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# Effects of Delayed Visual Information on the Rate and Amount of Prism Adaptation in the Human

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**Accurate reaching towards a visual target is initially disturbed when the visual field is displaced by prisms, but recovers with successive trials. To determine how the improvement depends on the visual error signals associated with the motor output, the time course of prism adaptation was studied with delayed visual information on the error. Subjects were trained to reach rapidly at a target on a tangent screen. Vision was always blocked during the movement, and allowed again only after the index finger touched the screen. One experiment consisted of three sets of 30 trials. In the first set, the subject wore no prisms and vision was allowed without delay. In the second, the visual field was displaced by prisms, and vision was available only after a delay period of 0-10,000 msec while the subjects maintained their final pointing position. Initially, the subject misreached the target by about the amount of visual displacement (60 mm). Errors decreased with trials by an amount proportional to the error in the preceding trial. The rate of decrease of error was generally largest when the delay was 0 msec, became significantly smaller when the delay was 50 msec, and showed only gradual change with longer delays. In the third set, the subject wore no prisms and vision was allowed without delay. Initial misreaching in the direction opposite to the visual displacement, reflecting the amount of adaptation in the second set, was generally largest with no delay (median of 46 mm) and significantly smaller with 50 msec and longer delays (17–33 mm). These results indicate that the rate and amount of prism adaptation depends critically on the availability of visual information within 50 msec of the completion of the movement.**

***[Key words: prism adaptation, visual displacement, visual delay, information feedback, reaching, human]***

When we see a target, we can reach to it accurately in a well-coordinated manner (Flash and Hogan, 1985; Uno et al., 1989). For the relatively fast and well-coordinated reaching movements, feedforward control mechanisms appear indispensable, since feedback control is limited by the physiological delays associated with the limited conduction velocities of efferent and afferent fibers and by the response delay included in the musculoskeletal systems (Katayama and Kawato, 1993). This delay, in turn, makes it difficult for the CNS to improve feedforward control over a discrete motor skill, since the improvement must rely on the error signals (Schmidt, 1975) fed back with the delay. As long as we can generate well-coordinated reaching movements, the CNS must be capable of improving the motor skill in spite of the delay. A fundamental question raised in this article is how much additional delay can be coped with by the CNS. More specifically, we address the question of whether the improvement of rapid reaching movements, which require feedforward control, is impeded by interposing further delays in feeding back the information on the error resulting from the movement.

Numerous investigators have already studied effects of interposing a delay between arm movements and the feedback of the error resulting from the movement. When the error information was given after discrete task movements, no reliable effects of delays were found on the improvement of the motor skill (for review, see Bilodeau, 1966; Salmoni et al., 1984; Adams, 1987). In these studies, however, verbal feedback was generally used. Hence, even "immediate" feedback was given only after a delay of 3–5 sec (e.g., Bilodeau and Bilodeau, 1958), which is already much longer than the physiological delays. Held and his colleagues (Held et al., 1966; Held and Durlach, 1989), in contrast, introduced much shorter delays of 30–3300 msec, feeding back a visually displaced hand position while the subject continuously moved his hand over a plane. They found that the aftereffects caused by the visual displacement significantly decreased when the visual delays were longer than 120 msec (Held and Durlach, 1989) or 300 msec (Held et al., 1966). However, there was no target to be reached in the continuous hand movements and therefore there were no errors to be reduced. Thus, their experiments were not designed to interpose a delay between a task movement and the error resulting from the movement.

In the present study, we examined the improvement in rapid reaching movements after the visual field is displaced by prisms: accurate reaching is initially disturbed by the visual displacement, but recovers with successive trials (for review, see Welch, 1978). In this situation, the visual image of the target and the hand at the end of reaching provides definite information on the error resulting from the movement. To elucidate the effects of delaying the visual error information, the rate and amount of adaptation were studied by presenting the terminal visual images with various delays from zero to 10 sec after the movement. We here report that a delay of as short as 50 msec reduced both the

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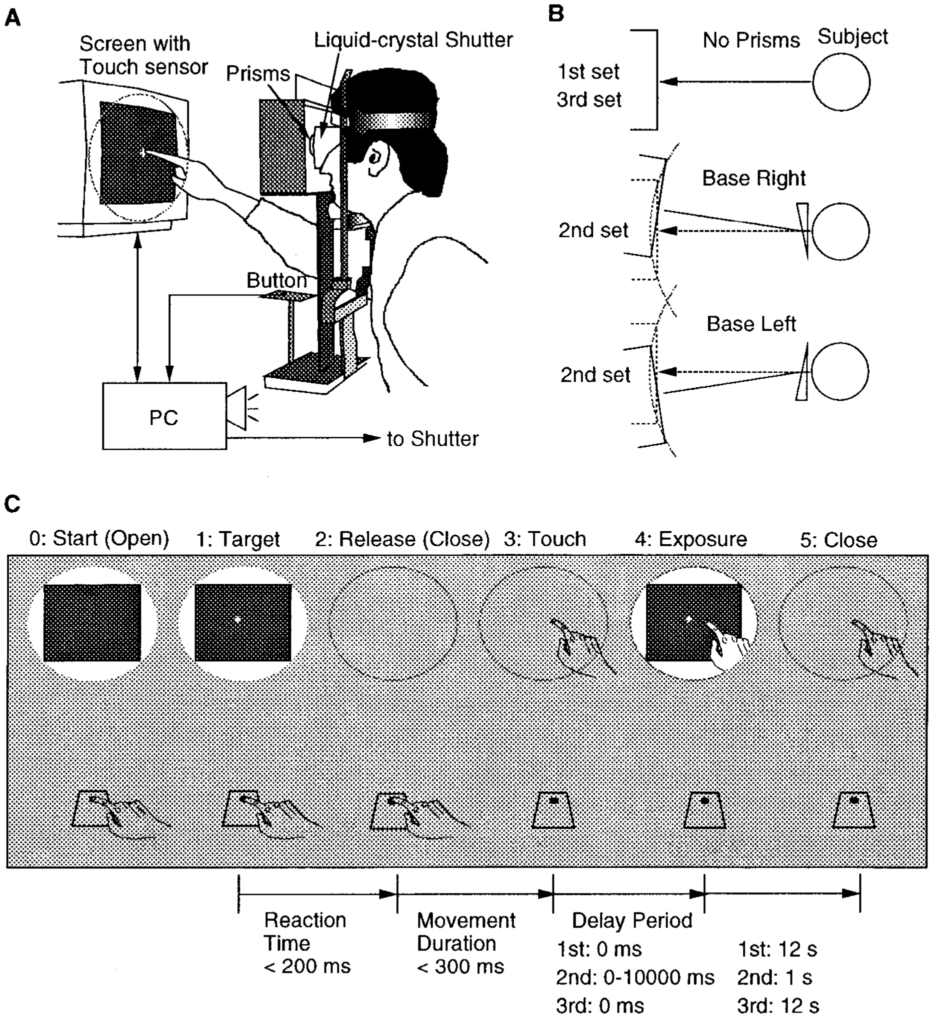

*Figure 1.* Design of experiments. *A,* The subject reached quickly at a target that appeared on a tangent screen (*Screen with Touch sensor*) placed 400 mm away from the subject. He wore a pair of spectacles with liquid-crystal shutters that were opened and closed by a personal computer (*PC*) used for data collection and task control. He viewed through eye pieces that restricted the visual field just over the screen (*oval shape*). Prisms were placed in the eye pieces in the second set (30 trials), while no prisms were used in the first and the third set (30 trials each). *B,* The screen was placed in a straight-ahead direction (*arrow*) of the subject when he wore no prisms in the first and third set (*1st and 3rd set, no prism*). In the second, the screen was displaced along an arc of 400 mm radius (*broken arcs*) according to the direction (*base right or left*) of the prisms (15 diopter), so that the subject viewed the screen in the same direction (*broken arrows*) as in the first set. The actual location of the screen is indicated by *solid lines*, while the perceived location by *broken lines*. Two prisms were placed in front of the eyes, though only one prism is schematically drawn in the figure. *C,* Time schedule of one trial is sequentially shown from left (*0*) to right (*5*). Each column schematically shows the status of the visual field (*oval shape*) and the position of the hand relative to the button and the screen. Shutters opened at 0 (*Start*) when the subject pressed the button. A target appeared at 1 (*Target*) after preceding beeps. Vision was blocked from 2 (*Release*) to 3 (*Touch*) and allowed again (*4, Exposure*) for 12 sec immediately after the touch (*1st and 3rd set*), or for 1 sec after a delay of 0–10,000 msec (*2nd set*). After 12 sec of the touch, a low-tone beep informed the subject to take his hand back from the screen to start the next trial. Intertrial intervals (*0 to the next 0*) were 15 sec throughout the experiment.

rate and amount of prism adaptation by 30–40% compared to those under zero delay.

A preliminary account of this study has appeared elsewhere (Kitazawa et al., 1994).

## Materials and Methods

*Subjects.* Eleven subjects (aged 20–31), one female and 10 male, were used for the experiments. All except one male subject were right-handed. The performance of the female and the left-handed subjects was similar to that of the others. All subjects were normal or corrected-to-normal in visual acuity and had no significant neurological history. All except the two authors (SK, TU) were naive as to the purpose of the experiments.

*Apparatus and general task procedures.* The subject was seated facing a tangent 14 inch CRT screen, 400 mm from the eyes, with his head restrained by a chin rest and a head band (Fig. 1*A*). The subject wore a pair of spectacles with liquid-crystal shutters (PLATO spectacles, Translucent Technology, Toronto), and viewed through opaque tubes that restricted his view of the screen as shown in Figure 1*A,C*. The shutters could change from opaque white to transparent within 1 msec, or vice versa within 5–10 msec (Milgram, 1987) by a control signal from a personal computer (NEC, PC9801DA). A trial was initiated (Fig. 1*C*, 0: Start) by three middle-tone beeps of 800 msec intervals in succession while the subject pressed a button (Button, Fig. 1*A*) with his right index finger (Fig. 1*C*, 0). The button was positioned 300 mm below and 100 mm ahead of the eyes in the midsagittal plane (Fig. 1*A*). These middle-tone beeps were followed by a high-tone beep, at which time a target (cross, 10 mm width) appeared at a random place in a square area (40 × 40 mm) on the screen (Fig. 1*C*, 1: Target). The subject was required to release the button (Fig. 1*C*, 2: Release) within 200 msec of the appearance of the target, to touch the screen (Fig. 1*C*, 3: Touch) within 300 msec of the release, and to hold the final position of the hand and the arm for 12 sec until a low-tone beep instructed the subject to return his hand to the starting position within 1 sec.

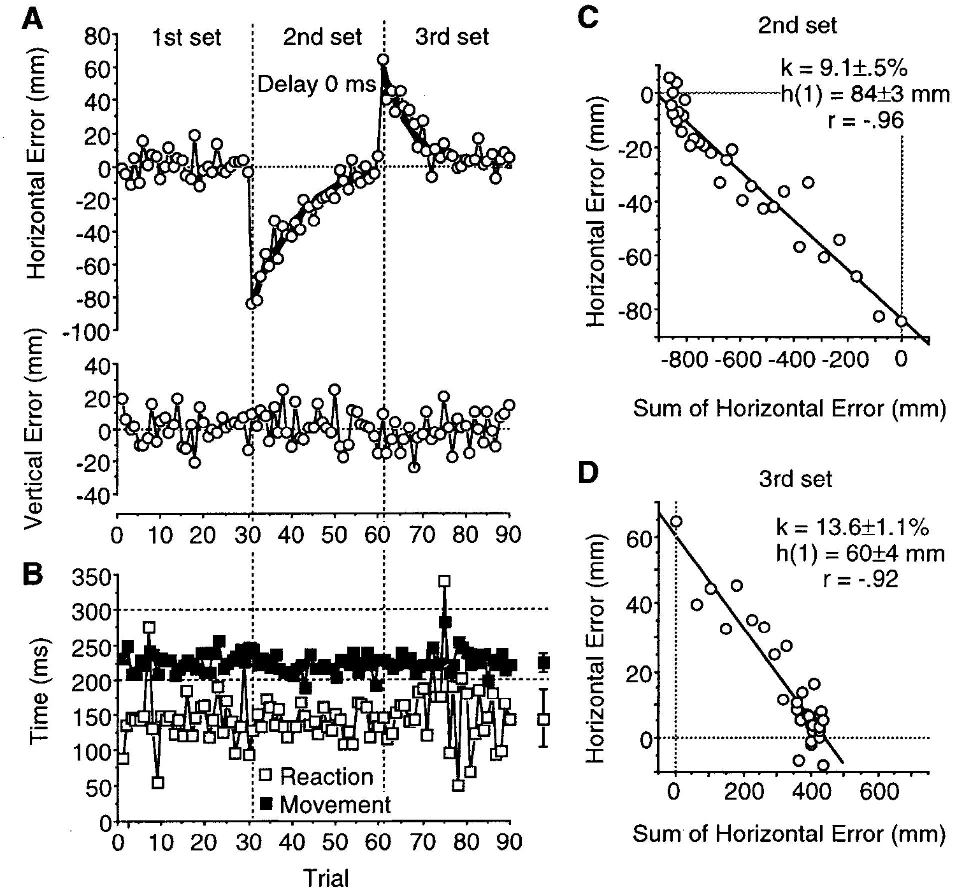

*Figure 2.* Prism adaptation with a 0 msec delay (*subject SK, base left*). *A,* Horizontal and vertical errors relative to the target (*ordinates*) plotted against trial sequence (*abscissa*). Rightward and upward errors are indicated as positive in each plot. *Thick lines* indicate the model predictions using the model eq. (1) described in the Results. *B,* Reaction time (*open squares*) and movement duration (*filled squares*). Means are indicated to the right with error bars (SD). *C* and *D,* Horizontal errors in the second (*C*) and the third (*D*) set are plotted against their summation (error-summation scattergram, see Results for more detail). Slopes (*k,* correction rates) and y-intercepts [*h(1)*, estimated initial errors for each set] of the regression lines are indicated with standard errors estimated by the linear regression analysis. Correlation coefficients (*r*) are also indicated.

Vision of the hand and the arm was blocked at the release of the button (Fig. 1*C*, 2: Release) by the liquid-crystal shutters to eliminate visual feedback during the movement. The shutters were opened again (Fig. 1*C*, 4: Exposure) only after the touch (3: Touch) to allow the subject to see the target and the final static position of the hand.

The reaction time (from 1 to 2 in Fig. 1*C*) and movement duration (from 2 to 3) were measured with a time resolution of 1 msec by the same PC used for the shutter control. The experimenter monitored these values on another PC (Epson, PC286L) connected with the former by an RS232C cable, and informed the subject of the values whenever he failed to respond within the time limits. The position of touch was detected by a transparent sheet of touch sensor (NPC-2000, Nihon Binary, Tokyo, Japan, sampling frequency 100 Hz, resolution 0.15 mm) that tightly covered the surface of the screen. These measured variables and target locations were stored for off-line analyses.

Each subject was instructed to react and reach the target as rapidly as possible, within a limit of 200 msec for the former and 300 msec for the latter. In addition to the rather strict time constraints, subjects were encouraged to touch within 10 mm of a randomly appearing target with no visual feedback to rely on. The subjects were trained until they could perform the task within the time constraints in more than 90% of trials, and within the spatial constraints (< 10 mm) in more than 50%.

*Design of experiments.* One experiment consisted of three sets of 30 trials. In the first set, the subject performed the reaching task without prisms, and visual information was allowed after a 0 msec delay for 12 sec (Fig. 1*C*, 3, 4, 5).

In the second set, the visual field was displaced to the right (base left, Fig. 1*B*) or to the left (base right) by prisms (15 diopters) placed inside the opaque tubes (Fig. 1*A*, prism) through which the subject viewed the screen. The CRT screen was displaced (rotated) around the vertical axis that passed the middle point of the subject's eyes to compensate for the visual displacement of the screen caused by the prisms: it was displaced by the amount of refraction (8.5 degree) to the right or to the left according to the base right or left conditions, respectively (Fig. 1*B*). Since the distance between the screen and the eyes was 400 mm, the screen was displaced 60 mm along an arc of 400 mm radius. This procedure kept the visual image of the screen in the second set almost identical to that in the first set: the subject viewed the tangent CRT screen in the same straight ahead direction (broken arrows, Fig. 1*B*) as in the first (solid arrow, no prisms). Mere parallel transport was avoided since the procedure rotates the subjective surface of the screen. In preliminary experiments without these corrections, the reaction time tended to become longer in the initial trial because of the abrupt apparent change in the visual field. In a given experiment, visual information was available only after a given delay period, while the subjects maintained their final pointing positions. The delay period was varied randomly from one experiment to another (11 delay periods of 0, 10, 20, 50, 100, 200, 500, 1000, 2000, 5000, and 10,000 msec).

In the third set of trials, the screen was placed back in the same position as in the first set, and the subject performed the reaching task without prisms. Visual information was allowed without delay for 12 sec.

It should be noted that intertrial intervals were kept constant (about 15 sec) through the experiments irrespective of the delay periods. Interset intervals were about 1 min, during which the subjects waited for the ready instruction with their vision blocked by the liquid-crystal shutters. It took about 25 min to complete one experiment.

In the design of this experiment, there were 22 alternative conditions that consisted of two directions of displacement and 11 delay periods. Ten conditions, which consisted of two directions and five delay periods of 0, 50, 100, 500, and 5000 msec, were chosen as core conditions. All subjects completed at least 10 experiments to cover the core conditions. Ten to 22 conditions were selected beforehand for each subject and were randomly ordered. Each subject completed the designated 10–22 experiments, once each, in 10–50 d. A total of 146 experiments were carried out.

## Results

### *Prism adaptation with 0 msec delays*

In the first set of trials, errors in reaching distributed around zero in both horizontal and vertical directions as exemplified in Figure 2*A* (first set). The absolute errors in this case were less than

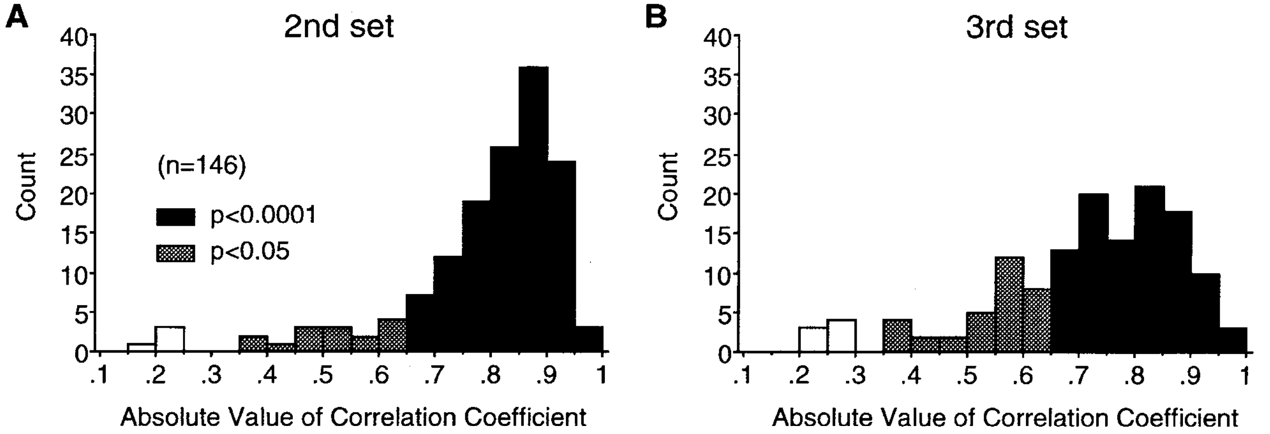

*Figure 3.* Distribution of the absolute values of the correlation coefficients between horizontal errors and their summation, obtained from the data in the second (*A*) and the third (*B*) set. Significance levels of the linear regressions are indicated by *filled* ($p < 0.0001$) and *shaded* ($p < 0.05$) *columns*.

10 mm in 17 of 30 trials (10.3 ± 4.1 mm, mean ± SD). This shows that the subject could reach accurately to a target that appeared at a random location in a 40 × 40 mm square area.

In the initial trial of the second set (Fig. 2*A*, trial 31), errors were observed in the same direction as the visual displacement. In the case shown, the visual field was displaced to the left by base right prisms and the CRT screen was displaced to the right by 60 mm to compensate for the displacement of the visual field (Fig. 1*B*, base right). The subject misreached about 80 mm to the left, which was more than the full extent of the visual displacement, in the initial trial. The horizontal errors decreased with trials in an exponential manner and almost returned to the control level in the last trials of the second set (55–60 trials). Errors in the vertical direction, in contrast, were not affected by the displacement and were distributed around zero (1.9 ± 10.7 mm, mean ± SD) as in the first set (0.5 ± 9.4 mm).

In the third set of trials, the prisms were removed and the screen was placed back in the same position as in the first set. Horizontal errors opposite to those in the second set were observed. In the example, the subject made an error of about 60 mm to the right in the initial trial of the third set (Fig. 2*A*, trial 61). This initial error is considered to reflect the amount of adaptation accomplished during the exposure to the visual displacement in the second set. The error again decreased exponentially with trials. Errors in the vertical direction had a similar distribution around zero (−1.4 ± 10.3 mm) as in the previous sets. Since vertical errors showed no significant difference among the three sets (ANOVA, $p > 0.4$), they are not mentioned in the following.

Figure 2*B* shows that the requirements for a reaction time < 200 msec and a movement duration < 300 msec were satisfied in 86 of the 90 trials.

### *A discrete model describing prism adaptation*

Horizontal errors seemed to decrease in an exponential fashion (see Fig. 2*A*). Since trials were carried out in a discrete manner, a discrete model was developed on the analogy of a differential equation for the exponential function as follows:

$$h(n) = h(n-1) - kh(n-1), \qquad (1)$$

where $h(n)$ and $k$ denotes the horizontal error in the $n$th 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 in proportion to the error in the preceding trial. Equation (1) can then be transformed into

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

which predicts that the error in the $n$th 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 if the model could explain the data. Figure 2*C*, drawn from the data in the second set shown in Figure 2*A*, shows a linear relation between the error and its summation ($r = 0.96$, $p < 0.0001$). 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. In the present case, the correction rate was 9.1% and the initial error given by the intercept was 84 mm. In other words, the initial error was 84 mm and decreased at a rate that was on average 9.1% of the error in the preceding trial. The thick line superimposed in Figure 2*A* (2nd set) shows the model prediction and indicates that it provided a good fit to the data.

The model was applied to all data in the second set and provided a reasonable approximation of the data as shown by the large absolute values of the correlation coefficients in Figure 3*A*. The correlation was significant in 127 (87%, filled columns) and 142 (97%, filled and hatched) of 146 experiments at the level of $p = 0.0001$ and 0.05, respectively. Estimates for the initial error in the second set distributed around 60 mm (61 ± 23 mm, mean ± SD, $n = 146$) as expected from the amount of displacement (see Fig. 6*C*, 2nd set).

The data in the third set of trials in Figure 2*A* were also well explained by the model: the error-summation scattergram (Fig. 2*D*) showed a linear decrement in the error ($r = -0.92$, $p < 0.0001$). The values given by the model (thick line in Fig. 2*A*, 3rd set) agreed well with the actual data (open circles), and this was the case for the majority of the data in the third set as indicated by the distribution of the correlation coefficients in Fig. 3*B*. However, the model did not fit the data in the third set as well as in the second, as shown by the broader distribution of the correlation coefficients. This difference could be explained by the smaller initial errors in the third set (Fig. 6*C*, 3rd set) rendering the data more sensitive to noise.

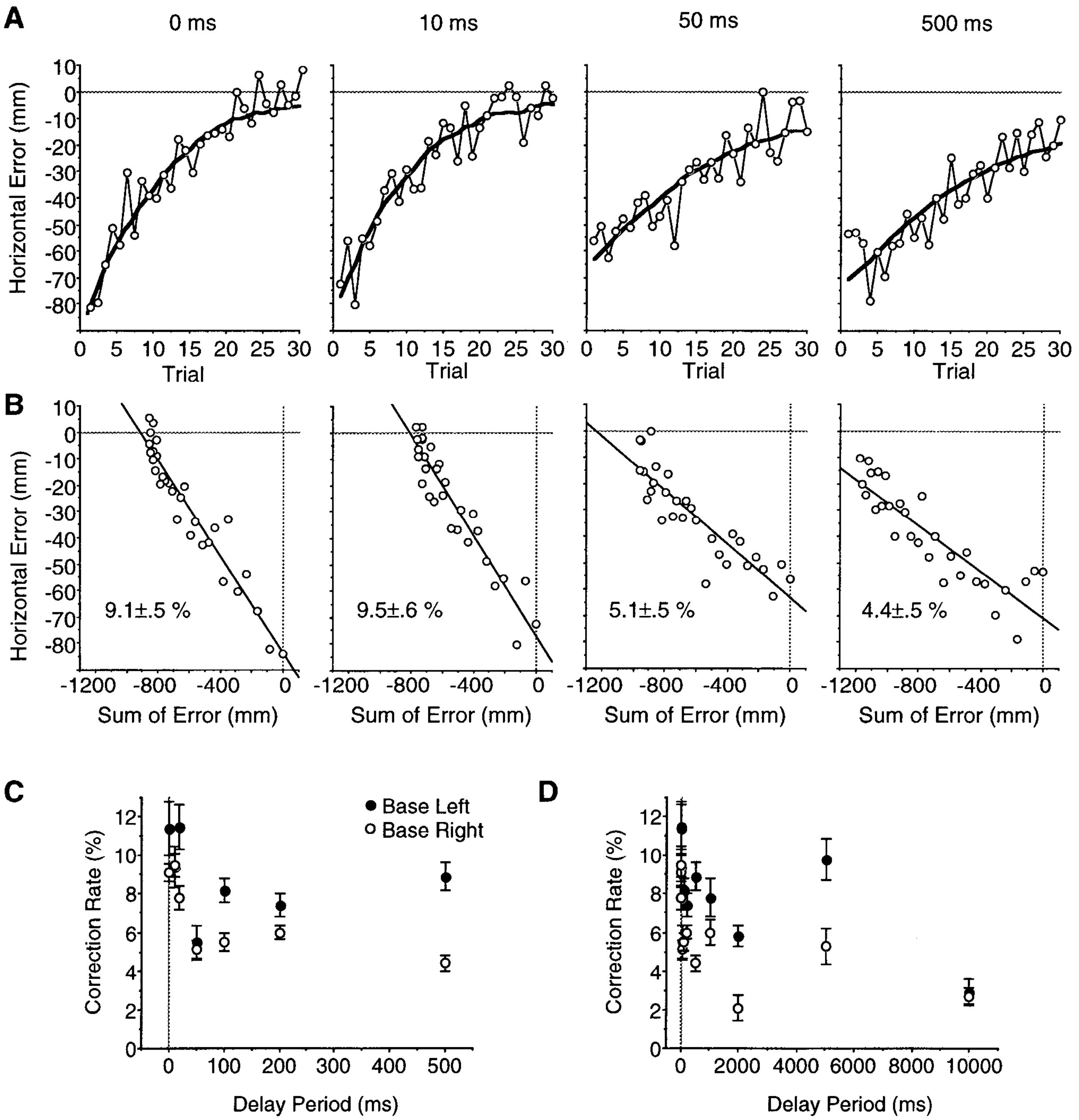

*Figure 4.* Decrease of horizontal errors in the second set obtained with different delay periods. *A*, Horizontal errors (*subject SK, base right*) are plotted against trial sequence obtained from four experiments with delays of 0, 10, 50, and 500 msec. *Thick lines* indicate the model predictions using the model eq. (1). *B*, Error-summation scattergrams with regression lines. Each corresponds to the data shown above in *A*. Correction rates are indicated with estimated standard errors. *C* and *D*, Correction rates (*ordinates*) plotted against delay periods (*abscissa*) from 0–500 msec (*C*) and 0–10,000 msec (*D*). They were obtained from 22 experiments of the same subject (SK) with base right (*filled*, $n = 11$) and left (*open circles*, $n = 11$) prisms. Error bars indicate standard errors estimated by the linear regression analysis.

### *Effects of delay on the rate of prism adaptation*

Figure 4*A* shows the time course of the decrease of the horizontal error for delay periods of 0, 10, 50, and 500 msec for subject SK with base right prism. With a delay of 10 msec, errors decreased in a manner similar to that with a 0 msec delay. The rate at which errors decreased was apparently slowed down with a delay of 50 msec and changed little with a much longer delay of 500 msec. These impressions are confirmed by the error-summation scattergrams in Figure 4*B*: the slopes of the regression lines show quantitatively that the correction rates were similar under conditions of 0 (9.1%) and 10 (9.5%) msec delays, while they were almost halved with 50 (5.1%) and 500 (4.4%) msec delays. The correction rates thus obtained from 11 experiments with different delay periods (same subject, base right prisms) are shown by the open circles in Figure 4*C* and *D*. The correction rates were greatest with the 10 and 0 msec delay (9.1–9.5%) and began to decrease with the 20 msec delay (7.8%), reducing to half with the 50 msec delay (5.1%); the rates main-

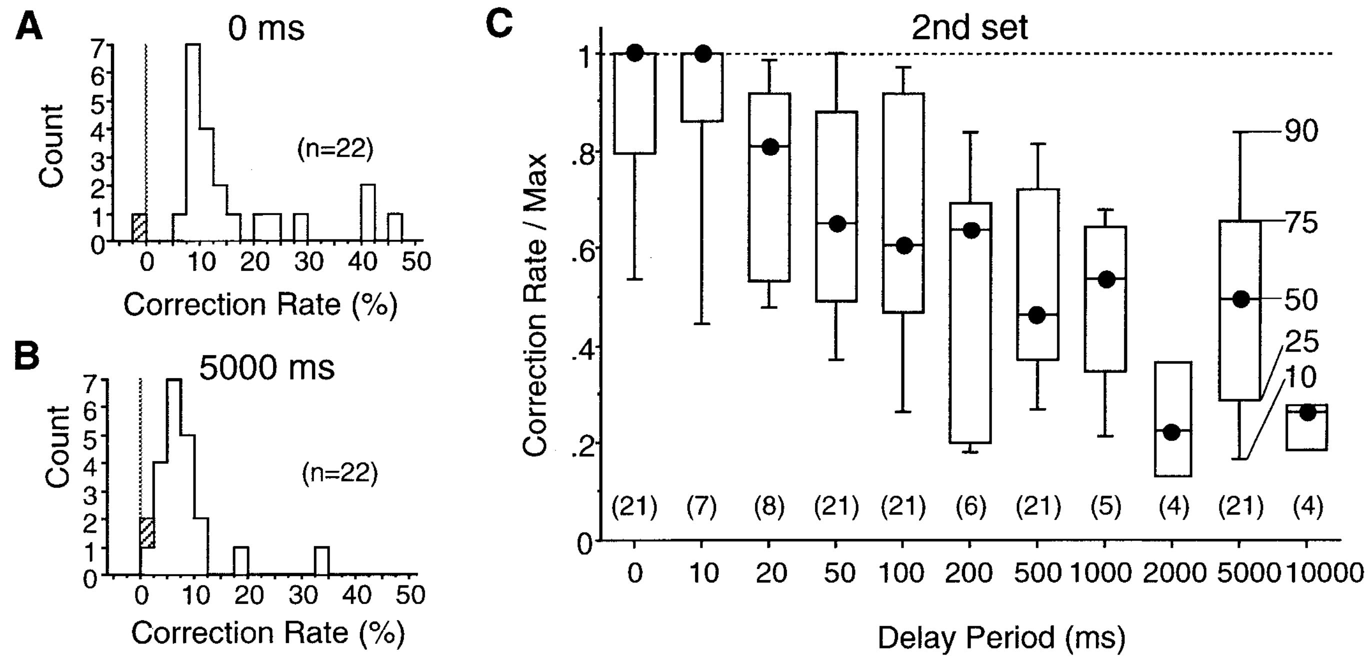

*Figure 5.* Correction rates in the second set compared among different delay periods. *A* and *B*, Histograms of correction rates from experiments with 0 msec (*A, n*X *= 22) and 5000 msec (B, n* = 22) delays. Eleven subjects completed two experiments with each delay, once with base left and once with base right prisms. *Hatched columns* show data from experiments of a subject TK with base right prisms, in which little decrease of error was observed. *C*, Distribution of normalized correction rates (*ordinate*) plotted against delay periods (*abscissa*). A group of correction rates, obtained from a given subject with a given direction of displacement, were normalized by the largest value in the group. Each box plot shows 10, 25, 50, 75, and 90 percentiles of thus normalized correction rates. Fifty percentiles are indicated by *filled circles* in particular. At delays of 0 and 10 msec 50–90 percentiles are overlapping at 1. Ten and 90 percentiles cannot be calculated at 2000 and 10,000 msec because only four data were collected. Numbers of experiments are shown in *parentheses*.

tained a similar level (4.6–6.0%) with longer (100, 200, and 500 msec, Fig. 4*C*) and much longer (1000 and 5000 msec, Fig. 4*D*) delay periods, though occasionally (2000 and 10,000 msec, Fig. 4*D*) they could be smaller (2.1–2.8%).

The filled circles in Figure 4*C* and *D* show the correction rates obtained from the same subject with base left prisms. These correction rates again showed an apparent decrease with the 50 msec delay (5.5%) compared to those (9.4–11.5%) with the shorter delay periods (0–20 msec). Correction rates with 50 msec and longer delays were always smaller than that of the 0 msec delay (11.3%), though they distributed over a wide range from 2.9% (10,000 msec) to 9.8% (5000 msec). It is also apparent that correction rates obtained with base left prisms (filled circles) were larger than those with base right prisms (open circles) for 10 of the 11 delay periods. This difference was significant at the level of $p = 0.005$ according to a Wilcoxon signed rank test (nonparametric correspondent of the two-tailed paired *t* test), which will be used for all statistical tests in the following. The result shows that the subject tended to adapt more quickly to the rightward displacement (base left) than to the leftward. Correction rates were significantly different in 7 of the 11 subjects depending on the direction of visual displacement, but the "preferred" direction seemed to distribute randomly among the subjects: four, including the one female, showed larger correction rates for the rightward displacement, and the other three, including the one left-handed, for the leftward. These results indicate that the correction rates depended not only on the delay periods but also on the subjects and the direction of visual displacement.

Figure 5*A* shows the distribution of the correction rates obtained from 11 subjects in 22 experiments with the 0 msec delay. There was a sharp peak around 10% but the correction rate could be as large as 46%. The distribution was shifted to the left (Fig. 5*B*) with a delay of 5000 msec, but the distributions overlapped considerably because of the inter- and intrasubject variability described above. If we compare pairs of correction rates obtained from a given subject with a given direction of visual displacement, correction rates of 0 msec delays were larger than those of 5000 msec delays in 20 of 22 such pairs ($p < 0.0002$). Thus, a group of correction rates, obtained from a given subject with a given direction of displacement, were normalized with respect to the largest value in the group. One exceptional group (subject TK, base right), in which little adaptation was observed with any delay periods from 0 to 5000 msec (e.g., hatched in Fig. 5*A,B*), were excluded from the normalization. Figure 5*C* shows the correction rates, thus normalized, as a function of the delay period. The medians (indicated by filled circles) were 1 at 0 and 10 msec delays. This reflects the fact that the correction rates were maximal in 15 of 21 groups for one of these delay periods. The normalized correction rates began to decrease with the 20 msec delay (median, 0.81), decreased further to 0.65 with a delay of 50 msec, and showed only a gradual decrease with longer delays (0.50 at 5000 msec). Correction rates were not significantly different from those with a 0 msec delay when the delay was 10 ($p = 0.61$, smaller than those of 0 msec in 3 of 7) and 20 ($p = 0.21$, 5/8) msec, but became significantly smaller when the delay reached 50 msec ($p = 0.011$, 17/21) or more: 100 msec ($p = 0.002$, 18/21), 200 msec ($p = 0.046$, 5/6), 500 msec ($p = 0.0003$, 19/21), and 5000 msec ($p = 0.0003$, 20/21). This decrease was also apparent for other delays of 1000 ($p < 0.08$, 4/5), 2000 ($p < 0.07$, 4/4) and 10000 ($p < 0.07$, 4/4) msec. The correction rates obtained with delays longer than 50 msec

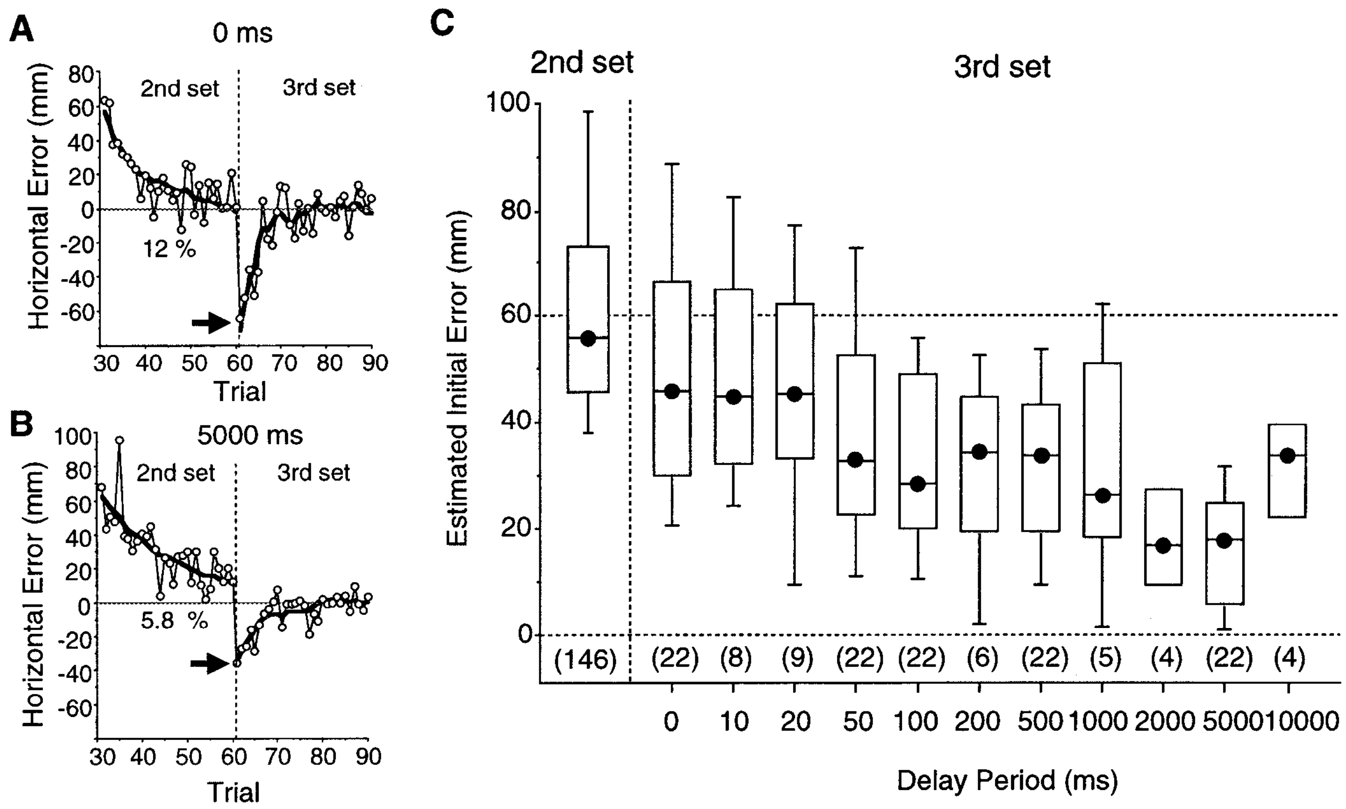

*Figure 6.* Initial errors in the third set compared among different delay periods. *A* and *B*, Horizontal errors in the second and third set plotted against trial sequence, obtained from experiments (*subject MY, base right*) with 0 msec (*A*) and 5000 msec (*B*) delays. *Thick lines* indicate the model predictions. Note the difference of the initial errors in the third set (*arrows*). Correction rates in the second set are also indicated. *C*, Absolute initial errors in the third set estimated by the model (*box plots, ordinate*) shown against delay periods (*abscissa*). Those in the second set ($n$ = 146) are shown to the left.

were not significantly different from one another with only one exception: those obtained with a 5000 msec delay were smaller than those obtained with a 50 msec delay in 14 of 21 groups ($p$ = 0.01). In summary, correction rates were maximal with the shortest delay periods (0 and 10 msec), decreased significantly with a delay of 50 msec and decreased only gradually thereafter.

### *Effects of delay on the amount of adaptation*

The initial misreaching in the third set (e.g., Fig. 2*A*) was used as a measure of the amount of adaptation induced by exposure to the visual displacement during the second set. Examples in Figure 6*A* and *B* (subject MY, base left) show that the initial error in the third set after a 0 msec delay (arrow in Fig. 6*A*) was larger than that after a 5000 msec delay (arrow in Fig. 6*B*). Since the model eq. (1) could fit most of the data in the third set (Fig. 3*B*) as well as the data in Figure 6*A* and *B* (thick lines), these estimates of the initial error were used to indicate the amount of adaptation. These initial errors were in general largest with the shorter delay periods of 0–20 msec (Fig. 6*C*, median of 45–46 mm) and decreased with longer delays (median of 17–33 mm). The initial errors were not significantly different from those obtained with a 0 msec delay when the delay was 10 msec ($p$ = 0.26, smaller in 6/8) or 20 msec ($p$ = 0.051, 6/9), but became significantly smaller when the delay reached 50 msec ($p$ = 0.017, 17/22) or more: 100 msec ($p$ = 0.003, 16/22), 200 msec ($p$ = 0.046, 5/6), 500 msec ($p$ = 0.019, 15/22), 1000 msec ($p$ = 0.043, 5/5), and 5000 msec ($p$ = 0.0003, 20/22). The initial errors were smaller than those with the 0 msec delay in all experiments with 2000 ($p$ < 0.07, 4/4) and 10,000 msec ($p$ < 0.07, 4/4) delays. The initial errors decreased little with delays of 50–500 msec: the initial errors were not significantly different from those obtained with a 50 msec delay when the delays were 100 msec ($p$ = 0.96, smaller in 10/22 than those of 50 msec), 200 msec ($p$ = 0.35, 4/6), and 500 msec ($p$ = 0.10, 14/22). They tended to be smaller with a 1000 msec delay ($p$ = 0.22, 4/5) and were minimal with delays of 2000 ($p$ = 0.14, 3/4) and 5000 msec ($p$ = 0.0006, 19/22). These results show that the amount of adaptation decreased significantly with a delay of 50 msec and further decreases were only gradual.

## Discussion

In the present study, we reported the effects of delaying the visual error information on the rate and amount of prism adaptation by presenting the terminal visual images of the hand and the target with various delays from zero to 10 sec after the reaching movement. The visual images available to the subjects were almost stationary and identical irrespective of the delay period. The striking result is that these almost identical visual images had different effects on both the rate and amount of adaptation, depending on whether they were made available just after the reaching movement, or after a further delay as short as 50 msec.

Since the interval between trials was kept constant in the present study, it might be argued that it is not the delay interposed between the movement and the exposure to visual information, but rather the shortening of the interval from the exposure to the next response (postexposure interval) that is responsible for the decreased rate and amount of adaptation (Bilodeau, 1966). However, the delay of 50 msec shortened the postexposure interval by less than 0.5% of that with the 0 msec delay, which was approximately equal to the intertrial interval of 15 sec. It is thus strongly suggested that the rate and amount of prism adaptation depend critically on the delay in the availability of visual information about the movement. In other words, the adaptation mechanism must utilize visual information as early as 50 msec after the movement.

It should be noted, however, that even with longer delays of 1 sec or more, adaptation was still evident in terms of both rate (Fig. 5*C*) and amount (Fig. 6*C*). Forty to 50% of the rate and amount of adaptation observed with a 0 msec delay was still evident with a 5000 msec delay. The results suggest that there is another different mechanism of adaptation that works even with delays of seconds interposed between the dynamic motor output and information on the error. Such a mechanism might also explain the improvement of rapid positioning tasks with delays longer than several seconds (Bilodeau and Bilodeau, 1958; Bilodeau, 1966). Another possible explanation is based on the equilibrium-point hypothesis (Bizzi et al., 1991). According to this hypothesis, the brain learns to control arm movements through temporal sequences of equilibrium postures. Since the subject in the present study was required to hold the final position of the hand and the arm until the visual information was made available again, the subject was at least allowed to adjust the representation of the final equilibrium posture using the direct visual information. Thus, the hypothesis of Bizzi et al. predicts and may explain the present result that a certain extent of adaptation was observed even with the longer delays.

### A discrete model of adaptation

Our model of the adaptive process had only two parameters—correction rate and initial error—and yet could fit the data in the second as well as the third set (Fig. 3*B*). This practical success of the model in fitting the data gives us the impression that there is only one mechanism or site for adaptation that changes at the unique correction rate. However, there could be two adaptation mechanisms that depend on delay periods in different ways as discussed. Other evidence has been interpreted to suggest that there are several different mechanisms in the process of adaptation to visual displacement (Welch et al., 1974; Welch, 1978; Redding and Wallace, 1988). Our model can be extended to allow for several different mechanisms simply by regarding $k$ as the summation of the correction rates of $m$-different mechanisms as

$$k(t) = k_1(t) + k_2(t) + \ldots + k_m(t) \quad (3)$$

in which $k$ is described as a function of the delay period $t$.

Assuming the two-mechanism model, the model could be expressed as

$$h(n) = h(n-1) - k_1(t)h(n-1) - k_2(t)h(n-1) \quad (1')$$

in which $k_1(t)$ is a rapidly decaying function of $t$ and $k_2(t)$ is a more slowly decaying function. Thus, the correction rate $k(t)$ shown in Figure 5*C* could be a summation of correction rates of different mechanisms that depend on delay periods in different ways. Though the present study does not give an exact idea on how many different mechanisms are involved, it is suggested that the learning rule applies to the respective submechanisms as well as to the overall mechanisms.

### Size of aftereffects in the third set

Initial errors in the third set are considered to be an aftereffect of the exposure to the visual displacement in the second set. A variety of tasks during the period of visual displacement have been known to produce such aftereffects in pointing or reaching toward visual targets. The size of the aftereffect in the present study (51 mm in the mean with a 0 msec delay) that amounted to about 80% of the size of visual displacement (60 mm) is among the largest of those (20–55%) previously reported (e.g., Harris, 1963; Cohen, 1966; Held et al., 1966; Freedman, 1968; Hardt et al., 1971; Taub and Goldberg, 1973; Welch et al., 1974; Weiner et al., 1983; Redding and Wallace, 1988; Held and Durlach, 1989). Since the total time of exposure to the visual displacement (30 sec) and the number of reaching during the displacement (30 trials) were not larger than those in the previous studies, these factors cannot explain this difference in the size of the aftereffect.

Freedman (1968) reported that exposure to prisms produced larger aftereffects in reaching tasks when the subject reached for a target than when they simply viewed their moving hand without targets during the period of prism exposure. On the basis of the study of Freedman (1968), Foley and Maynes (1969) argued that larger aftereffects may be produced when tasks during the period of prism exposure are more similar to those used after prism exposure. Tasks in the present study were strictly designed to be as identical as possible through the prism-exposure (second set) and post-prism-exposure (third set) periods. The large size of the aftereffects in the present study agrees with the argument of Foley and Maynes (1969) in that it could be explained by the identity of the tasks during and after exposure to the visual displacement.

Held and his colleagues interposed a delay (300–3300 msec in Held et al., 1966; 30–570 msec in Held and Durlach, 1989) before showing a subject the position of his moving hand, which was visually displaced, and studied the size of the aftereffects. Held et al. (1966) reported that aftereffects on target reaching disappeared with a delay of 300 msec or longer; Held and Durlach (1989) showed that aftereffects did not decrease with delays of 0–60 msec, but did decrease with delays of 120 msec. Since reaching was not used and there was no target to be reached during the period of exposure in their studies, mechanisms producing the aftereffects would be different (Redding and Wallace, 1988) from those in the present study. The smaller sizes of their aftereffects (20–30% of total displacement) and the longer delays (120 msec) required to produce significant decreases in the aftereffects in their studies might have been due to their experimental conditions being different from those of the present study.

### Implications for the underlying neural mechanisms

The present study has demonstrated the existence of a mechanism for prism adaptation that must utilize visual information as early as 50 msec after the movement. In addition, the model study suggested that the adaptive change had occurred in proportion to the error in the preceding trial. The next question to be addressed is where the mechanism is implemented in the brain. The cerebellum would be a candidate, since prism adaptation is impaired in patients with cerebellar deficits (Weiner et al., 1983; Thach et al., 1992) and in monkeys with cerebellar lesions (Baizer and Glickstein, 1974). In addition, there is evidence that the cerebellum is important for adaptive gain control of the vestibulo-ocular reflex (Lisberger et al., 1994a,b; for review, see Miles and Lisberger, 1981; Ito, 1984), and for Pavlovian conditioning of eyelid responses (Perrett and Mauk, 1995; for review, see Swain and Thompson, 1993).

Further neurophysiological studies are, indeed, required to draw conclusions on the site of adaptation in the present study, but the present findings at least yield criteria that must be satisfied by the underlying neural systems. (1) Signals that correlate with the spatial error (error signals) should be represented in the system. (2) The onset of the error signals should be tightly correlated with the onset of the visual input of the error. We look forward therefore to elucidating the neurophysiological basis of the present findings using the experimental paradigm in the present study and the criteria derived therefrom.

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