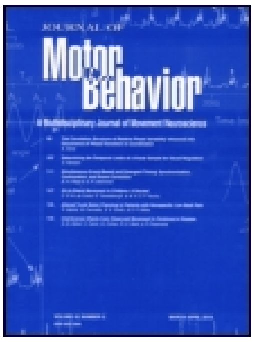

Journal of Motor Behavior

ISSN: 0022-2895 (Print) 1940-1027 (Online) Journal homepage: http://www.tandfonline.com/loi/vjmb20

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To cite this article: Gordon M. Redding & Benjamin Wallace (2001) Calibration and Alignment are Separable: Evidence From Prism Adaptation, Journal of Motor Behavior, 33:4, 401-412, DOI: 10.1080/00222890109601923

To link to this article: http://dx.doi.org/10.1080/00222890109601923

Journal of Motor Behavior, 2001, Vol. 33, No. 4, 401–412

Calibration and Alignment are Separable: Evidence From Prism Adaptation

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ABSTRACT. In 2 prism adaptation experiments, the authors investigated the effects of limb starting position visibility (visible or not visible) and visual feedback availability (early or late in target pointing movements). Thirty-two students participated in Experiment 1 and 24 students participated in Experiment 2. Independent of visual feedback availability, constant error was larger and variable error was smaller for target pointing when limb starting position was visible during prism exposure. Independent of limb starting position visibility, aftereffects of prism exposure were determined by visual feedback availability. Those results support the hypothesis that calibration is determined by limb starting position visibility, whereas alignment is determined separately by visual feedback availability.

Key words: limb movement, motor control, prism adaptation, spatial mapping

Sight of the limb in the starting position improves the accuracy of target pointing (Elliott, 1988; Elliott, Carson, Goodman, & Chua, 1991; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994). That phenomenon has been attributed to visual instead of proprioceptive calibration of limb position (Jeannerod, 1988, 1991; Jeannerod & Prablanc, 1983; Prablanc et al., 1979; Rossetti et al., 1994; Smith & Marriott, 1982). The greater precision of visual over proprioceptive representation (Bowditch & Southard, 1880; Desmurget, Rossetti, Prablanc, Stelmach, & Jeannerod, 1995) reduces variable error in performance.

When limb and target are both simultaneously visible before movement onset, one might attribute the advantage of sight of the limb to movement planning in an allocentric (rather than egocentric) frame of reference (Paillard, 1991) in which a movement vector is directly available on the retina (Desmurget, Rossetti, Jordan, Meckler, & Prablanc, 1997; Flanders, Helms-Tillery, & Soechting, 1992; Redding & Wallace, 1996, 1997b; Rossetti et al., 1994). Even when the target is the nonvisible contralateral hand, however, variable error in target pointing is reduced when the pointing limb is visible before movement (Desmurget et al., 1997). Thus, the more precise representation of initial limb position afforded by visual calibration reduces the variability in feedforward movement planning.

The advantage of visual calibration seems to depend, therefore, upon the greater precision of position representation, not necessarily on the veridicality of that representation. That interpretation suggests the interesting prediction that the reduction in variable error produced by visual calibration might persist even if a nonveridical visual representation produced a large constant error. Prism exposure produces such a situation. Viewing the limb in the starting position through displacing prisms produces a more precise representation than proprioception does; but the visual representation is not veridical, whereas the proprioceptive representation is. Thus, one would expect visual calibration during prism exposure to produce less variable error but greater constant error than that produced by proprioceptive calibration.

The prism adaptation paradigm also offers a means of testing the proposal that calibration and spatial alignment are separable (Redding & Wallace, 1997a). Calibration is the ordinary (everyday) process that establishes the present condition of the task–work space, and recalibration is necessary for different tasks or when the condition of the task–work space changes, or both. Alignment is the (usually implicit) process of applying "fixed-value transformation parameters to compensate for long-term, steady-state dif-

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ferences in origin location and axes orientation between coordinate systems" (Redding & Wallace, 1997a, p. 29). Such alignment is prerequisite to coordination (common action) in which spatial coordinates must be exchanged among sensorimotor systems. Realignment is the adjustment in parameters to compensate for ordinarily slowly developing misalignments that arise from natural processes, for example, growth and ordinary cell death.

Our present hypothesis is that calibration and alignment are distinct processes (Redding & Wallace, 1997a). Calibration provides information about the state of the task–work space within the current spatial mapping established by alignment and is blind to misalignment. Calibration is strategically variable, depending upon task structure, and some kinds of calibration may be more precise than others, but precision of representation is distinct from veridicality, which depends upon alignment. Alignment is transparent to calibration, as it is to other aspects of strategic control. According to the hypothesis, calibration and alignment should be differentially affected, respectively, by manipulations of starting position visibility and visual feedback availability.

Visual feedback availability has been shown to be a determinant of the kind of spatial realignment that occurs during prism exposure (Redding & Wallace, 1990, 1992b, 1994, 1997a, 2000; Uhlarik & Canon, 1971). When visual feedback is available early in a pointing movement, realignment aftereffects reside primarily in the hand–head sensorimotor system and are largely proprioceptive in nature. In contrast, when visual feedback is delayed until late in the pointing movement, aftereffects of prism exposure are largely visual in nature, residing in the eye–head sensorimotor system.

Visual feedback availability determines the locus of realignment by setting the direction of guidance linkage between visual eye–head and proprioceptive hand–head sensorimotor systems (Redding & Wallace, 1997a). A pointing movement is initiated on the basis of the erroneous (optically displaced) visual position of the target (feedforward control), and with early visual feedback the motor system uses the visible difference between limb and target online to achieve the target (feedback control). At the end of the pointing movement, the difference between the target position expected at the time the movement was initiated and the position achieved by the limb signals spatial discordance, which activates realignment in the guided hand–head system (i.e., proprioceptive adaptation). When visual feedback is delayed, a similar process occurs; but during the extended time when the limb is not visible, tracking eye movements are guided by the felt limb position. When the limb becomes visible late in the pointing movement, the difference between the expected visible position of the limb (based on limb proprioception) and its actual visible (but optically displaced) position signals spatial discordance, which activates realignment in the guided eye–hand system (i.e., visual adaptation).

In the present experiments, we tested for separable effects of starting position visibility and visual feedback availability on prism exposure performance and exposure aftereffects, respectively. If calibration and alignment are separable processes, one would expect the effect of starting position visibility on constant and variable error during prism exposure to be independent of the effect of visual feedback availability on visual and proprioceptive aftereffects. The predicted differential effect of starting position visibility on constant and variable error when visual feedback availability and the consequent realignment aftereffects covaried with starting position visibility was established in Experiment 1. The results of Experiment 2 confirmed the differential effect of starting position visibility on constant and variable error when visual feedback availability and the consequent realignment aftereffects were held constant.

EXPERIMENT 1

The control condition in the first experiment was similar to that used in previous research (e.g., Redding & Wallace, 1997b): Only the limb in the starting position was not visible; the entire movement path and the target were visible. We expected the availability of visual error feedback early in the pointing movement (sometimes called *concurrent exposure*; Uhlarik & Canon, 1971) to produce predominantly proprioceptive aftereffects, with realignment localized primarily in the hand–head sensorimotor system. That is, the spatial discordance between the final limb position expected on the basis of the feedforward movement command and the limb position achieved under visual feedback control would promote spatial realignment in the proprioceptive hand–head sensorimotor system. Because the limb was not visible in the starting position, we anticipated proprioceptive calibration, with consequently larger variable error and smaller constant error than would be found in the following experimental condition.

We expected visual calibration to occur in the experimental condition in which only the limb starting position and the target were visible and the movement path was occluded. Visual calibration should produce smaller variable error and larger constant error in that condition than in the control condition. Two different patterns of realignment aftereffects were possible in that condition, depending upon the strategic control deployed during exposure.

First, because visual feedback during movement was delayed, with sight of the pointing limb becoming available only at the terminus of the pointing movement (sometimes called *terminal exposure*; Uhlarik & Canon, 1971), one could expect visual aftereffects to appear predominantly in the eye–head sensorimotor system. Delayed visual feedback encourages proprioceptive guidance, with the eyes tracking the limb, especially during that portion of the movement path when the limb is not visible (Redding & Wallace, 2000). When the limb becomes visible at the end of the movement, spatial discordance between expected and achieved visible limb positions constitutes the signal for spatial realignment in the eye–head system (e.g., Redding & Wallace, 1997a).

Alternatively, simultaneous visibility of limb starting position and target might provide the basis for a vector code for controlling movement. That is, the central nervous system might use the visible difference between limb and target to compose a vector movement command (Rossetti, Desmurget, & Prablanc, 1995) for movement initiation (feedforward control).[1] Vector movement codes, however, do not produce the egocentric position information one needs to detect the spatial misalignment between eyes and limb produced by prismatic displacement (Redding & Wallace, 1996, 1997a, 1997b). Consequently, spatial realignment would not occur and realignment aftereffects would fail to appear.

The first experiment, therefore, bears on the issue of position versus vector codes in movement control. Redding and Wallace (1997a) have argued that vector (difference) coding is the natural kind of control for visual feedback error correction, whereas (absolute) position coding is the natural kind for feedforward control. According to their hypothesis, vector coding should not appear in the experimental condition because online visual feedback is largely not available; but position coding should occur with consequent realignment aftereffects, primarily in the visual eye–head system.

Method

Participants

The 32 participants were right-handed student volunteers at Cleveland State University. All participants had self-reported normal vision or vision that was corrected to normal by contact lenses. Participants were treated in accordance with the "Ethical Principles of Psychologists and Code of Conduct" (American Psychological Association, 1992).

Apparatus

The apparatus, which is illustrated in Figure 1, consisted of a two-layer, rectangular, wooden, box-like frame (24 cm high, 105 cm wide, and 74 cm deep) placed on a table and open on the side facing the participant. When participants placed their arm within the structure, on the lower layer, the arm was not visible. In that area, during tests before and after exposure, the experimenter noted limb position (i.e., the angle made by the hand relative to the body midline) by determining its position along a calibrated 180° arc.

During exposure, participants placed their arm upon the upper layer of the apparatus, which also had a measurement scale for recording exposure performance. The scale was positioned on the surface of the upper layer so that it was outside the visual field and not visible to the participant. A shelf was placed 15 cm above the upper layer of the apparatus, approximately just below the participant's nose. The middle portion of this shelf was a Plexiglas panel (22.9 cm wide × 25.4 cm deep × 1.3 cm thick) in which were embedded two black rods (each 1.27 cm in diameter and 5.08 cm long). The rods were located in the participant's sagittal plane and were separated by 21 cm, with the farther (distal) rod 54 cm from the participant. The distal rod projected above the Plexiglas panel, and the proximal rod projected below the panel. Except for those rods, all visible surfaces were homogeneously white in appearance. Attached to the front of the apparatus was a Marietta Instruments chinrest.

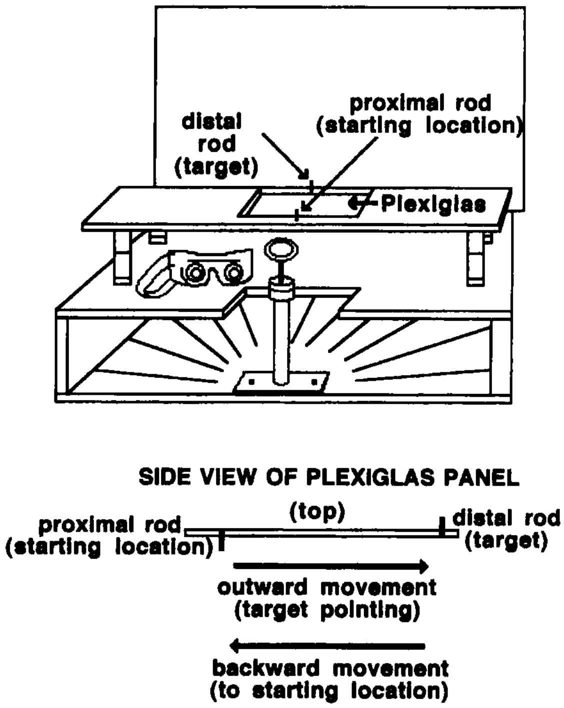

FIGURE 1. Apparatus. Participants were seated, with head constrained by a chin rest. For pretests and posttests, the participants' right arm was not visible on the lower level of the apparatus, the shelf containing the Plexiglas panel was removed, and target lines were introduced on the back vertical surface. For exposure, participants placed their arm on the top level, the shelf with the Plexiglas panel was in the position shown, and the visual field afforded by the goggles encompassed both target rods, but portions of the field were occluded by a black cloth draped over the Plexiglas panel (from Redding & Wallace, 1997b).

Participants wore welders' goggles, with a Risley prism mounted in each eyepiece that could be set to produce lateral displacement (right or left) of the optic array varying from 0 to 30 diopters (1 diopter = .57 arc deg) and which afforded binocular vision. Each circular eyepiece subtended a visual angle of approximately 30°, and the width of the binocular field was approximately 45°.

Design

A mixed design was used, with exposure task as the between-participants factor and exposure trials as the within-participant factor. Participants were randomly assigned to groups formed by the between-participants factor. Measures of terminal limb position in pointing were recorded for each exposure trial. Before exposure to optical displacement and after the exposure period, participants performed three alignment tests, without optical displacement and without visual feedback or knowledge of results. We designed the tests to obtain aftereffect measures of realignment of perceived visual position with perceived limb position (visual shift), realignment of limb position with visual position (proprioceptive shift), and total realignment between the eye and the limb (total shift). The order of the three alignment tests was differently randomized, both before and after prism exposure.

Procedure

Upon arrival in the laboratory, participants received a brief description of the experimental task, including the fact that perceptual-motor coordination tests would be given before and after a short period of eye–hand coordination activity while they looked through distorting prisms. Participants were not informed of the nature of the distortion: only that the prisms would affect their performance and that they should try to perform the task as accurately as possible. The participants were seated in a chair before the apparatus, with head positioned in the chinrest and wearing the prism-bearing goggles. The participants were then asked to perform each of the pre-exposure alignment tests.

The visual shift test involved no limb movement. Instead, the experimenter introduced a moving, visible vertical target line (.2 × 8 cm) on the back vertical surface of the upper layer of the apparatus and at the participants' eye level. When the experimenter moved that target laterally across the participants' visual field, the participants verbally indicated when the target appeared to be straight ahead of the nose. A total of 10 trials was given. Five trials started with the target placed randomly in the right half of the visual field, and 5 trials began with the target placed randomly in the left visual field. Order of left and right starting positions was also random. The duration of a test trial varied approximately between 5 and 10 s, depending upon the distance from the random starting position and the position that a participant judged to be straight ahead of the nose. The prisms were set to zero diopters for the visual shift test as well as for all other test situations. Because the visual shift test is referenced to the head, one can assume that the difference between that baseline, pre-exposure measure and performance on the same test administered after prism exposure provides an aftereffect measure of realignment in the visual (eye–head) system.[2]

In the proprioceptive shift test, the participants were required to place their right hand on the lower layer of the test apparatus, near the base of the chinrest, and to point sagittally to the position in space believed to be straight ahead of their nose. That task was performed 10 times at a rate of 1.5 s for each segment of the pointing movement and with vision occluded by a blindfold. Because the proprioceptive shift test is referenced to the head, one can assume that change in performance after prism exposure provides an aftereffect measure of realignment in the proprioceptive (hand–head) system.[3]

The total shift test was similar to the proprioceptive shift test, except that the participants were not blindfolded but pointed to a visible vertical target line (.2 × 8 cm) located physically straight ahead on the back vertical surface of the upper layer of the apparatus. During that test, the participants viewed the target with no visual displacement, but pointing accuracy was not known to the participants because their hand was on the lower level of the apparatus and was not visible. Ten measures were taken, with each movement segment requiring 1.5 s. Because that test involves the complete eye–hand coordination loop, one can assume that the difference between the baseline pre-exposure measure and performance on the same test administered after prism exposure provides an aftereffect measure of realignment in either or both the visual (eye–head) and the proprioceptive (hand–head) systems.

Following establishment of the pretest baselines, participants engaged in one of two exposure tasks. For the visible-starting-position group, we placed a black cloth over the Plexiglas panel to prevent sight of the movement path between the proximal and distal rods. In that condition, the visible portion of the movement path was limited to about 4 cm (2 cm at the beginning and the end), and both the limb in the starting position at the proximal rod and the distal target rod were visible. Then, with the participant's vision occluded, we set the prisms so that the visual field was displaced 11.4° (20 diopters) in the rightward direction, and we positioned the participants' right index finger, with the limb extended on the upper layer of the apparatus, so that the finger touched the proximal rod. Participants were then instructed to open their eyes and point sagittally from the starting rod toward the distal target rod. Upon completion of an outward movement, participants immediately reversed and pointed toward the proximal rod, then again toward the distal rod, and so on, with continuous out-and-back movements. Each segment (out or back) of movement required approximately 1.5 s. Participants pointed in that manner 30 times at each rod.

For the nonvisible-starting-position group, the procedure was the same, except that we placed the black cloth over the Plexiglas panel to prevent sight of the proximal rod and limb starting position. In that condition, the visible portion of the movement path was reduced by only about 2 cm (from 21 to 19 cm), and sight of the limb was available early in the pointing movement, but only after movement initiation.

For both groups, terminal accuracy in pointing at the distal target rod was recorded for each participant on each trial. Those observations were made when the participants' finger paused briefly, signaling primary movement completion. Movements after a pause but not in the opposite (return) direction were considered secondary corrections. Such secondary movements were discouraged and, in fact, occurred only infrequently. In any case, terminal position of the pointing finger was recorded before any such secondary movements. The two groups were not discernibly different in their pointing behavior. Thus, the use of visual feedback was almost entirely restricted to online control of the primary movement, and participants made little use of visual feedback to initiate secondary corrections after the primary movement had been completed. Of course, participants could have used visual information about terminal error (knowledge of results) on the previous trial as the basis for initiating the next primary movement on the next trial.

After the exposure period, the prisms were reset to zero diopters, the participants were told that the distortion had been removed, the shelf containing the Plexiglas panel was removed, and the three alignment tests were repeated (i.e., 10 trials for each kind of test). The predicted posttest adaptive change from pretest baseline was opposite the direction of displacement for the proprioceptive shift and total shift tests but in the direction of displacement for the visual shift test (Harris, 1974; Redding & Wallace, 1998, 2000; Welch, 1978).

All measurements were to the nearest degree. Throughout the experiment, the participants' head was constrained by the chinrest, and we monitored head position to correct any changes. All pointing movements, both during exposure and testing, were paced by a metronome set to beat every 1.5 s (.67 beats/s). Participants began an outward movement on one beat, completed it on the next beat, and immediately began a backward movement, which was completed on the third beat. The third beat served as the signal to begin the next outward movement, and so on, for 30 out-and-back movement cycles; each segment of the cycle was performed in about 1.5 s. With those instructions, participants achieved a smooth cycle of movements. The same pointing rate was employed for both exposure trials and aftereffect tests in which pointing was required (i.e., proprioceptive shift and total shift tests).

Results and Discussion

Aftereffects of prism exposure and direct effects of the prismatic distortion on performance during exposure are not directly commensurable measures (but see Redding & Wallace, 1993). For that reason, we analyzed the two kinds of measures separately, before considering their joint implications. Data are reported in degrees. By using a constant multiplier of 1.29, one can convert aftereffect data into centimeters at the 74-cm distance to the back of the apparatus, and by using a constant multiplier of .94, one can convert exposure performance data into centimeters at the 54-cm distance to the distal target.

Exposure Performance

For each participant, constant error was calculated as the average difference over trials between the target and the finger at the terminus of the pointing movement, whereas variable error was the standard deviation over trials of the terminal response around the participants' mean terminal response (Schmidt, 1988). For that purpose, we grouped the data into six blocks of 5 trials to minimize confounding with variable error the large differences in constant error over the 30 exposure trials. Thus, constant error provided a measure of the veridicality of response with respect to the target, and variable error independently measured the variability of response. Figure 2 illustrates the measures of performance accuracy for the six blocks of trials.

As can be seen in Figure 2, average constant error was larger for the visible- (2.1) than for the nonvisible- (0.4) starting-position group, $F(1, 30) = 49.21, p < .001$. Constant error decreased for both groups over blocks of trials, $F(5, 150) = 227.90, p < .001$, but the Group × Block interaction, $F(5, 150) = 12.26, p < .001$, supported the conclusion that constant error decreased more rapidly for the nonvisible-

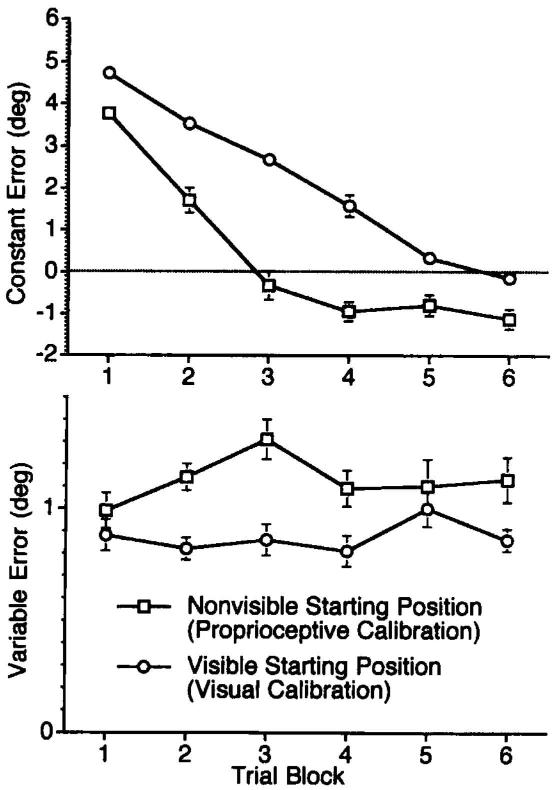

FIGURE 2. Mean constant and variable errors during prism exposure in each of six blocks of five pointing trials for different groups when the limb starting position was visible (the target was simultaneously visible, but the movement path was occluded) and visual calibration of limb position was possible or when the limb starting position was not visible (but the target and movement path were visible) and only proprioceptive calibration of limb was possible. Error bars denote standard errors. Where error bars are not visible, they are obscured by the data point symbol. Experiment 1.

starting-position condition. The visible-starting-position group achieved the target only toward the end of the exposure period, but the nonvisible-starting-position group achieved the target by the third block of trials, showing substantial overcompensation thereafter.[4] Those results confirmed the expected detrimental effects of nonveridical visual calibration.

As can also be seen in Figure 2, average variable error was larger for the nonvisible- (1.1) than for the visible- (0.9) starting-position group, $F(1, 30) = 30.07, p < .001$. The nonsignificant trial block main effect, $F(5, 150) = 1.09, p = .367$, suggested that variable error did not change over trial blocks, and the nonsignificant Group × Trial Block interaction, $F(5, 150) = 1.32, p = .257$, suggested that the difference between groups persisted across blocks of trials. Those results confirmed the expected lower variability in performance with visual calibration than with proprioceptive calibration.

The differential development of adaptive behavior during exposure for the two groups suggests something of the nature of the strategic control deployed under the different conditions. The nonvisible-starting-position group showed an early improvement in performance, whereas the visible-starting-position group improved much more slowly. The standard errors displayed in Figure 2 suggest that the nonvisible-starting-position group acquired the target by about the third block of trials. In contrast, the visible-starting-position group achieved accurate pointing only between the fifth and sixth (last) blocks of trials. The data also suggested that overcompensation for the prismatic distortion appeared for the nonvisible-starting-position group after the third block of trials but did not appear for the visible-starting-position group until the last block. That pattern of results suggested the following interpretation.

When the starting position was not visible, participants initiated movement under feedforward control by using the erroneous position of the target; once the limb became visible early in movement, by using online visual feedback control participants were able to reduce the terminal error. They achieved subsequent improvement in part by using error information (knowledge of results) from a preceding trial to select a compensatory virtual target position to the side of the actual target (feedforward control, side-pointing strategy). By using a combination of visual feedback and knowledge of results, participants appeared to be able to achieve the target in about three blocks of trials.

When starting and target positions were simultaneously visible, the terminal error produced by the erroneous target position when the movement was initiated was compounded by the erroneous visual calibration signal, which indicated a displaced initial limb position. Improvement in performance was retarded both because online visual feedback control was not available and because the persistent erroneous initial limb position provided by visual calibration slowed development of an adaptive side-pointing strategy (knowledge of results).

The developing overcompensation beyond Trial Block 3 for the nonvisible-starting-position group and in the last trial block for the visible-starting-position group suggested that an additional compensatory process was at work. Developing realignment is transparent to strategic control (Redding & Wallace, 1993, 1997a), and such changes in the apparent position of both the target (visual shift) and the limb (proprioceptive shift) produce errors opposite the prismatic displacement. Such transparent realignment appears as overcompensation. Aftereffect evidence for realignment is considered in the next section.

Aftereffects

Examination of the pre-exposure measures revealed stable performance across each of the 10 measures for both groups. We therefore did not misrepresent the data by averaging those measures. There were, however, significant differences among the averages for each pre-exposure measure, $F(2, 60) = 28.19, p < .001$, which differed for the two groups, $F(2, 60) = 3.81, p = .028$.

All pre-exposure measures showed a slight leftward bias that was less for the total shift and proprioceptive shift measures but greater for the visual shift measure in the visible-starting-position group. The leftward pretest bias for the nonvisible- and visible-starting-position groups, respectively, was 1.0° and 0.3° for the total shift baseline, 1.1° and 0.6° for the proprioceptive shift baseline, and 1.6° and 1.8° for the visual shift baseline. Thus, neither the pre-exposure measures nor the groups were exactly equivalent before prism exposure. Consequently, we calculated the usual pretest–posttest change scores to minimize the effects of nonequivalence. All subsequent analyses were performed on those aftereffect measures.

The average aftereffects for the two groups are shown in Figure 3. On average, the total shift (TS) measure and the sum of the visual and the proprioceptive shift measures (VS + PS) had identical values (3.8°), $F(1, 30) = .72, p = .402$. The groups did not differ on the average of those two aftereffect measures, $F(1, 30) = 2.48, p = .126$, and the Exposure Task × Aftereffect Measure interaction, $F(1, 30) = .63, p = .433$, further indicated that the two measures did not differ within each group. Such additivity provides a converging check on the assumption that those aftereffects measure realignment, independent of contributions from strategic control processes, such as memory of movements practiced during prism exposure, that might transfer to the postexposure tests (Redding & Wallace, 1978, 1993).

Figure 3 also displays the data for the component tests of VS and PS. Those results also confirmed our prediction. On average, the aftereffect measures of visual and proprioceptive realignment were not different for the two groups, $F(1, 30) = 1.36, p = .253$. The sum of those two measures (VS + PS) indicated that spatial realignment was about 3.5° for the nonvisible-starting-position group and was nonsignificantly larger at 4.0° for the visible-starting-position group. Therefore, total spatial realignment was about the same for the two groups, but the nature of the realignment was different.

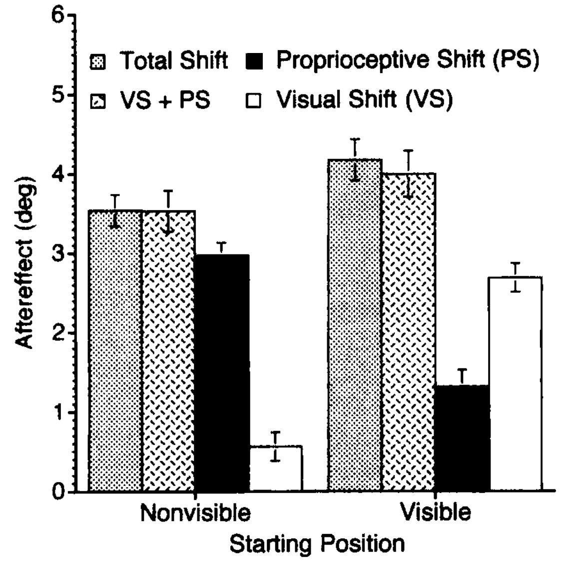

FIGURE 3. Aftereffects of prism exposure for different groups when the limb starting position was visible (the target was simultaneously visible, but the movement path was occluded) or the limb starting position was not visible (but the target and movement path were visible). Error bars denote standard errors. Results are shown separately for the visual shift test for realignment in the eye–head system, the proprioceptive shift test for realignment in the hand–head system, the sum of those two tests, and the total shift test for realignment in both systems. Experiment 1.

On average, proprioceptive aftereffects in the hand–head system (2.1°) were larger than visual aftereffects in the eye–head system (1.6°), $F(1, 30) = 10.16$, $p = .003$, but as indicated by the Exposure Task × Aftereffect Measure interaction, $F(1, 30) = 132.50$, $p < .001$, that was not true for both groups. As can be seen in Figure 3, when the starting position was not visible, proprioceptive realignment in the hand–head system (3.0) was greater than visual realignment in the eye–head system (0.6), but when the starting position was visible, visual realignment (2.7) was greater than proprioceptive realignment (1.3). Those results replicate many previous studies (e.g., Redding & Wallace, 1993, 1998, 2000) and support a similar interpretation.[5]

The early availability of visual feedback when the starting position was not visible largely favored visual guidance throughout the exposure. The local discordance in the controlled hand–head system between the target position code with which movement was initiated and the limb position required to achieve the target enabled misalignment detection and realignment localized in the proprioceptive hand–head system.

The late availability of visual feedback when the movement path was occluded in the visible-starting-position condition produced substantial proprioceptive guidance. The local discordance in the controlled eye–head system between the expected position of the nonvisible limb and its actual position when it became visible enabled misalignment detection and realignment localized in the visual eye–head system.

The small amount of visual shift when the starting position was not visible suggests that some proprioceptive guidance can occur even when the moving limb is continuously visible (Redding & Wallace, 2000), especially early in exposure when feedback control is not sufficient to enable the participant to achieve the target. The eyes may initially track the preprogrammed (feedforward) limb movement, with feedback correction delayed until the error becomes obviously large. The more substantial amount of proprioceptive shift found when the starting position was visible arose because the movement was initiated under visual guidance even when the movement path was occluded.

Realignment was incomplete (about 3.8° or 33% of the 11.4° optical displacement) because some of the strategies deployed during exposure precluded misalignment detection (Redding & Wallace, 1997a). For example, knowledge of results compensation replaces the actual target position with a virtual position that a performer can achieve by using feedforward control, and there is no discrepancy between expected and achieved positions, which would signal misalignment. A balance of strategic control and realignment is reached and maintained at least until changes in the exposure task disrupt the balance (Redding, 1981).

The developing realignment evidenced by those aftereffects is transparent during exposure and appears as a perturbation (Redding & Wallace, 1993, 1997a): Perceived target and limb positions actually change over exposure trials! When added to the control strategies already applied, realignment produces overcompensation. Such overcompensation was especially apparent when strategic control was sufficient to quickly achieve the target in the nonvisible-starting-position condition (see Figure 2). But the developing realignment also contributed to target achievement in the visible-starting-position condition by reducing both the misalignment and the error in visual calibration, and the rate of target achievement a performer could reach by using strategic control in that condition might even have been slower than is apparent in Figure 2.

Note that the presence of realignment aftereffects in the visible-starting-position conditions argues against the idea that vector-coded movement commands are used in feedforward control. Realignment aftereffects would not have appeared if feedforward vector commands had been deployed because those commands do not provide the spatial discordance information necessary for misalignment detection (Redding & Wallace, 1996, 1997a, 1997b). The fact that realignment-preventing vector codes were not computed even though sufficient information was available (i.e., visible target and starting limb positions) suggests that such codes are reserved for feedback control (Redding & Wallace, 1997a).

EXPERIMENT 2

The results of the first experiment support the hypothesized separability of calibration and alignment. The more precise, but erroneous, initial limb position produced by sight of the displaced limb in the starting position (visual calibration) slowed target acquisition (constant error) but enabled more precise pointing movements (variable error) than the movements produced when the starting position was not visible (proprioceptive calibration). Nevertheless, realignment aftereffects occurred in the usual manner predicted for the differing availabilities of visual feedback in the two exposure conditions. An alternative explanation is possible, however, for the differences in constant and variable error.

The differential availability of proprioceptive and visual calibration for the two exposure conditions was confounded by the difference in availability of visual feedback. When the starting position was not visible but the movement path was visible, visual error feedback became available almost immediately after movement initiation. However, when the starting position was visible but the movement path was occluded, visual error feedback was less available because the limb disappeared almost immediately after movement initiation and reappeared only after the movement was near completion. In that condition, terminal error could function as knowledge of results, but less readily as online visual feedback, to enable the performer to correct movement initiation on the next trial. Thus, the lower constant error for the nonvisible-starting-position condition might be explained by online correction based on the available visual feedback.

Moreover, the higher variable error observed in the nonvisible-starting-position condition might also be explained by the additional source of movement control afforded by online visual feedback. In contrast to the visible-starting-position condition, where movement was arguably under feedforward control with little feedback control, the nonvisible-starting-position condition afforded feedforward control in movement initiation and feedback control after movement initiation. On the assumption that no control signal is perfectly precise, the additional feedback control could have added variable error to the imprecision inherent in feedforward control, thereby producing larger variable error for the nonvisible-starting-position condition.

In short, the differences in constant and variable errors found in the first experiment might have arisen because of the differences in visual feedback availability, not because of differences in visual and proprioceptive calibration. We designed the second experiment to control for visual feedback availability between conditions affording visual and proprioceptive calibration.

The condition of visible starting position with movement path occlusion used in Experiment 1 was repeated in the second experiment, but that condition was compared with a condition in which both starting position and movement path were occluded; the limb became visible only near the terminus of the pointing movement. The opportunity for visual error feedback correction was therefore minimized for both conditions, and we expected that differences in constant and variable error would disappear if online feedback control was the sole reason for the differences in those measures found in Experiment 1.

Because in this experiment we used two delayed visual feedback exposure conditions that encourage proprioceptive guidance, we expected realignment aftereffects to be similar; namely, we expected visual realignment in the eye–head system to be greater than proprioceptive realignment in the hand–head system.[6]

Method

The method for Experiment 2 was the same as that for Experiment 1, with the following exceptions: Participants in the nonvisible-starting-position group saw only the target and 2 cm of the fingertip when it appeared at the end of the pointing movement; the movement path was otherwise occluded, including the starting position. Twenty-four participants were tested, 12 in each group. Participants were different from those who had taken part in Experiment 1 but were recruited from the same source and were given the same ethical consideration.

Results and Discussion

As for the first experiment, the two kinds of measures, direct effects of the prismatic distortion on exposure performance and aftereffects of prism exposure, were analyzed separately before we considered their joint implications.

Exposure Performance

Figure 4 illustrates the mean constant and variable error measures of performance accuracy for the six blocks of exposure trials. Although the difference in constant error between groups was smaller, results were similar to those of the first experiment.

Constant error was on average larger for the visible- (1.5) than for the nonvisible- (0.6) starting-position group, $F(1, 22) = 15.03$, $p = .001$ (Figure 4). Constant error decreased for both experimental groups over blocks of trials, $F(5, 110) = 151.16$, $p < .001$, but the Group × Block interaction, $F(5, 110) = 3.06$, $p = .013$, supported the conclusion that constant error decreased more rapidly for the nonvisible-starting-position condition. The visible-starting-position group achieved the target only toward the end of the exposure period, but the nonvisible-starting-position group achieved the target by the third block of trials, showing substantial overcompensation thereafter.[7] Those results confirmed the detrimental effects of nonveridical visual calibration found in Experiment 1.

As can also be seen in Figure 4, average variable error was larger for the nonvisible- (1.0) than for the visible- (.8) starting-position group, $F(1, 22) = 11.57$, $p = .003$. The nonsignificant trial block main effect, $F(5, 110) = 1.33$, $p = .258$, suggested that variable error did not change over trial

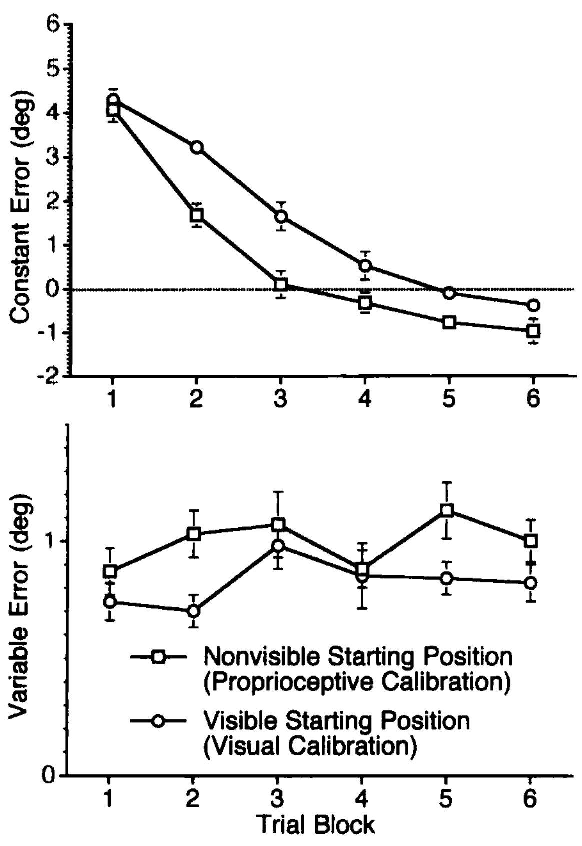

FIGURE 4. Mean constant and variable errors during prism exposure in each of six blocks of five pointing trials for different groups when limb starting position was visible (the target was simultaneously visible, but the movement path was occluded) and visual calibration of limb position was possible or when only the target was visible (starting position and movement path were occluded) and only proprioceptive calibration of the limb was possible. Error bars denote standard errors. Where error bars are not visible, they are obscured by the data point symbol. Experiment 2.

blocks, and the nonsignificant Group × Trial Block interaction, $F(5, 110) = .61, p = .689$, suggested that the difference between groups persisted across blocks of trials. Although variable error was smaller than that found in the first experiment, the average difference between conditions was the same, and those results confirmed the lower variability in performance with visual calibration than with proprioceptive calibration found in the first experiment.

Thus, one cannot attribute the differences in constant and variable error found in Experiment 1 to differences in the availability of visual feedback. The same differences appeared in the present experiment, in which visual feedback was not differentially available. The larger constant error and smaller variable error when starting position was visible can be safely attributed to the nonveridical, but more precise encoding of limb starting position afforded by visual calibration.

The nearly identical constant error values shown in Figure 4 for both groups in the first block of trials is puzzling; it may suggest that visual calibration is slow to develop. Like other aspects of strategic control, visual calibration may depend upon task conditions and, in the present case, may have been strategically deployed only after participants became familiar with task structure in the first few trials. The absence of a similar result in the first experiment (see Figure 2) might be attributed to greater terminal accuracy afforded by online visual feedback for the nonvisible-starting-position group. Consistent with that interpretation was the observation that the difference in variable error between groups was small in the first block of trials in both experiments, although it was not statistically different across blocks of trials in either experiment.

In any case, the slower reduction in constant error beyond the first block of trials for the visible-starting-position group likely reflected the detrimental effect of visual calibration. Participants in both groups may have initiated movement on the basis of the erroneous target position and then used terminal error (knowledge of results) to develop a side-pointing strategy to improve performance on following trials. Improvement in performance was retarded for the visible-starting-position group because the persistent erroneous initial limb position provided by visual calibration slowed development of an adaptive side-pointing strategy.

As in the first experiment, the late-appearing overcompensation may be attributed to perturbation produced by slowly developing but transparent realignment. Moreover, the tendency for both groups to converge on the same final value for constant error might be explained if the visual realignment expected for the delayed feedback conditions reduced the detrimental effects of visual calibration. Evidence for aftereffects is examined next.

Aftereffects

As in the first experiment, significant differences were found among the averages for each pre-exposure measure, $F(2, 44) = 35.78, p < .001$; but unlike Experiment 1, those differences were the same for the two groups, $F(2, 44) = 1.70, p = .195$. TS and PS baselines were biased in the leftward direction (1.8 and 0.1°, respectively), but the VS baseline was biased in the rightward direction (0.5°). Although the two groups appear to have been equivalent on the pretest measures, the measures themselves were not equivalent. Consequently, we calculated the usual pretest–posttest change scores to minimize the effects of nonequivalence. All subsequent analyses were performed on those aftereffect measures.

The average aftereffects for the two groups can be seen in Figure 5. On average, the TS measure and the VS + PS measure were nearly identical (3.7 and 3.9°, respectively), $F(1, 22) = 1.50, p = .233$. The groups did not differ on the average of those two aftereffects, $F(1, 22) = 0.16, p = .698$, and the Exposure Task × Aftereffect Measure interaction, $F(1, 22) = 0.01, p = .919$, further indicated that the two measures were not different within each group. As in the first experiment, such additivity supports the assumption that those aftereffects measure realignment, free of transfer contributions from strategic control processes deployed during prism exposure (Redding & Wallace, 1978, 1993).

In Figure 5 are also displayed the data for the component tests of VS and PS. The results also confirmed prediction. On average, aftereffect measures of visual and proprioceptive realignment were not different for the two groups, $F(1, 22) = 0.14, p = .715$. The sum of those two measures (VS + PS) indicated that spatial realignment was about 3.8° for the nonvisible-starting-position group and was nonsignificantly larger at 4.0° for the visible-starting-position group. Total spatial realignment was about the same for the two groups.

Furthermore, unlike the first experiment, the Exposure Task × Aftereffect Measure interaction, $F(1, 22) = .73, p = .403$, indicated that the nature of the realignment was the same for the two groups. As can be seen in Figure 5, when the starting position was visible results were much like those of Experiment 1: Visual realignment in the eye–head system (2.5°) was greater than proprioceptive realignment in the hand–head system (1.4°). When the starting position was not visible, however, realignment in the eye–head system (2.7°) was also greater than proprioceptive realignment in the hand–head system (1.2°). Thus, the differential availability of visual and proprioceptive calibration did not differentially affect realignment; therefore, spatial alignment is a process separable from calibration.

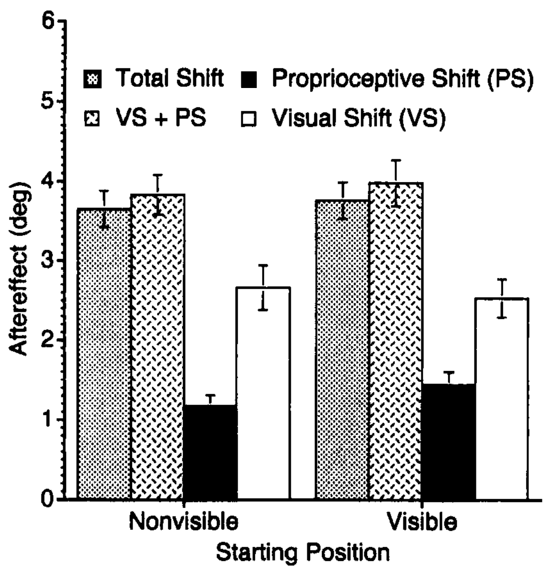

FIGURE 5. Aftereffects of prism exposure for different groups when the limb starting position was visible (the target was simultaneously visible, but the movement path was occluded) or when only the target was visible (starting position and movement path were occluded). Error bars denote standard errors. Results are shown separately for the visual shift test for realignment in the eye–head system, the proprioceptive shift test for realignment in the hand–head system, the sum of those two tests, and the total shift test for realignment in both systems. Experiment 2.

Conclusions

Independent of visual feedback availability, constant error was larger and variable error was smaller during prism exposure when limb starting position was visible for target pointing than when it was not. Independent of limb starting position visibility, aftereffects of prism exposure were predominately proprioceptive in nature when visual feedback was available early in pointing movements and was predominately visual in nature when visual feedback was delayed until the terminus of the pointing movement. Those results support the hypothesized separability of calibration and alignment.

Visibility of limb starting position determines the source of the calibration signal. Visual calibration when the limb starting position is visible during prism exposure specifies limb position more precisely (Bowditch & Southard, 1880; Desmurget et al., 1995), but nonveridically, because of the prismatic distortion of position. Visual feedback availability determines the direction of guidance linkage between visual eye–head and proprioceptive hand–head sensorimotor systems (Redding & Wallace, 1992b, 1994, 1997a, 2000; Uhlarik & Canon, 1971). Early visibility of the limb during pointing movements causes the selection of predominantly visual guidance of the limb, with consequent proprioceptive realignment in the hand–head system. Delaying sight of the limb until near the terminus of the pointing movement causes the selection of predominantly proprioceptive guidance of the eyes, with consequential visual realignment in the eye–head system.

Further investigation is needed, but the present results support the hypothesis that calibration and alignment are distinct processes (Redding & Wallace, 1997a). Calibration provides information about the state of the task–work space within the current spatial mapping established by alignment and is blind to misalignment. Calibration is strategically variable, depending upon task demands, and some kinds of calibration may be more precise than others, but precision of representation is distinct from veridicality, which depends upon alignment. Alignment is transparent to calibration, as it is to other aspects of strategic control.

The present data also have implications for the issue of position versus vector codes in the control of movement (Fu, Suarez, & Ebner, 1993; Georgopoulos, 1990; Grobstein, 1988; Rossetti et al., 1995; see also Rosenbaum, Loukopoulos, Meulenbroek, & Vaughan, 1995; Rosenbaum, Meulenbroek, Vaughan, & Jansen, in press). In previous research, Redding and Wallace (1996, 1997b) showed that when conditions are optimal for vector computation (i.e., when the entire movement path is visible, including target and starting limb positions), realignment aftereffects of prism exposure do not appear. The presence of realignment aftereffects in the visible-starting-position conditions of both of the present experiments suggests that realignment-preventing vector codes were not computed, even though sufficient information was available (i.e., visible target and limb starting positions). It seems reasonable, therefore, to conclude that vector codes are used in feedback control, whereas position codes are used in feedforward control (Redding & Wallace, 1997a).

Vector codes are an expression of the difference between effector endpoint and target position, that is, an expression of the direction and amplitude of movement necessary to achieve the goal position. As such, vector codes are ideally suited to feedback control, and the vector-coded nature of feedback control enables a performer to make online corrections more efficiently (Bullock & Grossberg, 1988; Bullock, Grossberg, & Guenther, 1993). However, vector codes represent only the position of target and effector relative to each other, not their egocentric positions. Consequently, vector codes cannot serve spatial-mapping functions among sensorimotor systems having different spatial reference frames; relative position will be the same for coordinate systems having different origins and orientations. Furthermore, vector codes are insensitive to changes in the alignment of sensorimotor spaces.

Position codes are an expression of effector endpoint and target positions independently, that is, an expression of coordinates within a particular reference frame. As such, position codes do not directly express the difference between effector and target but do provide the necessary information for the computation of a set of spatiotemporal predictions (i.e., a feedforward movement plan) about the sequence of effector positions that will achieve the movement goal (Rosenbaum et al., 1995; Rosenbaum et al., in press). Consequently, position codes serve spatial-mapping functions among sensorimotor systems having different spatial reference frames; absolute position will be different in coordinate systems having different origins and orientations. In addition, position codes are sensitive to changes in alignment of sensorimotor space.

ACKNOWLEDGMENT

A preliminary report of Experiment 1 was given at the 40th annual meeting of the Psychonomic Society (1999, November) in Los Angeles, CA. Similarly, Experiment 2 was preliminarily reported at the 41st annual meeting of the Psychonomic Society (2000, November) in New Orleans, LA.

NOTES

1. The formation of a vector movement command (direction and amplitude) does not necessarily depend upon simultaneous visibility of starting and ending positions; the command might be formed in movement planning from positional information. In recent proposals, however, a positional (postural) basis for movement plans has found favor (e.g., Rosenbaum et al., 1995; Rosenbaum, Meulenbroek, Vaughan, & Jansen, in press).

2. We use the term *visual shift* to designate adaptive change in the eye–head system that has phenomenal consequences for visual perception. The basic nature of such change may be realignment of either retinal local sign or direction of gaze (e.g., Crawshaw & Craske, 1974; Harris, 1980). Current theory development does not permit a comparison between those two possible accounts of visual change (but see Redding & Wallace, 1997a), and the aftereffect test for visual shift used in the present experiments is sensitive to either or both kinds of change.

3. We use the term *proprioceptive shift* to designate any adaptive change in position sense at joints between the head and the hand or even the fingers. We assume that the hand–head system is hierarchically organized (Redding & Wallace, 1992a, 1997a; see also Jeannerod, 1988) such that any proximal change extends to positioning of more distal joints. We designed the present proprioceptive shift test to detect all position sense changes in the hand–head system. Indeed, we think of the spatial map for the limb as being defined by the combination of joint positions (e.g., Churchland, 1986).

4. The large difference in average constant error between groups was caused in part by the negative values in later trial blocks. To control for the influence of overcompensation, we performed an analysis of absolute constant error (Schmidt, 1988). Results were the same. Absolute constant error was larger for the visible- (2.3) than for the nonvisible- (1.6) starting-position group.

5. We believe that the local nature of realignment aftereffects means that transformations among sensorimotor spaces are mediated by a central noetic spatial representation (Redding & Wallace, 1992a, 1992b, 1993, 1997a). That topic, however, is beyond the scope of the present problem, and discussion has been correspondingly abbreviated.

6. Our principal reason for allowing starting position visibility and visual feedback availability to covary in the first experiment was to avoid the null hypothesis prediction for aftereffects when visual feedback availability was held constant, as it was in the second experiment.

7. As in the first experiment, we performed an analysis on absolute constant error to control for the influence of overcompensation. Results were again the same. Absolute constant error was larger for the visible- (1.9) than for the nonvisible- (1.5) starting-position group.

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Submitted May 24, 2000
Revised January 17, 2001