NeuroReport 7, 2357–2361 (1996)

Learning of scaling factors and reference axes for reaching movements

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To further understand visuomotor transformations in reaching, we compared adaptation to display rotation and altered gain in planar movements. Healthy subjects moved a cursor on a screen by moving an indicator on a horizontal digitizing tablet with their unseen hand. Adaptation to rotation was less complete and was accompanied by markedly increased directional variability. Adaptation training on a single target generalized broadly for gain change, but poorly for rotation. We propose that the difficulty in adapting to rotation arises from the substantial demands on short-term working memory imposed by the need to determine the new reference direction. Adaptation to gain change makes more modest demands on short-term memory to recalibrate the visuomotor scaling factor.

Key Words: Multi-joint arm movements; Reaching; Accuracy; Movement errors; Coordinate transformations; Motor programs; Human; Adaptation

Introduction

It is now generally accepted that the nervous system plans reaching movements in a schematic representation of extrinsic space. This simplified representation does not take account of joint and segment motions explicitly,[1] but is understood to include both the hand and the target, and to be egocentered (on the eye, head, body or shoulder).[2–4] It has also been hypothesized that movement is specified as a vector (distance and direction) according to a global scaling factor, with the vector origin at the initial hand position.[5,6] This hypothesized origin is supported by the occurrence of directional biases when the initial position of the unseen hand deviates from its habitual location near the body midline.[7,8] Practice in local regions away from the midline results in new biases in previously error-free regions, perhaps due to local resetting of a reference direction for movement.[9]

If movements are indeed planned according to a global scaling factor and a locally learned reference direction, subjects should adapt readily to a change in visuomotor scale. However, because of the inherent complexity of computing an egocentric reference axis,[10] they should have more difficulty in adapting to changes in this reference direction. We now report two experiments testing this idea by comparing adaptation to changes in gain and rotation of hand path displays in reaching movements. The first experiment shows that for equivalent changes imposed over a fixed number of trials, adaptation to rotation is less complete, and is associated with increases in response variability that do not occur with changes in gain. The second experiment, examining generalization of adaptation, shows that training with a single target at an altered gain generalizes to a full range of directions, whereas for rotation generalization is limited. Preliminary accounts of this work have been published.[11,12]

Materials and Methods

Subjects and apparatus: Nineteen healthy right-handed subjects (aged 24–34 years; 15 males) were studied (7 in experiment 1, 12 in experiment 2). All were naive to the purpose of the study, signed an institutionally approved consent form and were paid for participating. They were familiarized with making point-to-point movements in a single training session under control conditions. In both experiments, subjects sat facing a computer monitor (17 × 12 cm) at eye level (distance 72 cm), and were required to reposition a screen cursor from a common central origin to a series of peripheral targets (see below) by moving an indicator on a horizontal digitizing tablet (resolution: 0.0025 cm) with their right hand. Vision of the upper extremity was blocked, but the starting position for all movements was the same for all movements and subjects (elbow angle 90°, shoulder angle 45°).

Experiment 1 – time course of gain and rotation adaptation: At the beginning of individual trials, subjects positioned a screen cursor within a 6 mm start circle; after a tone, they were instructed to move when ready in a single uncorrected movement to a target circle. The screen cursor was blanked during movement to prevent visual corrections, but its path was displayed on the screen afterwards to provide information about movement errors. Targets in nine different locations were presented in a repeating pseudorandom sequence (without successive targets in the same direction or distance), in blocks of 45–117 trials. Targets were at each of three screen distances (1.5 cm, 3.0 cm and 4.5 cm) and along three directions from the starting point (horizontal to the right, vertical upwards, and at a 45° angle upwards and to the right). Each subject was studied in two sessions on separate days, in which either a gain change or a rotation of the display was imposed. Sessions included six groups of 108 trials, alternating between control and adaptation conditions (gain or rotation). In three subjects the gain session was prior to the rotation session and in four subjects the order was reversed.

In the control condition, the gain of the path display (screen:hand) was 0.47:1. The screen targets at 1.5 cm, 3.0 cm and 4.5 cm thus required hand movements of 3.2 cm, 6.4 cm, and 9.6 cm. Right and forward for the hand corresponded to right and upward on the screen. Performance was considered to have stabilized after 54 trials, and the subsequent 54 responses were used to derive baseline error measurements for comparison with adaptation conditions.

In the gain session, the control condition was followed by an adaptation condition with an increase in gain to 0.63 ($\mathrm{Gain}_{.63}$), designed to cause an initial overshoot of 35% of the screen target distance. The $\mathrm{Gain}_{.63}$ condition was followed by a return to the control condition ($\mathrm{Gain}_{.47}$) to observe after-effects, and so on in alternation until the $\mathrm{Gain}_{.63}$ condition had been repeated three times. In the rotation session, the control condition was followed by a 20° counterclockwise rotation of the displayed hand path around the initial position (Rot_{20}), but no change in gain.

The parameters for the $\mathrm{Gain}_{.63}$ and Rot_{20} conditions were chosen to equalize the magnitude of the predicted linear errors (defined here as the straight-line distance from the movement end point to the target). Additionally, in the $\mathrm{Gain}_{.63}$ and Rot_{20} conditions, the altered hand to screen transformations were not implemented during the initial cursor alignment to the start circle, but only in displaying the path after each movement. Thus, visual information about movement errors was only available after movement, through the displayed hand paths.

Experiment 2 – generalization of adaptation to gains and rotations: In this experiment, we examined generalization of adaptation following extensive training to a single target location. To maximize efficiency of training, we modified our paradigm two ways. First, subjects moved their hand from the central location to the designated target, and back to the center, at regular 2 s intervals. Second, subjects were provided with real time feedback of cursor position both during the control condition and during training. Separate subjects were tested for adaptation to gain changes (six subjects) and rotation (six subjects) to avoid cross-over effects. Three separate blocks of 44 trials were repeated four times for each subject in each session using different training directions in each of the four sessions. Each session consisted of a control condition with eight equidistant targets (see Figure 3 caption), a training condition (gain or rotation) with a single target and a testing condition with the eight control targets. As in experiment 1, changes in gain and rotation were chosen to produce equal linear errors. In the control condition the display gain was 1:1 (screen:hand), and subjects were presented with the eight targets in pseudorandom order. Subjects were provided with cursor feedback when moving to the target used later for adaptation training (once every four movements). No feedback or path display was provided for the other targets. The training condition consisted of 88 trials in which a single target was presented and either the gain of the display was increased to 1:1.5 (gain session), or cursor motion was rotated by 30° counterclockwise (rotation session). In the test condition, which followed immediately, the degree of adaptation was assessed for the remaining seven targets without cursor feedback. Cursor feedback was provided in refresher trials aimed to the training target every four movements. Extent or direction of accuracy of these test movements were then compared to the movements to the same targets in the control condition.

Data analysis: Automatic routines were used to mark the movement onset and movement end point of each trial; these critical points were checked visually and re-marked manually if wrong. Movement extent was defined as the straight line distance between the starting point and the end point of the movement, irrespective of curves in the movement path. Similarly, movement direction was defined as the direction in degrees of the linear vector from the starting point to the end point. Linear error was defined as the straight line distance between the movement end point and the target; extent error was movement extent minus target distance; directional error was defined as movement direction minus target direction. These measures of error were all defined in terms of screen cursor movement relative to the screen target. Statistical hypothesis testing employed paired or unpaired *t*-tests and ANOVA. Statistical significance was set at $p = 0.05$, and all *t*-tests were two-tailed.

Results

Experiment 1. Differences in degree of adaptation with changes in display gain and rotation: Subjects produced relatively accurate responses at the control gain of 0.43. Mean percentage extent error was 6.7 ± 1.8% (s.e.m.; $n = 14$), while mean directional error was –1.4 ± 1.0° ($N = 14$) across subjects in the two sessions. Figure 1 shows, for the aggregate data, that the alterations in display conditions produced the expected initial extent or direction biases in the first trial, and that adaptation occurred thereafter in both gain and rotation sessions. Thus, the 35% change in gain produced a mean increase in movement extent in the first trial of 32.5 ± 8.7% ($n = 7$). Figure 1A shows that the hypermetria decreased rapidly in the ensuing two nine-trial averages, with the mean scaling error becoming similar to that in the baseline period. When the control condition was imposed again, movements were initially hypometric but this bias was again rapidly lost. In fact, response scaling to the varied target distances was more accurate during the last 36 trials of the gain session (mean slope 1.00 ± 0.04; $n = 7$) than during the baseline condition (mean slope 0.86 ± 0.03; $n = 7$).

Following the imposed 20° rotation (Rot_{20}), the first trial showed a mean counter-clockwise error of 19.4 ± 1.1° ($n = 7$) relative to baseline across subjects. Like the hypermetria in the gain session, this bias also decreased progressively (Fig. 1B), and a reverse clockwise bias of –15 ± 1.7° occurred when the display was returned to control conditions (Rot_0).

The final degree of adaptation achieved by each subject under the $\mathrm{Gain}_{.63}$ and Rot_{20} conditions was calculated from the last 36 trials of each session. The mean final linear error across all subjects in the $\mathrm{Gain}_{.63}$ condition was less than that in the Rot_{20} condition (47 ± 4.2 mm, $n = 7$ *vs* 61 ± 6.6 mm, $n = 7$; $p < 0.05$, paired *t*-test).

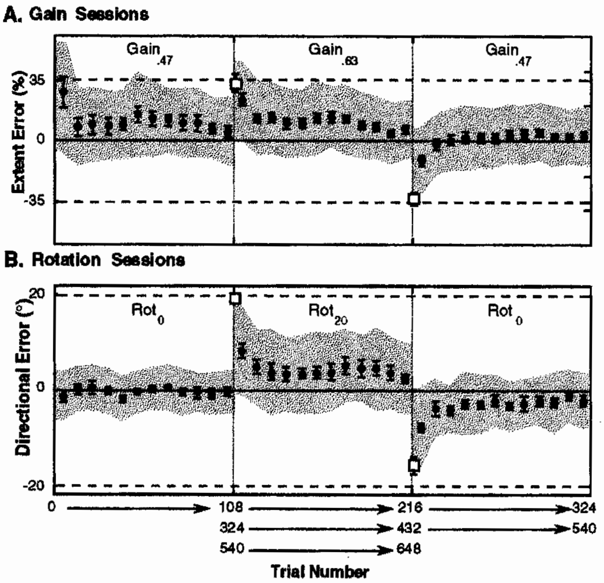

FIG. 1. Adaptation to display gain change (**A**) and rotation (**B**) (experiment 1). Filled circles show means across seven subjects for nine-trial epochs. Open squares show means across seven subjects for the initial trial under a given condition. Errors bars show s.e.m. Gray zone indicates mean variability across seven subjects (± mean of s.d. of each nine-trial epoch). Horizontal lines indicate expected initial errors.

In order to obtain comparable measures of extent and direction errors in the two adaptation conditions, we normalized them with respect to the variability during the baseline period. This was performed by computing a standardized error score for each trial. This consisted of the difference between the error (extent error for the gain session and directional error for the rotation session) on that trial and the mean baseline error, divided by the standard deviation of the baseline interval. Across subjects, the final standardized extent error in the gain sessions (–0.11 ± 0.13, $n = 7$) was less than final standardized direction error in the rotation sessions (1.30 ± 0.38, $n = 7$; $p < 0.03$, paired *t*-test). This standardized directional error in the rotation sessions was significantly different from baseline (i.e. greater than zero, $p < 0.02$) whereas the final standardized extent error in the gain sessions was not ($p > 0.04$). These findings indicate that a greater degree of adaptation was achieved for gain increase than for rotation.

Figure 2 shows that extent variability increased transiently after increases in gain, but returned rapidly to control levels and remained unchanged from baseline in the post-gain control condition. By contrast, directional variability markedly increased throughout the rotation condition, and remained substantially higher than baseline during the post-

A

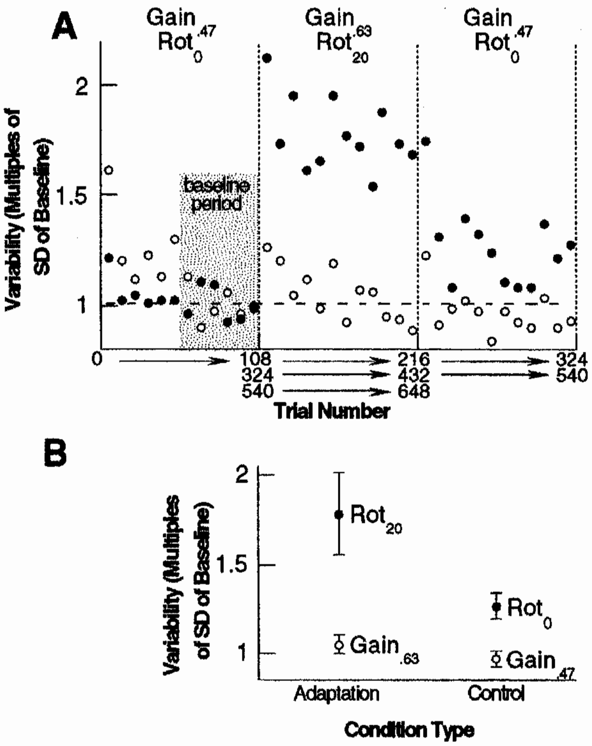

FIG. 2. Changes in movement variability during adaptation to display gain change and rotation (experiment 1). Open circles show variability in extent error during gain sessions; filled circles show variability in directional error during rotation sessions. (**A**) Data points indicate mean variability across seven subjects for nine-trial epochs. (For each nine-trial epoch by each subject, variability was calculated as the s.d. of the pertinent error divided by the mean s.d. during the same subject's baseline period for that session.) (**B**) Mean variability across seven subjects (± s.e.m) for each condition. Rotation sessions show higher variability than gain sessions ($p < 0.02$); adaptation conditions ($Gain_{.63}$ and Rot_{20}) show higher variability than control conditions ($Gain_{.47}$ and Rot_0; $p < 0.04$, ANOVA).

rotation trials. A two-factor ANOVA with session type (gain *vs* rotation) and condition type (adaptation *vs* control, excluding the initial control condition) as factors confirmed that rotation sessions had higher variability than gain sessions ($p < 0.02$; Fig. 2B). Adaptation conditions ($Gain_{.63}$ and Rot_{20}) had higher variability than control conditions ($Gain_{.47}$ and Rot_0; $p < 0.04$); the interaction almost reached statistical significance ($p = 0.057$). In addition, variability was significantly above baseline (i.e. > 1) in Rot_{20} ($p < 0.02$) and Rot_0 ($p < 0.01$) but was not significantly above baseline in $Gain_{.63}$ or $Gain_{.47}$ conditions.

Experiment 2. Adaptation to a locally learned change in gain generalizes across directions while adaptation to rotation fails to generalize: The increase in directional variability following imposed rotation (experiment 1) suggested that subjects had difficulty using error information to form a general transformational rule suitable for targets in various directions. Therefore, in experiment 2 we examined generalization of adaptation to gain change and to rotation after extended practice to a single target with visua feedback. At the end of training there were no significant differences in directional variability, extent erro or linear error between movements made in the two training conditions. (There was, however, a small 2 residual increase in directional error after rotation) When tested for generalization, without feedback, to the full range of targets, subject performance differed markedly for the two training conditions. As Figure 3 shows, adaptation to the gain change at a single target location allowed subjects to correctly aim movements to the seven other targets. In contrast adaptation to rotation at a single target location generalized poorly: directional biases increased progressively with greater directional disparity between the target direction and the training direction and when the disparity exceeded 90° mean directional errors matched the degree of imposed rotation. Thus adaptation to a change in display gain during repeated movements to a single target generalizes across directions, whereas adaptation to a rotated path display using a single target remains local.

Discussion

Our data with multiple target locations indicate that movement errors induced by a display gain change result in rapid and incremental rescaling o movement extent across sequential trials, withou substantial changes in response variability. In contrast, subjects do not compensate as rapidly fo imposed directional errors, and response variability increases markedly. Our findings are in accord with many prior studies showing that adaptation to gain changes occurs readily,[13–15] but that prolonged practice is necessary when hand path displays are rotated.[16,17]

The relative ease and generalizability of adaptation to an altered gain fits with the idea that such adaptation involves recalibrating a global scaling factor,[15,18] according to observed extent errors. The difficulty in adapting to a rotated display, equivalent to rotating the reference axis around the hand, may in part be explained by the inherent ambiguity of a single path display: a given error may arise because the assumed reference axis was incorrect, and also because the movement origin was misrepresented.[9,19,20] A second difficulty may be the unusual nature of the transformation required. Whereas we have ample daily experience with reaching when our head or eyes are rotated relative to the body, this may not prepare us for rotations around the initial position of the hand.

In light of the need to resolve ambiguous error information, computing a new spatial reference

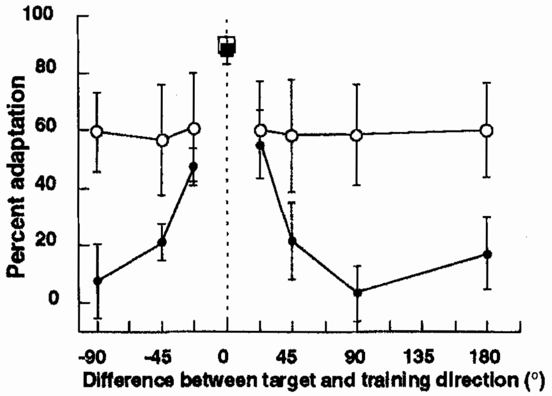

FIG. 3. Generalization of adaptation to display gain change and rotation (experiment 2). Mean error ± s.e.m. across six subjects and all sessions plotted as a percentage of complete adaptation to the imposed change. Filled symbols show the rotation condition; open symbols show the gain condition. Squares show mean error for the training direction prior to testing; circles show performance in the test condition. Training directions used were 45°, 135°, 225°, 315° (relative to the rightward direction). The targets were located 4.2 cm from the central starting position on the screen. Broad generalization in the gain condition contrasts with narrow generalization in the rotation condition.

direction requires storing successive targets and movement paths in multiple directions within short-term working memory (STWM). The difficulty in adapting to rotation with multiple targets may thus result from the known limitations in STWM.[21,22] In contrast, STWM demands for gain adaptation may be more modest, simply requiring the adjustment of the visuomotor scaling factor according to the extent error derived from each individual trial.

We have recently obtained important support for the idea that STWM is critically involved in adaptation to display rotation in hand movements, through studies of regional cerebral blood flow using [^{15}O]H_2O positron emission tomography. Using a similar task to that employed here in experiment 2, we found that, compared with movements made without rotation, adaptation to display rotations produced significant increases in blood flow in the contralateral posterior parietal cortex, area 46 and hippocampus.[23] Interestingly, the degree of labeling of this network, characterized using statistical subprofile mapping,[24] predicts subject performance.[25]

Conclusions

We compared adaptation to display rotation and altered display gain in planar reaching movements made without vision of the hand. With training on multiple targets, adaptation to rotation was less complete than to altered gain, and was accompanied by markedly increased movement variability. With training on a single target, adaptation generalized broadly for gain change, but poorly for rotation. Rotation adaptation involves establishing a new reference axis for movement, using directional error information. We propose that one explanation for the relative difficulty of rotation adaptation is the inherent ambiguity of directional errors in single movements. To resolve this ambiguity, errors from multiple successive movements in different directions must be stored and interpreted, making substantial demands on short-term working memory. In contrast, adaptation to gain change appears to make more modest demands on short-term memory to recalibrate a visuomotor scaling factor.

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ACKNOWLEDGEMENTS: Supported by HD 01018, NS 22713, and NS 07155.

Received 10 July 1996;
accepted 18 July 1996

General Summary

To further understand how the central nervous system plans reaching movements, we compared adaptation to display rotation and altered gain in planar movements by healthy humans. Subjects moved a cursor on a computer screen from a central origin to a series of peripheral targets, by moving an indicator on a horizontal digitizing tablet, without vision of the hand. Adaptation to rotation was less complete, and was accompanied by markedly increased movement variability. Adaptation training on a single target generalized broadly to seven new targets for gain change, but poorly for rotation. We propose that rotation adaptation imposes heavy short-term working memory demands to determine a general reference axis for movement, whereas gain adaptation requires modest short-term memory use in order to recalibrate a scaling factor.