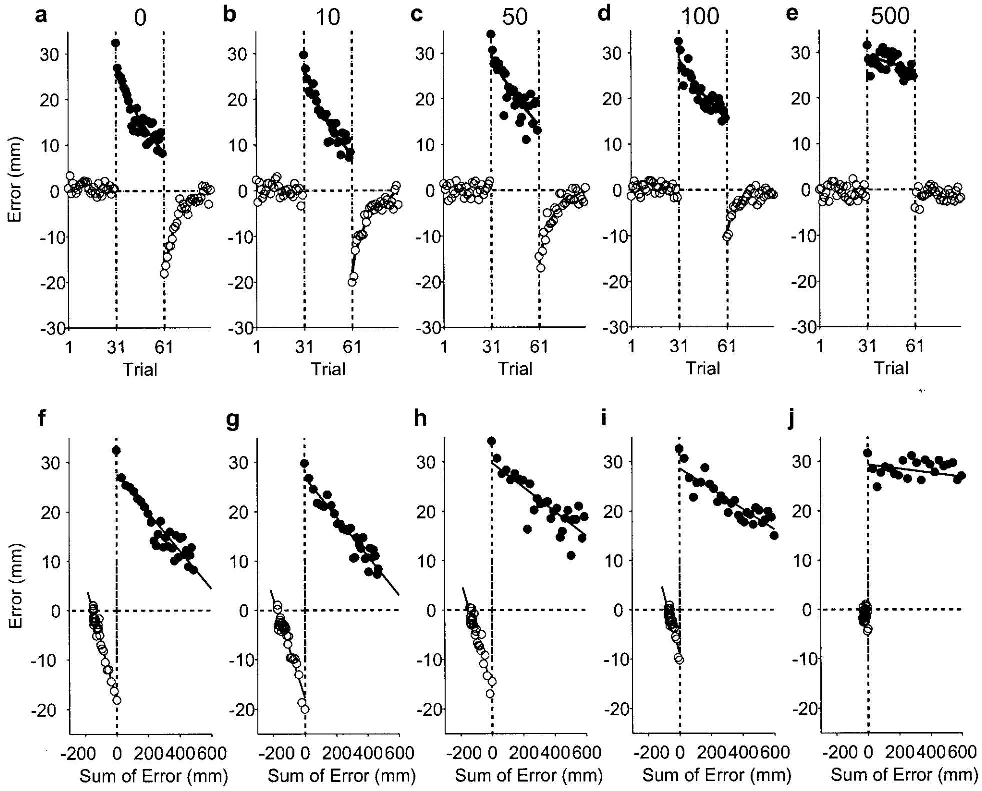

Fig. 1a–j Prism adaptation with visual delays. **a–e** Horizontal errors (*ordinates*) plotted against trial sequence (*abscissa*). Errors in the direction of prism displacement (right or left) are indicated as positive. Each *dot* represents the median of the errors from 20 experiments. *Black dots* show median errors during exposure to prism displacement (15 diopters, 30 mm) and *white dots* those during the pre- and postexposure periods under zero displacement. The length of visual delay in milliseconds during the exposure period is indicated above each panel. **f–j** Error-summation scattergrams for the exposure (*black dots*) and postexposure (*white dots*) periods. Data shown in **f–j** correspond to those in **a–e**. *Regression lines* are superimposed

(40×40 mm). One target was chosen randomly from nine targets that were evenly spaced 20 mm apart in a 3×3 grid. 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 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 its eyes. The shutters opened after a given delay after the touch, allowing the monkey to see the target and the final position of its hand for 300 ms. 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 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. In this study, one of two lateral displacements was used during the prism-exposure period, 15 diopters (8.5°) to the right or 15 diopters to the left, and zero displacement was used during the pre- and postexposure periods. A cylindrical screen was chosen so that the prismatic displacement would cause little, if any, changes (for example, 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).

One experiment consisted of three periods: pre-exposure (30 trials), exposure (30 trials) and postexposure (30 trials). During the pre- and postexposure periods, the prisms were set to zero displacement by the motor and the shutters were opened with no delay. During the exposure period, the prisms were set to one of the two displacements: 15 diopters to the right or 15 diopters to the left. The shutters were opened after a given delay period, which was varied randomly from one experiment to another. Five delay periods were used: 0, 10, 50, 100 and 500 ms. Thus, there were ten conditions consisting of two directions of displacement and five delay periods. The monkey completed 100 experiments to cover the ten conditions five times for each arm. Thus, there were 20 experiments with each delay period (two directions, two arms and five repetitions). The experiments were randomly ordered for each arm.

Data from 20 experiments with the same delay period were combined to make five groups of data. The median of the errors ($n=20$) measured in the direction of visual displacement was calculated for each of 90 trials. Errors during the exposure and postexposure periods were analysed using a discrete model (Kitazawa et al. 1995; Yin and Kitazawa 2001) formulated as:

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

where $h(n)$, $\tilde{h}(n)$ and k denote the estimated horizontal error in the nth trial, the observed 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 observed in the preceding trial. Equation (1) can then be transformed into

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

which predicts that the estimated error in the nth trial is linearly related to the sum of the observed errors from the first to the (n–1)th trials. The horizontal error $\tilde{h}(n)$ is then plotted against the summed errors (error-summation scattergram) to test whether the model could explain the data (Fig. 1f–j). 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 $h(1)$. The size of the after-effect was defined as the estimate of the initial error in the postexposure period.

Results

Effects of delay on the rate of adaptation

During the pre-exposure periods (Fig. 1a–e; trials 1–30), the horizontal error was distributed around zero (0.2±5.4 mm, mean ± SD; n=3,000). During the expo-

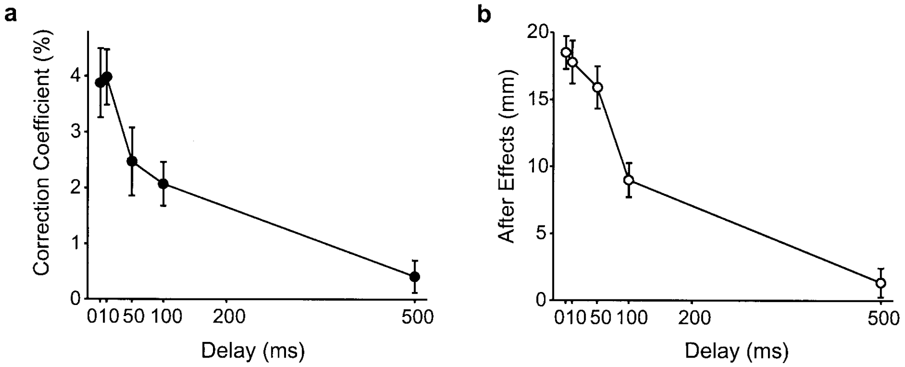

Fig. 2 Effects of visual delay on the rate (**a**) and amount (**b**) of prism adaptation. Correction coefficients (**a**) and the size of after-effects (**b**) are plotted against the visual delay during the exposure period. These values (*dots*) and 95% confidence areas (*error bars*) were estimated from the linear regressions shown in Fig. 1f–j

sure periods, the monkey initially made errors in the direction of displacement of about the size of the displacement (30 mm), irrespective of the visual delay (Fig. 1a–e, trial 31). When the terminal error was given the moment the monkey's hand touched the screen (zero delay; Fig. 1a), the initial error of about 30 mm decreased with trials to less than 10 mm at the end of the exposure period (trial 60). In contrast, when the error was given 500 ms after the touch (Fig. 1e), the error decreased little, and still exceeded 20 mm at the end of the exposure period.

To analyse the effect of the visual delay on the rate of adaptation, the error during exposure periods was plotted against the summation of errors (*black dots* in Fig. 1f–j). The slope of the regression line (k in Eqs. 1 and 2) superimposed on each scattergram shows the correction rate of error per trial. The correction rates were similar with 0- (3.9%; Fig. 1f) and 10-ms (4.0%; Fig. 1g) delays, while they were almost halved with 50- (2.5%; Fig. 1h) and 100-ms (2.1%; Fig. 1i) delays. When the delay was 500 ms (Fig. 1j), the correction rate was as small as 0.41%, one-tenth of that under the zero delay condition. The correction rates are shown with 95% confidence intervals in Fig. 2a. An overlap of two confidence intervals indicates that the two correction rates did not differ from each other significantly. By contrast, an absence of overlap indicates that the difference was significant. It is apparent that the correction rate decreased significantly when the delay was increased from 10 to 50 ms. The correction rate decreased significantly further when the delay was increased from 100 to 500 ms.

Effects of delay on the after-effects

The size of the initial errors in the postexposure periods (trial 61) decreased with visual delay (Fig. 1a–e). The after-effect was about 20 mm, more than half the size of the displacement, with a 0-ms delay (Fig. 1a), but almost disappeared with a 500-ms delay (Fig. 1e). From quantitative analyses with error-summation scattergrams (*white dots with regression lines* in Fig. 1f–j), the size of the after-effect (y-intercepts of the regression lines) was estimated as 18, 18, 16, 9 and 1 mm with 0-, 10-, 50-, 100- and 500-ms delays, respectively. Figure 2b shows that the size of the after-effect decreased significantly when the delay during exposure was increased from 50 to 100 ms and from 100 to 500 ms. It is also worth noting that the correction rates in the postexposure periods (*slopes of regression lines* in Fig. 1f–i) were around 11%, which is two to three times as large as the correction rate during an exposure period with zero delay (3.9%). This might reflect a general tendency that re-adaptation is faster than adaptation.

Discussion

In this study, we report the effects of delaying visual error information on prism adaptation in a monkey. The rate and amount of adaptation were almost halved with a delay of 100 ms. A significant decrease in the rate of adaptation was observed with a shorter delay as small as 50 ms. The results agree well with those for human subjects (Kitazawa et al. 1995), and suggest that the monkey and human share a common mechanism of adaptation that must utilise visual information within 50 ms after the movement.

However, there was a clear difference between these results and those for human subjects. In the monkey, the adaptation almost disappeared with a 500-ms delay, while in the human 40% to 50% of the rate and amount of adaptation observed with a 0-ms delay was evident with a 500-ms delay and was still evident even with a 5,000-ms delay (Kitazawa et al. 1995). Since we only tested one animal in this study, we should be careful in drawing any conclusion on the difference between the two species. However, it is worth noting that the mean rate of adaptation in 11 human subjects with a 500-ms delay (mean 11.4%, n=22) was significantly larger (t-test, P<0.001) than that of the monkey (0.41%) in this study. Therefore, we suggest that another mechanism of adaptation, one that still works even with delays of seconds in the human, (Kitazawa et al. 1995), is absent in monkeys. Such a mechanism, with a long working range in the time domain, would contribute to adaptation with much slower reaching movements, as seen in the human, which was shown to be acquired independently of the adaptation with fast movements (Kitazawa et al. 1997). Therefore, monkeys might not show as large an adaptation with slower movements as they do with fast movements.

This study demonstrated that a monkey can serve as a substitute for a human in studying the mechanism of prism adaptation that critically depends on visual information within a short time window of 50 ms after a movement. We suggest that the cerebellum is a likely candidate for the location of the implementation of such a mechanism, for three reasons. First, prism adaptation is impaired with cerebellar lesions in the macaque (Baizer et al. 1999). Second, the information on terminal errors in reaching is signalled by climbing fibres with an onset latency of 100 ms after the visual input of the error (Kitazawa et al. 1998). In addition, the peak information about the error conveyed by the climbing fibre signals is significantly decreased with a visual delay of 100 ms, compared with the peak information under a zero delay (Kitazawa et al. unpublished observation). Third, climbing fibre signals elicit plastic changes, long-term depression (for review see Ito 2001), in the synapses between the parallel fibres and the Purkinje cells only when the parallel fibre inputs are associated with the climbing fibre signals within a short period. This and other possibilities, such as the contributions of the ventral premotor cortex (Kurata and Hoshi 1999) and parietal cortex (Clower et al. 1996) to prism adaptation, should now be studied at the neuron level in the monkey.

Acknowledgements This work was partly supported by an HFSP Research Grant.

References

Baizer JS, Kralj-Hans I, Glickstein M (1999) Cerebellar lesions and prism adaptation in macaque monkeys. J Neurophysiol 81: 1960–1965

Clower DM, Hoffman JM, Votaw JR, Faber TL, Woods RP, Alexander GE (1996) Role of posterior parietal cortex in the recalibration of visually guided reaching. Nature 383:618–621

Harris CS (1965) Perceptual adaptation to inverted, reversed, and displaced vision. Psychol Rev 72:419–444

Ito M (2001) Cerebellar long-term depression: characterization, signal transduction, and functional roles. Physiol Rev 81: 1143–1195

Kitazawa S, Kohno T, Uka T (1995) Effects of delayed visual information on the rate and amount of prism adaptation in the human. J Neurosci 15:7644–7652

Kitazawa S, Kimura T, Uka T (1997) Prism adaptation of reaching movements: specificity for the velocity of reaching. J Neurosci 17:1481–1492

Kitazawa S, Kimura T, Yin PB (1998) Cerebellar complex spikes encode both destinations and errors in arm movements. Nature 392:494–497

Kurata K, Hoshi E (1999) Reacquisition deficits in prism adaptation after muscimol microinjection into the ventral premotor cortex of monkeys. J Neurophysiol 81:1927–1938

Welch RB (1978) Perceptual modification. Academic Press, New York

Yin PB, Kitazawa S (2001) Long-lasting after-effects of prism adaptation in the monkey. Exp Brain Res 141:250–253