Context-dependent Arm Pointing Adaptation*

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Abstract

We sought to determine the effectiveness of head posture as a contextual cue to facilitate adaptive transitions in manual control during visuomotor distortions. Subjects performed arm pointing movements by drawing on a digitizing tablet, with targets and movement trajectories displayed in real time on a computer monitor. Adaptation was induced by presenting the trajectories in an altered gain format on the monitor. The subjects were shown visual displays of their movements that corresponded to either 0.5 or 1.5 scaling of the movements made. Subjects were assigned to three groups: the head orientation group tilted the head towards the right shoulder when drawing under a 0.5 gain of display and towards the left shoulder when drawing under a 1.5 gain of display; the target orientation group had the home & target positions rotated counterclockwise when drawing under the 0.5 gain and clockwise for the 1.5 gain; the arm posture group changed the elbow angle of the arm they were not drawing with from full flexion to full extension with 0.5 and 1.5 gain display changes. To determine if contextual cues were associated with display alternations, the gain changes were returned to the standard (1.0) display. Aftereffects were assessed to determine the efficacy of the head orientation contextual cue compared to the two control cues. The head orientation cue was effectively associated with the multiple gains. The target orientation cue also demonstrated some effectiveness while the arm posture cue did not. The results demonstrate that contextual cues can be used to switch between multiple adaptive states. These data provide support for the idea that static head orientation information is a crucial component to the arm adaptation process. These data further define the functional linkage between head posture and arm pointing movements.

Introduction

Early work examining visuomotor adaptation of arm pointing movements led to the belief that only one visuomotor map existed at any given time, because subjects needed to re-adapt to a normal environment following an initial adaptation to an altered environment [12-14]. Pointing errors evident upon the return to the normal environment, opposite in direction to those observed when subjects were first exposed to the adaptive stimulus, have been termed aftereffects. Further investigations have since demonstrated that subjects can concurrently store two or more visuomotor maps by alternately switching back and forth between environments over blocks of trials [4, 7, 9, 19, 31]. Following repeated exposures, subjects require fewer trials to re-adapt and exhibit reduced aftereffects each time they switch between exposures. This has been demonstrated with a variety of adaptive stimuli, including wedge prisms [7,19,31], rotated visual feedback [5], varying VOR gains [25, 26, 28], and force fields perturbing the direction of limb movement [10].

Shadmehr and Brashers-Krug [23] have demonstrated that time is required (possibly for consolidation of learning) between exposure to multiple environments in order for subjects to be able to learn the new state without interference from the previous one. Furthermore, they have demonstrated using PET that the ventral prefrontal cortex may be involved in the inhibition of the initially acquired state during acquisition of a new one [24]. Without providing a consolidation time period, Kravitz and Yaffe [18] demonstrated that auditory tones were effective at helping subjects switch between pointing at different magnitudes of prism shifts, using a tone to signify a change between blocks. More recently, Cunningham & Welch [5] compared the effectiveness of auditory and visual cues to aid switching between multiple maps. The visual cue was simply a change in color of the target and cursor whenever the magnitude of feedback rotation was altered. Their results demonstrated only weak effects for both auditory and visual signals, with the cues appearing to be effective for switching between some, but not all blocks. There are further conflicting results as to whether visual cues can be associated with acquired adaptations; Donderi et al. [7] demonstrated color-contingent aftereffects following prism exposure. Gandolfo et al. [10], however, demonstrated that subjects could not associate a change in the color of the ambient room lighting with different perturbing force fields.

Shelhamer and colleagues [25, 26] examined whether subjects could associate eye position with multiple gains of the vestibulo ocular reflex (VOR). They exposed subjects to alternating periods of VOR gain, shifting the angle of gaze with each change in gain, After successive exposures, subjects were able to anticipate a new VOR gain automatically when the eye position was changed. In another example, Gandolfo et al. [10] had subjects adapt to a force field opposing their movement, with force magnitude proportional to the velocity of the moving limb. Subjects alternated between a clockwise- and a counter clockwise-directed opposing force field. Two types of stimuli were used as contextual cue conditions to aid subjects in switching between the two states. The first was color; the room was flooded with one color light for the clockwise field and another for the counter clockwise field. This was not effective, however, in enabling the subjects to switch from one state to another. The other type of contextual cue condition was the hand posture used to grasp the manipulandum. One posture was with the hand halfway between full pronation and full supination, and the other was fully pronated, effectively changing the muscle requirements to move the manipulandum. The use of these different postures was sufficient to enable subjects to switch automatically between the two mappings. That is, after associating the mapping with the cue, as soon as the posture was changed (i.e., from the first trial) subjects were able to perform movements that were appropriate for the environment. Similar results were obtained for goal-directed eye movements by Deubel [6] and Clendaniel et al. [3]. From the above data it appears that the contextual cues which are effectively associated with multiple adaptive states are those that are intrinsic to the task. This interpretation would explain the effectiveness of hand posture for arm pointing adaptation in the Gandolfo et al. [10] study and eye and head orientation for VOR adaptation observed by Shelhamer and colleagues [25, 26, 28].

Our previous work [20] suggests that the visuomotor map in use for arm pointing is functionally linked to that in use for head pointing, even when the head is restrained during arm pointing. The existing literature on eye-head-hand coordination provides substantial evidence for integrated, synergistic control of these body segments [2, 8, 29]. However, the bulk of these experiments have included investigation of dynamic head and hand control; it remains unclear how or whether static head posture is integrated into the control of arm pointing movements. Berger et al. [1] have demonstrated that the accuracy of arm pointing can be biased by variations in the head-to-trunk posture when subjects point with the eyes closed, particularly following microgravity exposure. Further support for this functional linkage between head posture and arm pointing would be obtained if subjects are able to switch between acquired adaptations for arm pointing movements using different head postures as opposed to other types of contextual cues.

The purpose of this experiment was to determine whether head posture is an effective contextual cue for switching between visuomotor maps. It was predicted that static head orientation could be easily incorporated into the arm adaptation process, in comparison to control cues. This was expected because of the linkage between head posture and arm movement control, making head orientation an integral aspect of the task. Subjects in the head orientation group tilted the head towards the right shoulder when drawing under a 0.5 gain of display (+20°

roll) and towards the left shoulder (-20° roll) when drawing under a 1.5 gain of display. Under one of the control conditions, subjects changed the elbow angle of the left arm (while drawing with the right arm) from full flexion to full extension with 0.5 and 1.5 gain display changes. Under the other control condition, the home & target positions were rotated counterclockwise when drawing under the 0.5 gain and clockwise for the 1.5 gain. These target orientation angles matched those of the head posture group. This was to rule out the possibility that changing head orientation is effective simply because it requires an additional transformation from the drawing movements made (horizontal line between targets) to the eye movements performed (oblique line between targets). This additional transformation could make the task more difficult than under the arm posture conditions, thereby making the stimulus more salient. The arm posture control condition changes posture of a body segment with changes in gain; it is presumed, however, that posture of the left arm is not integral to the task. It was predicted that head orientation would prove to be more effective than the contexts created by the control conditions, since static head orientation information is a crucial component to the arm adaptation process. The discovery of any contextual cue that aids subjects in switching between multiple adaptive states would be of benefit to adaptive training programs. For example, the appropriate context could be used to help astronauts to switch between multiple adaptive sets, a set appropriate for microgravity, the gravitational environment of Mars, and the gravitational environment of Earth.

It also appears that almost any type of cue can become effectively associated with multiple mappings following extensive alternating training periods. For example, Martin et al. [19] demonstrated that subjects could switch automatically between throwing with wedge prisms and without after six weeks of training sessions, with the only trigger being the presence or absence of the lenses. Even from the first trial the subjects pointed accurately. Since Martin et al. [19] have demonstrated that some cues can become effectively associated with multiple mappings when using an extensive training period, a secondary experiment was conducted in order to determine whether the effectiveness of these contextual cue conditions is dependent on the training period employed. New subjects were recruited and assigned to the same groups as in the main experiment; the participants performed twice as many trials. The purpose was to examine whether the two control conditions would become associated with the adaptive states following extensive training, and/or whether the effectiveness of the head posture condition would strengthen.

Methods (mark methods for small print)

Subjects. Three groups of twelve subjects were recruited from the Arizona State University campus to participate. Group 1 subjects (4 males, 8 females) were 24.8 (sd=4.5) years old; group 2 subjects (6 males, 6 females) were 25.7 (sd=4.2) years old, and group 3 subjects (4 males, 8 females) were 25.2 (sd=4.3) years old. After hearing an explanation of the experiment the subjects decided whether they wanted to volunteer. If they did, they provided written informed consent in accordance with the institution's human subjects' policies. Subjects were compensated with extra credit for an undergraduate motor learning course for their participation, which took an average of one hour. An additional four subjects per group were recruited to participate in the second experiment, aimed at determining how the strength of cue association increases over repeated exposures to visuomotor conflict.

Procedure. Subjects were seated in front of a computer monitor, with their arm resting on a digitizing tablet. The shoulder was flexed to 90° for the starting posture, and the table height was adjusted to support the arm in a posture parallel to the floor. The head was fixed to a support for the duration of the experiment. Subjects grasped the stylus in a whole hand grasp to prevent them from making adjustments to the pen position with their fingers. Subjects wore goggles that were blacked out on the lower half to prevent vision of the moving hand. The subjects performed aiming movements to various targets on a Wacom digitizer. Custom software was used to present the imperative stimulus (auditory go signal), the targets, and the pen trace, and to collect the x and y pen tip coordinates at 206 Hz during the course of the movements. Targets were displayed on a 30 cm by 40 cm monitor, placed at eye level 60 cm back from the subjects' eyes. The subjects were instructed to perform the movements as rapidly and as accurately as possible upon an auditory go signal. Although latency of response was not stressed, anticipation and no response trials were omitted by having subjects repeat trials in which they did not achieve a reaction time (RT) between 100 ms and 1000 ms. All other trials were retained, regardless of whether or not the target was achieved.

Subjects were randomly assigned to one of three groups, each receiving a different cue condition: 1) subjects changed static head posture from +20° of roll (towards the right) to -20° of roll (towards the left) with the gain of display changing from 1.5 to 0.5, 2) the target orientation was changed by tilting the computer monitor from +20° to -20° of roll with the gain changing from 1.5 to 0.5 and the head remaining fixed, 3) the left arm posture (all subjects were right handed and drew with their dominant hand) varied from full elbow extension to full elbow flexion while again the gain changed from 1.5 to 0.5.

All three groups performed a pre test with the gain of display at 1.0 (20 trials), an adaptation block in which the gain of display alternated between 0.5 and 1.5 every 20 trials for three successive sets (120 trials total), and a post test (32 trials) in which the gain was returned to 1.0 (see Table 1 for an overview of trial presentation). No cues were provided during the pre test, but cues were present throughout the adaptation and post tests. The 0.5 gain of display requires subjects to travel twice the distance on the tablet compared to the distance displayed on the monitor, and the 1.5 gain of display requires subjects to travel two thirds of the distance on the tablet compared to the displayed pen trace. During the adaptation block, the level of cue was changed with every gain change (i.e., head orientation went from +20° to -20° of roll, target orientation and arm posture changed in a similar fashion). Cue levels and corresponding gains of display are presented in Table 1.

To examine whether there was any interference between cue effectiveness and recency effects arising from the last gain experienced during the adaptation block, the groups were subdivided into two. One half received one cue level for the first half of the post test (for example, +20° of head roll, which was associated with the 0.5 gain during adaptation) and the other received the remaining cue level (for example, -20° of head roll, which was associated with the 1.5 gain during adaptation). The level of cue was changed halfway through the post test (at 16 trials) to determine whether the direction of aftereffect changed accordingly with the gain previously associated with the level of cue during the adaptation block. Subjects participating in the second, smaller experiment (four subjects for each of the three cue groups) followed the same protocol except that they performed the adaptation block two times (240 total adaptation trials) before continuing on to the post test.

Data Analysis. The position data were subjected to a residual analysis in order to determine the appropriate cutoff frequency for data filtering [33]. This method compares the residual difference between the filtered and the raw data using multiple cutoff settings. Thus the user can select the cutoff that maximizes noise elimination and minimizes signal distortion. The resulting value used was 7 Hz. The resultant path was computed by taking the square root of the sum of the squared x and y coordinate data. The tangential speed and acceleration profiles were then found by successive differentiation. The optimal algorithm of Teasdale, Bard, Fleury, Young, and Proteau [27] was used to determine movement onset from the velocity profiles. The algorithm works as follows: Locate the sample at which the velocity time series first exceeds 10% of its maximum value (Vmax); working back from this point stop at the first sample (call it S) less than or equal to (Vmax/10)-(Vmax/100); find the standard deviation of the series between sample 1 and sample S (call this sd); working back from S stop at the first sample less than or equal to S-sd; this is the onset sample. As sampling was terminated when subjects remained stationary for 300 ms, the same algorithm was used in reverse to determine movement offset.

Subjects typically perform movement corrections during adaptation experiments, evident as corrective submovements in the velocity profile [16, 20], especially towards the beginning of the adaptation blocks when they are learning the task and adapting to the change in the gain of display. Since the focus of interest was more in how the subjects preplanned the movements and less in the on-line corrections that they made, we decomposed the movement into its primary and secondary submovements. The primary submovement is thought to be mostly under ballistic control whereas the secondary submovement reflects a feedback-based correction [20]. The existence of secondary submovements was determined using an algorithm that searches for a positive acceleration value following a period of deceleration, or a change in the sign of the velocity, signifying a change in movement direction. The end of the primary submovement was also considered the beginning of the secondary submovement. While it is acknowledged that multiple corrective submovements may occur, they were considered as one corrective phase for the purposes of this analysis. Trials not containing corrective submovements were excluded from mean calculations of secondary submovement amplitude and duration (i. e., rather than entering values of 0.0 cm amplitude and 0 ms duration).

Using these methods of submovement decomposition allowed us to portion the movement into ballistic and corrective phases. This enabled us to compute the distance covered in the primary submovement. This variable is reflective of programming errors rather than errors in any feedback-based corrections. For example, the primary submovement should cover approximately 50% of the total distance for the initial trials of the 0.5 gain of display adaptation blocks and 150% of the total distance for the initial trials of the 1.5 gain blocks.

A within subjects MANOVA (group $\times$ block $\times$ trial) with repeated measures on trial and block was used to determine how performance varied across each block. The Huynh-Feldt epsilon [15] was evaluated to determine whether the repeated measures data met the assumption of sphericity ($\Sigma > .75$). In cases where sphericity was met, the univariate tests were used to maintain power. Otherwise, the repeated measures were treated as multivariate. Note that the significance of the F value is assessed using different degrees of freedom depending on whether the univariate or multivariate tests are used. The observed power was computed for all variables, as was ω^2, an estimate of the total population variance that is explained by the variation due to the treatment [17]. Its value does not depend on sample size or power of the experiment. Its values can range between 0.0 and 1.0, with negative values a possibility when the associated F value is less than 1.0. Cohen suggests that a small effect is comparable to an ω^2 of .01, a medium effect is .06, and a large effect is .15 or greater [4]. These standards were employed in our assessment of treatment effect sizes. Data analyses for the second experiment were identical, except that the majority of the interpretation focused on the effect sizes rather than the p values since only four subjects per group participated.

Results

The observed power for all significant reported effects for the first experiment ranged from .86 to .99. There were small learning effects in the pre-test as subjects became accommodated to the task, as seen in Figure 1. The error bars have not been plotted for Figures 1 and 3, as they obscure the visual assessment of the pattern of results for the three subject groups. Further, the groups are pooled across cue condition in these plots because there were neither significant main effects nor interactions involving condition for the pre test and adaptation blocks. There were significant main effects on both block ($F(1, 31) = 22.6$, $p < .001$, $\omega^2 = .23$, large effect size) and trial ($F(9, 279) = 17.9$, $p < .001$, $\omega^2 = .30$, large effect size) for the pre test, reflecting increases in the primary submovement distance both within and across blocks for all three cue groups. It should be noted that there were no group differences in performance at the pre test.

Sample trajectories from the adaptation block (Figure 2) reveal that subjects initially undershoot the target when exposed to the 0.5 gain of display and overshoot it when exposed to the 1.5 gain, followed by corrections to achieve the target. This pattern of results is reflected in the primary submovement distance data, presented in Figure 3. Again the groups are pooled across cue condition as there were neither significant main effects nor interactions during the adaptation blocks. There was a significant block x trial interaction ($F(45, 1395) = 29.4$, $p < .001$, $\omega^2 = .44$, large effect size). Follow up contrasts revealed significant linear and quadratic trends across trials within each adaptation block (Linear trends: Block 1: $F(1, 34) = 143.4$, $p < .001$, $\omega^2 = .22$, large effect size; Block 2: $F(1, 34) = 49.5$, $p < .001$, $\omega^2 = .40$, large effect size; Block 3: $F(1, 34) = 84.4$, $p < .001$, $\omega^2 = .53$, large effect size; Block 4: $F(1, 34) = 66.4$, $p < .001$, $\omega^2 = .47$, large effect size; Block 5: $F(1, 34) = 134.0$, $p < .001$, $\omega^2 = .64$, large effect size; Block 6: $F(1,$

34) = 46.0, $p < .001$, $\omega^2 = .38$, large effect size. Quadratic trends: Block 1: $F(1, 34) = 21.4$, $p < .001$, $\omega^2 = .22$, large effect size; Block 2: $F(1, 34) = 110.5$, $p < .001$, $\omega^2 = .60$, large effect size; Block 3: $F(1, 34) = 38.8$, $p < .001$, $\omega^2 = .53$, large effect size; Block 4: $F(1, 34) = 80.0$, $p < .001$, $\omega^2 = .52$, large effect size; Block 5: $F(1, 34) = 50.0$, $p < .001$, $\omega^2 = .40$, large effect size; Block 6: $F(1, 34) = 58.4$, $p < .001$, $\omega^2 = .44$, large effect size).

The post-test data for experiment 1 revealed moderate effectiveness of both the target orientation and the head posture cues (Figure 4). The groups are split by condition (level of cue) for this plot, as there were significant effects involving condition during the post-test. There was a group x block x condition interaction for the post test ($F(2, 31) = 5.2$, $p = .01$, $\omega^2 = .07$, medium effect size). Follow up tests for block 1 of the post test revealed main effects for condition ($F(1, 31) = 10.0$, $p < .01$, $\omega^2 = .11$, medium effect size). Furthermore, condition contrasts on the first trial of block 1 revealed that there was no significant effect of condition for group 1 (arm posture cue group) ($F(1, 10) = 2.02$, $p > .10$), a trend for a condition effect with group 3 (head orientation cue group) ($F(1, 10) = 3.3$, $p < .10$), and a condition main effect for group 2 (target orientation cue group) ($F(1, 10) = 15.1$, $p < .01$). Condition contrasts on the first trial of post test block 2 revealed that there was no significant effect of condition for groups 1 and 2 (Group 1: $F(1, 10) = 3.03$, $p > .10$, Group 2: $F(1, 10) < 1.0$, $p > .10$), but that there was a condition main effect for group 3 ($F(1, 10) = 5.62$, $p < .05$).

Subjects participating in the second experiment also exhibited small learning effects during the pre-test (Figure 5). There was a block by trial interaction ($F_{9,81}=2.78$, $p<.01$, $\omega^2= .29$, large effect size), reflecting that greater changes occurred across trials in the first block in comparison to the second. Similar to the first experiment, however, there were no group differences in performance from the outset of the experiment.

As in the main experiment, there were no group differences in the disruptions in performance that were seen each time the gain was changed during the first set of six adaptation blocks for the second experiment (upper row, Figure 6). Subjects demonstrated patterns that were similar to those observed in the first experiment for these first six adaptation blocks; that is, they initially undershot the target when presented with the 0.5 gain of display and overshot it with the 1.5 gain, resulting in significant linear and quadratic trends across trials within each of the blocks (Linear trends: Block 1: $F_{1,9}$=24.9, p<.01, ω^2=.37, large effect size, Block 2: $F_{1,9}$=16.9, p<.01, ω^2=.28, large effect size, Block 3: $F_{1,9}$=23.5, p<.01, ω^2=.36, Block 4: $F_{1,9}$=14.0, p<.01, ω^2=.24, large effect size, Block 5: $F_{1,9}$=.31, large effect size, Block 6: $F_{1,9}$=17.8, p<.01, ω^2=.30, large effect size. Quadratic trends: Block 1: $F_{1,9}$=15.5, p<.01, ω^2=.27, large effect size, Block 2: $F_{1,9}$=38.6, p<.01, ω^2=.48, Block 3: $F_{1,9}$=26.8, p<.01, ω^2=.39, large effect size, Block 4: $F_{1,9}$=13.0, p<.01, ω^2=.23, large effect size, Block 5: $F_{1,9}$=40.3, p<.01, ω^2=.49, large effect size, Block 6: $F_{1,9}$=10.3, p=.01, ω^2=.19, large effect size).

The performance disruptions occurring due to gain changes were diminished across the second set of six adaptation blocks for the head posture group, resulting in group x trial interactions for some of these blocks (Figure 6, lower row; only the first five trials are plotted to increase clarity of the initial group separations). Although the interactions were not always statistically significant (which was not surprising given the small number of subjects participating), the effect sizes were moderate to large. These occurred in the odd-numbered blocks only (0.5 gain of display, Block 1: $F_{2,9}$=2.0, p>.10, ω^2=.20, large effect size, Block 3: $F_{2,9}$=3.7, p<.10, ω^2=.40, large effect size, Block 5: $F_{2,9}$=1.9, p>.10, ω^2=.18, large effect size with both head posture and target orientation groups differing from the arm posture cue group). There were no group differences in the quadratic trends across trials in the even-numbered adaptation blocks, in which the gain was 1.5 (trial main effects, Block 2: $F_{1,9}$= 24.3, p<.01, ω^2=.70, large effect size, Block 4: $F_{1,9}$=19.9, p<.01, ω^2=.65, large effect size, Block 6: $F_{1,9}$=.81, large effect size).

Similar to Experiment 1, the post-test for the second experiment demonstrates moderate effectiveness of both the head posture and the target orientation cues (Figure 7). The groups have been divided by condition (level of cue) to demonstrate the effectiveness of the cues. There were large condition effect sizes in some cases, indicating cue effectiveness. In the first portion of the post test, only the head posture cue was effective (condition main effect: $F_{1,2}$=2.8, p>.10, ω^2=.47, large effect size for the head posture group; ω^2 values were negative for the other two cue groups and F<1.0). For the second portion of the post test, both the head posture and the target orientation cues were effective (condition main effect head posture: $F_{1,2}$=2.4, p>.10, ω^2=.41, large effect size, target orientation: $F_{1,2}$=5.4, p>.10, ω^2=.69, large effect size, arm posture: ω^2 was negative and F<1.0).

Discussion

It was predicted that changing head orientation would be more effective than the control contextual cues to aid switching between visuomotor maps, due to the functional linkage between head and arm control. This linkage makes head orientation an integral aspect of arm movement control. Indeed, this group was the only one (in the first experiment) showing a significant elevation of distance covered in the primary submovement (for subjects in the post test condition level 2) when the level of cue was switched halfway through the post test block. The head posture contextual cue was also consistently effective for the subjects participating in the second experiment. Shelhamer and colleagues [25, 26, 28] have obtained similar results, demonstrating that head and eye orientation are salient cues to associate with differing gains of the VOR. They found that subjects could increase the gain of the VOR while the eyes were directed upward and decrease it for downwardly directed eye movements [25]. Similarly, Gandolfo et al. [10] demonstrated that the use of different hand postures was an effective contextual cue to discriminate between adaptive states for counteracting perturbing force fields. It appears, therefore, that the most effective cues are those that are integral to task execution. Thus, our results support the existence of interactions between head position and hand control, with even static head postures taken into account for arm movement control. Similarly, Berger and colleagues [1] have demonstrated that arm pointing movements (with the eyes closed) can be biased by static head posture. This effect is exaggerated by exposure to microgravity. Combined, these data support the idea of a functional head-hand linkage, with head orientation influencing limb control.

The target orientation cue also proved to be moderately effective. The fact that both of these cues worked may provide some insight into the mechanisms of contextual association. Both the target orientation and head posture cues resulted in subjects making oblique eye movements; thus, proprioceptive information regarding eye position may have served to transduce the cue information. The oblique eye movements may also have created the need for an additional transformation between this obliquely oriented eye movement and the horizontally oriented movement required by the hand. This additional step could increase the task difficulty and enhance association of the cue.

The arm posture contextual cue condition was not associated at all with the gain experienced during adaptation. It is not entirely surprising that the arm posture cue was ineffective, since it did not serve to change any aspect of the task performance (subjects drew with the right arm and changed posture of the left arm). It is unlikely that subjects could have utilized the cues to formulate an explicit rule; data suggests that visuomotor adaptation does not incorporate such processes. For example, Welch [30] has demonstrated that prism shift aftereffects occur even when subjects are made aware that the prism lenses have been removed.

The mechanism by which cues enable switching between adaptive states is unclear. They could potentially facilitate priming of the appropriate visuomotor map and/or simultaneously inhibit the competing mappings. Shadmehr and Holcomb [24] have demonstrated that a learned pattern needs to be inhibited before acquisition of a competing pattern can occur. Their work suggests that this occurs over time (5.5 hr was sufficient for their task) and involves the ventral prefrontal cortex [24]. The data presented in this experiment suggest that appropriate cues can expedite this process.

The adaptation paradigm used in the first experiment followed a relatively short time course (120 trials, approximately 20-30 minutes) in comparison to other investigations of dual adaptation. This likely contributed to the lack of evidence for dual adaptation appearing within these training blocks. The addition of another sequence of adaptation blocks in the second experiment was sufficient for subjects in the head orientation cue group to demonstrate a mitigation of the disruption occurring with each gain change, providing evidence of dual adaptation. Thus it appears that cue association is a dynamic process that evolves gradually over time. Surprisingly, this occurred only when subjects performed under the 0.5 gain of display and not the 1.5 gain of display. The target orientation group appeared to exhibit signs of dual adaptation towards the end of the second adaptation block, but there seemed to be no difference for the arm posture group. It is possible that, provided adequate exposure to the alternating blocks, the arm posture contextual cue group would also eventually achieve dual adapted states. For example, Martin et al. [19] demonstrated that subjects could switch automatically between throwing with wedge prisms and without after 20 training sessions over six weeks. In their study, the only cue available to the subjects was the existence of the prism lenses over the eyes. Similarly, Cunningham and Welch [5] found a reduction in initial errors when subjects alternated between normal and rotated visual feedback after five hours of training. Perhaps less salient contextual conditions (i.e., presence or absence of lenses) are associated with adaptive states over longer periods of alternating exposures. Shelhamer and colleagues [25] investigated this by having subjects take on and off clear lenses while alternating between increased and decreased VOR gain for one hour, without providing any additional cues. Subjects did not exhibit context dependency on the glasses following this training. However, following the six weeks of prism training sessions in the experiment by Martin et al. [19], subjects were able to use the prism lenses as a contextual cue.

These results have significant implications for the design of adaptive training programs. Firstly, they add to the accumulating evidence that humans can simultaneously store multiple adaptive states [5, 7, 10, 19, 21, 25, 26, 28, 31, 32]. Secondly, the data leads to a cohesive theory regarding the effectiveness of contextual cues to aid switching between these states. It appears that even simple cues, such as wearing prismatic lenses, can be effective over many hours of training [5, 19]. The current study and others [10, 25, 26], however, have demonstrated that some cues can also be effectively associated with an adaptive state after a short time period of training. These cues are those that are an integral aspect of the task. Additionally, the data demonstrate that head orientation information is incorporated into arm movement control.

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Table 1

Trial Descriptions

Block Number	Arm Posture Cue Group	Target Orientation Cue Group	Head Orientation Cue Group
Block 1. Pre Test	10 trials right-to-left, 10 trials left-to-right, 8.0 cm, gain = 1.0, neutral arm posture.	10 trials right-to-left, 10 trials left-to-right, 8.0 cm, gain = 1.0, neutral monitor position.	10 trials right-to-left, 10 trials left-to-right, 8.0 cm, gain = 1.0, neutral head orientation.
Block 2. Adaptation			
A1:	20 trials 16.0 cm, gain = 0.5, non-dominant arm in full flexion.	20 trials 16.0 cm, gain = 0.5, monitor in +20° roll.	20 trials 16.0 cm, gain = 0.5, head in +20° roll.
A2:	20 trials 5.3 cm, gain = 1.5, non-dominant arm in full extension.	20 trials 5.3 cm, gain = 1.5, monitor in -20° roll.	20 trials 5.3 cm, gain = 1.5, head in -20° roll.
A3:	Identical to A1.	Identical to A1.	Identical to A1.
A4:	Identical to A2.	Identical to A2.	Identical to A2.
A5:	Identical to A1,3.	Identical to A1,3.	Identical to A1,3.
A6:	Identical to A2,4.	Identical to A2,4.	Identical to A2,4.
Block 3. Post Test	32 trials, 8.0 cm, gain = 1.0, non-dominant arm flexed first 16 trials, extended last 16 trials (half subjects extension first, flexion second).	32 trials, 8.0 cm, gain = 1.0, monitor in +20° roll first 16 trials, -20° roll last 16 trials (half subjects +20° first, -20° second).	32 trials, 8.0 cm, gain = 1.0, head in +20° roll first 16 trials, -20° roll last 16 trials (half subjects +20° first, -20° second).

Figure Captions

1. Pre-test primary submovement distance (Panel A is right-to-left movements and Panel B is left-to-right, see Table 1 for trial definitions). There was a main effect for both trial and block, with all three groups increasing primary submovement distance during the pre-test.
2. Sample position and velocity trajectories from early in the adaptation blocks. The left panels depict trials from the 0.5 gain of display, characterized by target undershoots followed by corrections to achieve the target. The right panels plot trials from the 1.5 gain of display, characterized by target overshoots with corrections necessary to achieve the target.
3. Primary submovement distance across the adaptation blocks. Block numbers are defined in Table 1; the first half of each block consists of leftward movements while the second half are rightward movements. There were significant linear and quadratic trends across trials in each block as subjects adapted performance to the altered gain of display within each block.
4. Post-test primary submovement distance (1.0 gain of display, plotted by level of cue). The upper row plots the first 16 trials and the lower row plots the second 16 (following the change in cue level). The target orientation group exhibited a cue effect for the first post-test block, while the head posture group exhibited a trend for a cue effect for the first post-test block and a significant cue effect for the second post-test block.
5. Experiment Two pre test primary submovement distance (Panel A is right-to-left movements and Panel B is left-to-right). There was a block x trial interaction, with greater changes occurring across trials in the first block than in the second.
6. Experiment Two adaptation primary submovement distance (upper row first six adaptation blocks, lower row second six adaptation blocks). Only the first five trials of each block are presented for the second set of adaptation blocks. There were significant linear and quadratic

trends across trials in all blocks. Additionally, there were large effect sizes for the group x trial interaction in blocks A1, A3, and A5 of the second set of adaptation blocks (lower row). In these blocks, the head posture group exhibiting a lessening of performance disruptions upon switching between the two gains of display.

7. Experiment Two post-test primary submovement distance (1.0 gain of display, plotted by level of cue). The upper row plots the first 16 trials and the lower row plots the second 16 (following the change in cue level). There were large condition effect sizes, with the head posture cue effective for both the first and second post blocks and the target orientation cue effective for the second post test block only.

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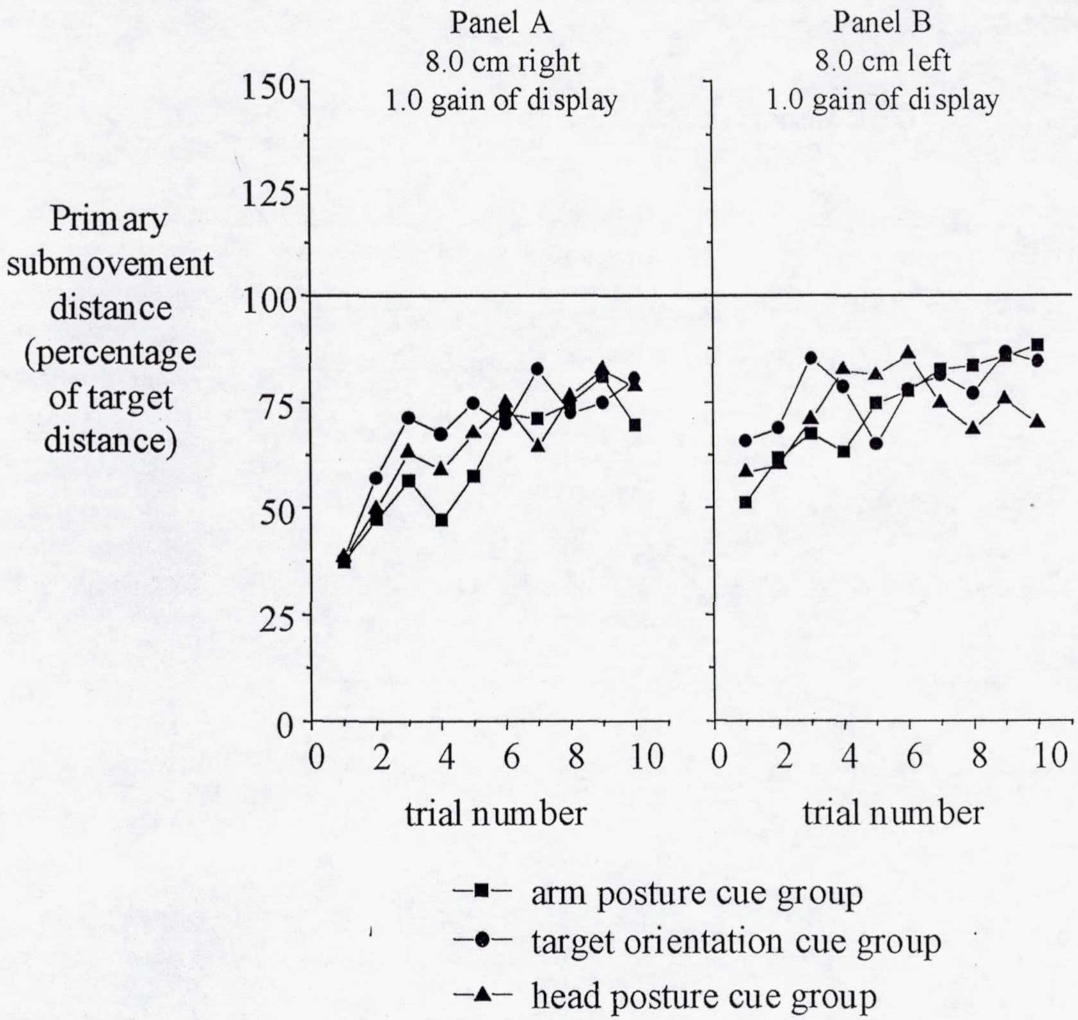


Panel A
8.0 cm right
1.0 gain of display
Panel B
8.0 cm left
1.0 gain of display
Primary submovement distance (percentage of target distance)
150
125
100
75
50
25
0
0 2 4 6 8 10
0 2 4 6 8 10
trial number
trial number
arm posture cue group
target orientation cue group
head posture cue group

Fig. 1

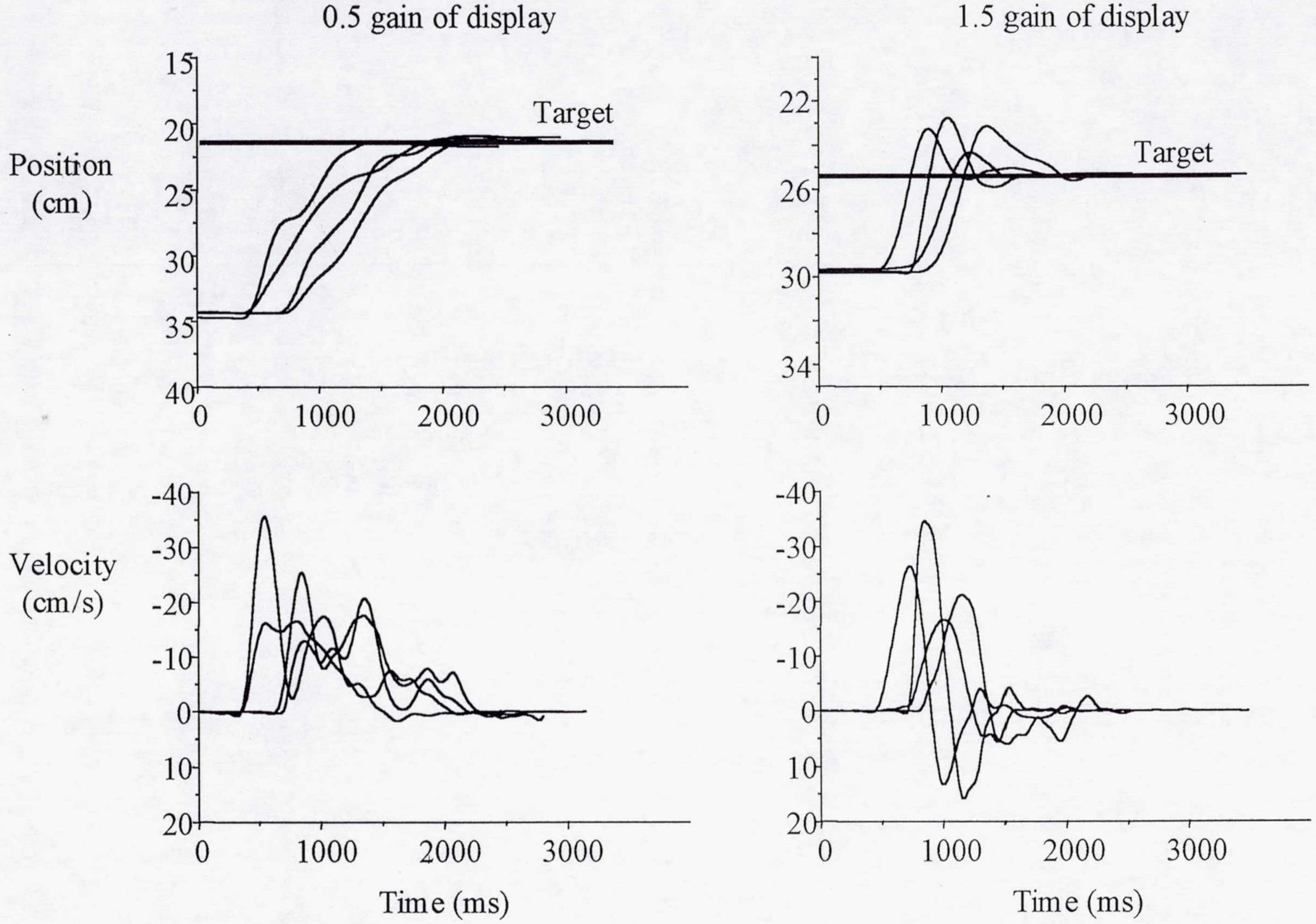

0.5 gain of display
1.5 gain of display
Position
(cm)
Velocity
(cm/s)
Target
Target
15
20
25
30
35
40
22
26
30
34
-40
-30
-20
-10
0
10
20
0
1000
2000
3000
Time (ms)
Time (ms)

Fig.2

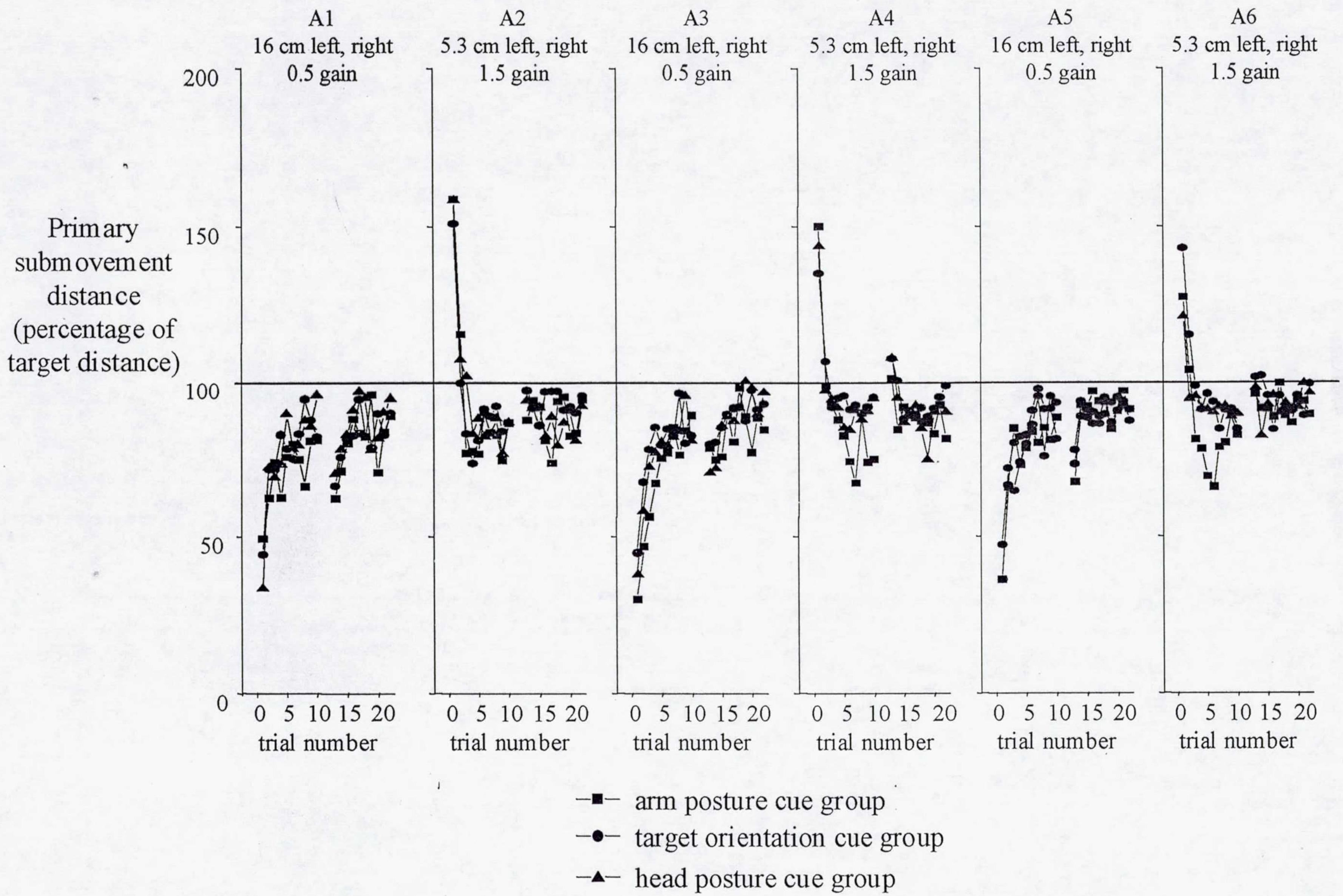

A1
16 cm left, right
0.5 gain
A2
5.3 cm left, right
1.5 gain
A3
16 cm left, right
0.5 gain
A4
5.3 cm left, right
1.5 gain
A5
16 cm left, right
0.5 gain
A6
5.3 cm left, right
1.5 gain
Primary submovement distance (percentage of target distance)
200
150
100
50
0
0 5 10 15 20
trial number
arm posture cue group
target orientation cue group
head posture cue group

Fig. 3

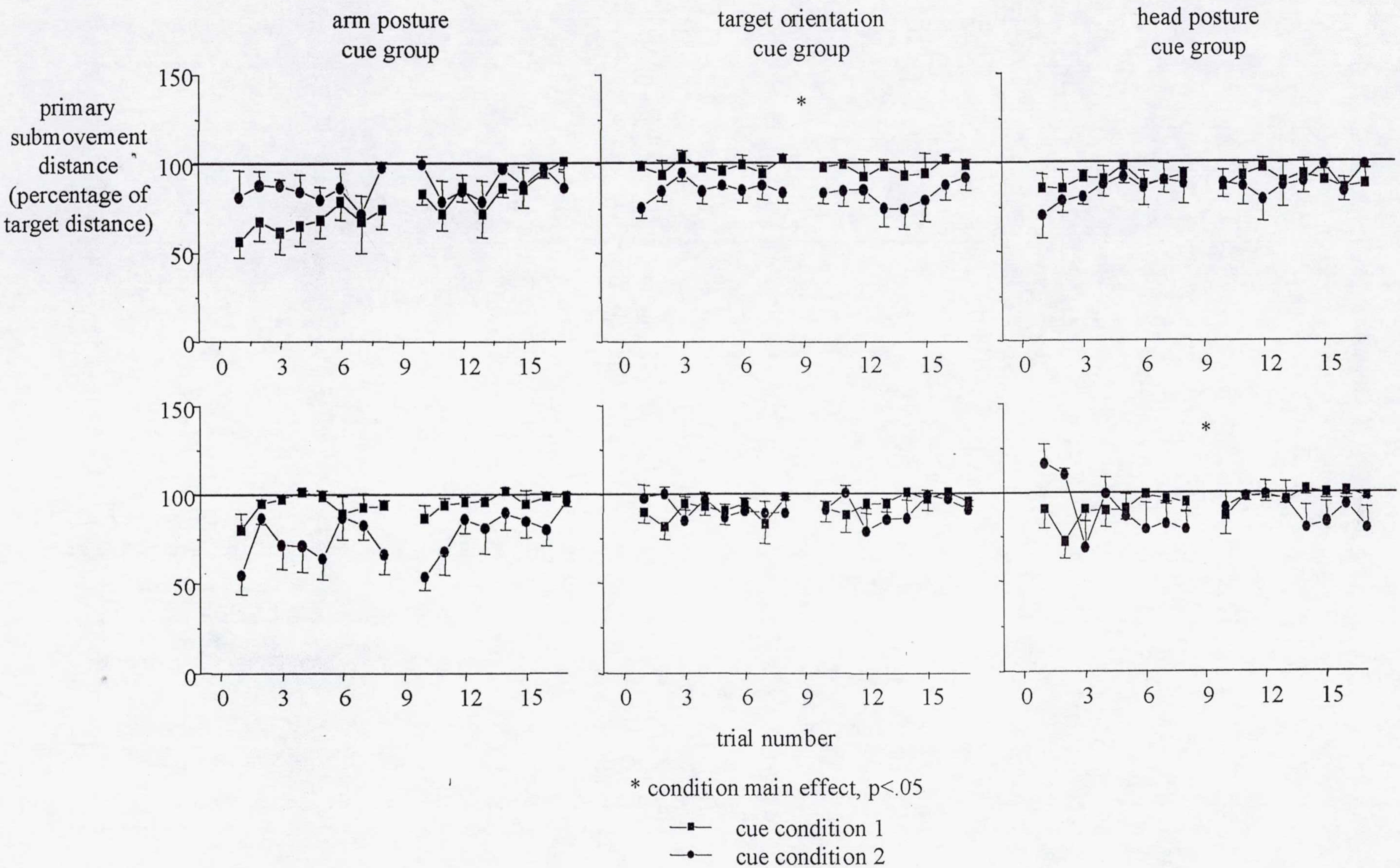
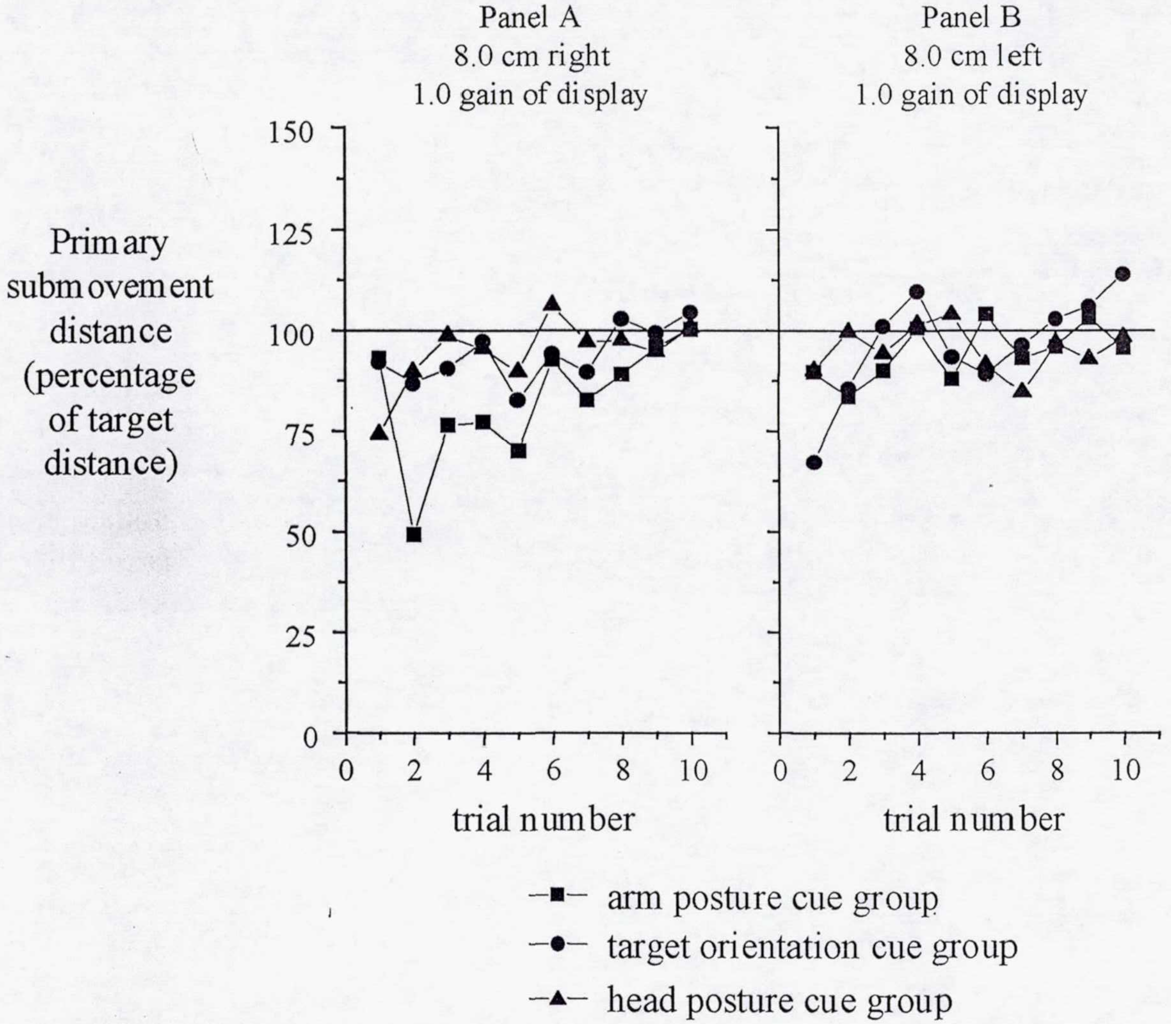

arm posture
cue group
target orientation
cue group
head posture
cue group
primary
submovement
distance
(percentage of
target distance)
150
100
50
0
0
3
6
9
12
15
*
trial number
* condition main effect, p<.05
cue condition 1
cue condition 2

Fig. 4



Panel A
8.0 cm right
1.0 gain of display
Panel B
8.0 cm left
1.0 gain of display
Primary submovement distance (percentage of target distance)
150
125
100
75
50
25
0
0 2 4 6 8 10
trial number
arm posture cue group
target orientation cue group
head posture cue group

Figure 5

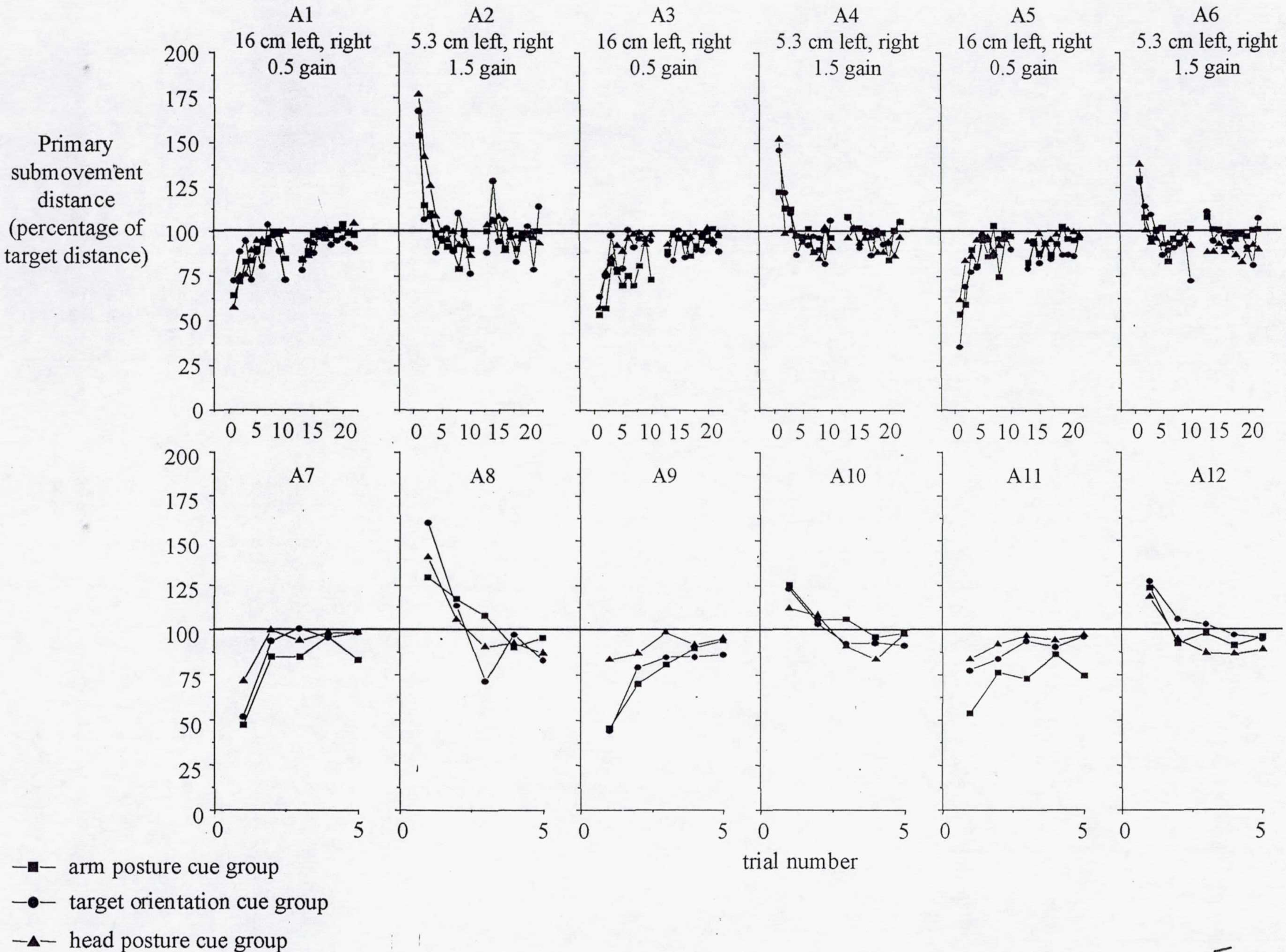

A1
16 cm left, right
0.5 gain
A2
5.3 cm left, right
1.5 gain
A3
16 cm left, right
0.5 gain
A4
5.3 cm left, right
1.5 gain
A5
16 cm left, right
0.5 gain
A6
5.3 cm left, right
1.5 gain
A7
A8
A9
A10
A11
A12
Primary submovement distance (percentage of target distance)
trial number
arm posture cue group
target orientation cue group
head posture cue group

Figure 6

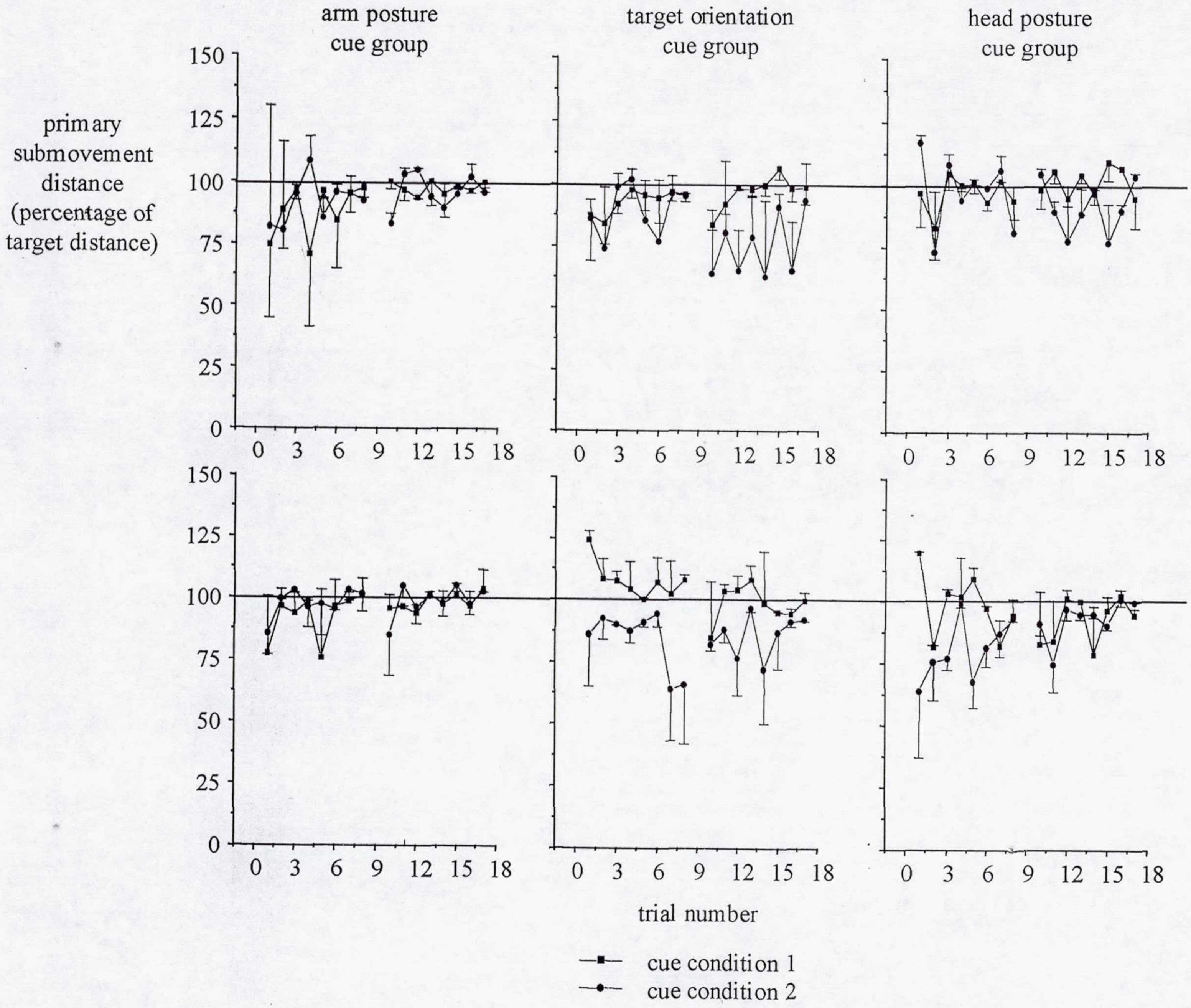

arm posture
cue group
target orientation
cue group
head posture
cue group
primary
submovement
distance
(percentage of
target distance)
150
125
100
75
50
25
0
0 3 6 9 12 15 18
trial number
cue condition 1
cue condition 2

Figure 7