Straight Reaches are Due to Standard Visual Feedback

By

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THESIS

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Natarajan Vaidyanathan,

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SUMMARY

It is generally understood that reaching movements that aim to be efficient, for example by minimizing metabolic costs or mechanical power, will arc the hand along curved paths. Yet behavioral studies consistently find that subjects move the hand along a straight path. It has also been shown that visual feedback depicting hand and target locations influences how subjects move. Could this influence explain the lack of path curvature in experimental results? In particular, would reaches examined under different feedback conditions elicit curvature indicative of efficient movements? To address these questions, we reproduced an early and influential study (Morasso 1981) along with two variations that progressively reduced the extent of visual feedback of the hand and target locations in two experiments. As is often found, subjects moved their hands along relatively straight paths when provided with the standard visual feedback. In contrast, the two new conditions in the Experiment elicited curved paths (as quantified by perpendicular errors, angular errors, and path length). Notably, this curvature increased as the extent of visual feedback decreased. The changes in curvature could not be attributed to increases in task difficulty, but rather appear to reflect the motor system's intentional strategies for reaching when the visual feedback of the task is diminished. Furthermore, in order to check if the observed curvature in the absence of visual feedback was actually a preference and not a mere chance or an artifact of unclear picture of accurate target location, we devised another experiment. Here subjects reached for the same targets, but the standard visual feedback was removed either in the first or the second half of the experiment. The results from this experiment while showcased a preference for curved trajectories in the absence of visual feedback irrespective of the order in which the feedback was removed, also displayed the strong influence of the standard visual feedback even after it was removed. Our results are further

evidence that the straight reaches often observed may be due to a bias to move the displayed feedback along straight paths. Eliminating this visually-induced bias may expose innate reaching behaviors more appropriate for investigating the motor system, possibly revealing a preference for efficient reaches.

1. Introduction

Our brain is essentially a controller that constantly receives inputs from the surroundings, understands it, takes appropriate decisions and performs actions simultaneously. It is essential to understand how the brain encodes these information and what control mechanisms it incorporates in order to execute a movement. Motor control research investigates, how the brain learns, represents, adapts and executes movements. Research involves experiments including but not limited to examining lesions, EEG (Electro Encephalogram) recordings, behavioral studies and computational modeling as well. Here we discuss in detail one such investigation that aims at comprehending the control of reaching movements through a simple behavioral experiment.

Reaching studies are broadly applied as a tool to examine the motor system and the control of movements. In many studies, subjects make point-to-point reaches to a displayed target. These studies consistently find that the hand follows a straight path during both unperturbed reaches (Morasso 1981, Flash and Hogan 1985) and those made with perturbed visual feedback (Krakauer, Pine et al. 2000). When given adequate practice, subjects also make straight reaches when interacting with disturbing loads, such as a force field (Uno, Kawato et al. 1989, Shadmehr and Mussa-Ivaldi 1994), a Coriolis force (Dizio and Lackner 1995), or an external mass (Krakauer, Ghilardi et al. 1999, Sainburg, Ghez et al. 1999). The fact that reaches are straight under these very different circumstances seems to imply that the goal of the motor system is to move the hand straight.

Despite this evidence, there are several reasons to believe that the goal of the motor system is to move the hand in curved paths. Everyday movements outside the laboratory setting are often curved (Ramanathan, Eberhardt et al. 2000). Since our limb's joints rotate, not translate, it seems sensible that our hand movements may naturally follow arced paths. Another reasonable logic is the effect the control of movements has due to metabolic considerations. Firing of neurons is a highly energy-expensive process and the brain should have evolved to produce movements that do not have a huge toll on the energy expenditure of the body. Reduced metabolic activity with extensive practice can also be seen in M1 hinting at an evidence for control for efficiency (Picard, Matsuzaka et al. 2013). To gain more insights from a biological standpoint, researchers often model movements optimizing metabolic efficiency.

Reaching models that minimize metabolic costs predict curved reaches (Rosenbaum, Loukopoulos et al. 1995). Minimizing mechanical precursors of metabolic costs, such as joint torque rates, energy and work also predict curved reaches (Uno, Kawato et al. 1989, Alexander 1997, Kang, He et al. 2005). More broadly, studies on human locomotion find that legs are controlled for efficient movement (Selinger, O'Connor et al. 2015). Indeed, the movements of many animals are consistent with mechanical and metabolic efficiency (Hatze and Buys 1977, Rayner 1993). This wealth of data suggests reaches should be curved, yet in experimental settings reaches are straight. What can account for this discrepancy?

Many studies have found that the feedback displayed during reaching studies can influence how subjects move. For example, subjects move in the opposite direction of visual perturbations, such that the displayed feedback follows a straight path (Wolpert, Ghahramani et al. 1995). This is also true when the visual feedback is nonlinearly perturbed (Flanagan and Rao 1995). Even when a cursor's trajectory is defined through a complex association of finger orientation and movements, subjects alter their movement to force the feedback along a straight trajectory (Danziger and Mussa-Ivaldi 2012). The effect of visual feedback on reaches can also be seen in object manipulation experiments, where the type of feedback provided can change how subjects interact with the environment (Kluzik, Diedrichsen et al. 2008, Farshchiansadegh, Melendez-Calderon et al. 2016). Thus visual feedback can bias reaching movements and how they are controlled.

Here we test whether reaches are inherently controlled to be straight, or whether the standard visual feedback provided biases them to be straight. In Experiment 1, we systematically reduced the extent of visual feedback: the visually displayed information that subjects could use to track hand and target location. The first group provided the standard visual feedback of small solid circles for hand and target locations. In the second group, subjects were shown the target location and their hand's distance from it, but not its exact location. In the third group, subjects were shown their distance from the target but neither their hand nor the target's location. As the extent of visual feedback decreased, the movement curvature (as quantified by perpendicular error, angular error and path length) increased. In Experiment 2, we test how the same subject reach for the targets in the presence and absence of visual feedback (condition similar to the first and the third group in Experiment 1). One group reached with no visual feedback during the first half of the experiment and was later provided with the standard visual feedback, while the other group performed the task with standard visual feedback right from the beginning, which was removed later for the second half. An increased curvature was observed when reaches were made in the absence of standard visual feedback. An induced bias was also evident from the less curved trajectories for the reaches made in the no visual feedback condition after practicing in the standard visual feedback condition.

We suggest that removing visual feedback of the hand and target locations may eliminate a visually-induced bias for straight reaches, and reveal behavior similar to what would be observed outside the laboratory setting. We suggest prior studies may have unintentionally biased reaching behavior, masking evidence for efficiency as is often found in the control of our lower limbs (and the movement of other animals).

2. Materials and methods

2.1. Subjects

A total of 34 subjects (23 ± 2.7 yr, 12 females) were assigned to one of three groups in experiment 1 and 23 subjects (24 ± 2.8 yr, 2 females) were assigned to one of the two groups in experiment 2. All subjects were healthy with normal or corrected-to-normal vision and provided written consent prior to participating. Subjects completed the Edinburgh Inventory Test to ensure right-handedness. Subjects were paid to participate with a baseline compensation and a bonus proportional to performance. Two subjects were removed from this study (1 in Experiment 1 and 1 in Experiment 2) due to especially poor performance. All experimental procedures were approved by the University of Illinois Chicago Institutional Review Board.

2.2. Experimental setup

Subjects sat in a height-adjustable chair and made point-to-point reaching movements with their index finger (Figure 1A). They were instructed to reach by moving their shoulder and elbow in the workspace plane without rotating their wrist. Reaches were made to 6 different targets in an ordered sequence of 8 movements (identical to (Morasso 1981), see Figure 3.1 B). A block was defined as a sequence of these 8 reaches.

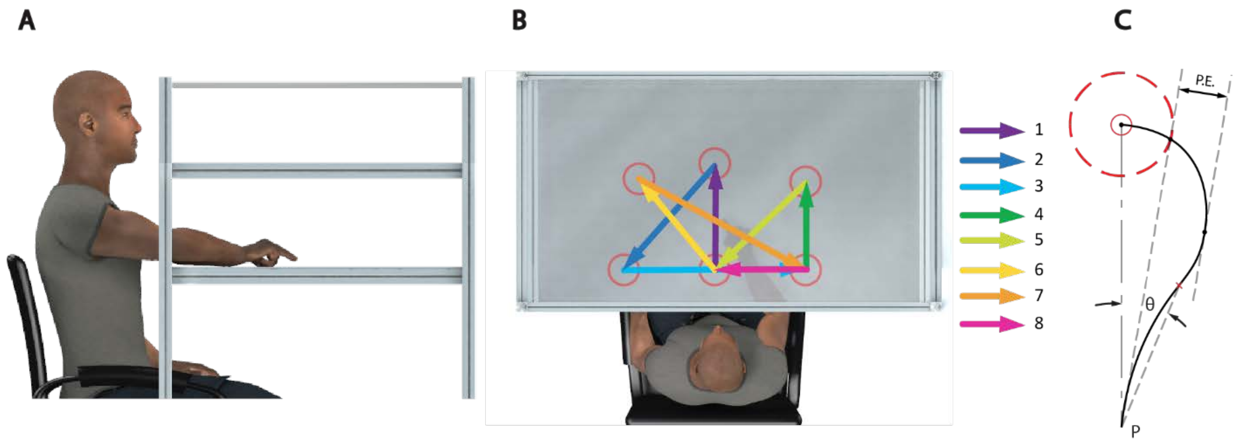

Figure 3.1 ***- Experimental setup for experiment 1 and 2 and definition of metrics that were used to compare reach curvature.*** *(a) A side-view of the experimental apparatus. The top, middle and bottom levels on the structure represent the projector screen, one-way mirror, and workspace respectively. Subjects were adjusted to an appropriate height at which the arm was relatively planar. (b) A birds-eye view of the apparatus with the projector screen hidden. The one-way mirror reflects the eight reaches from Morasso 1981. Note that there is overlap between the trajectories of reach 3 and reach 8. (c) An example of a reach 1 trajectory and locations that pertain to the curvature metrics. Location P is the starting hand location. The "trigger state" is defined as the hand position as it crosses a threshold (red dashed circle). The perpendicular error (PE) is defined as the largest perpendicular deviation of the hand's trajectory from the straight line between P and the trigger state. The angular error (theta) is defined as the angle between the straight trajectory between starting and ending targets and the position of the hand where velocity was at a maximum (red hash line). Finally, the path length is defined as the integrated distance of the subject's trajectory normalized by the distance from Location P to the trigger state.*

2.3. Feedback conditions

Full Visual Feedback or Cursor condition: Subjects made reaches with continuous feedback of their finger location displayed as a 10 mm diameter filled white circle. The target was displayed with a 20mm diameter open white circle. The target's color changed when the feedback was provided, as described above. This condition provided full visual feedback of the finger's location as well as the exact target location, similar to Morasso 1981. Behavior under this condition was used as a control and point of reference for the following two conditions.

Partial Visual Feedback or Ring condition: A ring centered on the target provided feedback of the hand's location. The radius of the ring was equal to the hand's distance to the target such that their exact hand location was somewhere along the ring's perimeter. The target display was identical to Condition 1 above. To land on target subjects decreased the ring's radius to that of the target's. The center of the target changed color when feedback was provided. This condition, in contrast with Condition 1, did not display the subject's exact hand location and was our first test for examining a potential visually-induced bias. Though more difficult than in Condition 1, with practice subjects were quickly able to make successful reaches.

No Visual Feedback or Bar condition: This displayed a rectangle in a fixed location of the workspace. The height of the rectangle was constant but the right edge of the rectangle moved such that the overall length was equal to the subject's distance to the target. A thin vertical line on the rectangle indicated the threshold for landing inside the target. In this condition, the color of the rectangle changed when feedback was provided. To indicate the current reach a target number was displayed at the top of the workspace. In this condition neither target nor hand location was displayed and subjects had to rely on remembered target locations and proprioception. Though also more difficult than Condition 1, subjects were able to make successful reaches.

3. Experimental Apparatus

A one-way mirror sitting below a projector screen (20 cm and 48 cm above the workspace plane respectively) reflected the visual display and blocked the hand from the subject's view (see Figure 3.1 A). The reaching workspace was a smooth, flat surface supporting the hand and elbow. Subjects were instructed to move their right hand along the surface with their index finger resting inside a small, light plastic wand that held infra-red sensors.

Limb data was recorded with an Optotrak 3D Investigator at 250 Hz with sub-millimeter precision. Small, light-weight (~2 grams) infra-red sensors recorded finger location and limb orientation. Three sensors were placed on the finger's wand so it could be viewed from a wide range of angles and during all the required movements. Subjects wore a compression sleeve on the right upper and forearm. Three sensors affixed to the forearm and 6 more on the upper arm allowed us to compute limb joint angles and limb motion throughout a trial, though none of this data was used in the analysis provided here. Before each experiment, the Optotrak and Projector system were calibrated to the workspace.

4. Experimental method

4.1. Experiment 1

Subjects were divided into 3 groups, and performed the reaching task for each visual feedback condition: Cursor, Ring and Bar. An initial 5 blocks (40 reaches) were used to familiarize subjects with the setup, target locations, desired movement times, and the provided visual and auditory feedback. These familiarization trials were followed by 70 blocks with a brief (~3 minutes) break halfway through the experiment. In total subjects made 600 reaches (75 to each target).

4.2.Experiment 2

Subjects were divided into 2 groups: (i) Bar-to-Cursor (B2C), which was provided with No visual feedback in the first half of the experiment and later provided with full visual feedback and (ii) Cursor-to-Bar (C2B), which had complete visual feedback for the first half of the experiment which is removed for the second half. After an initial 5 blocks (40 reaches) of familiarization and 32 blocks (256 reaches) of trials in first visual feedback condition, subjects reached for targets in the other visual feedback condition for the next 37 blocks (298 reaches). A brief break (~3 minutes) was provided in the middle of the experiment. Thus, subjects performed 600 reaches in total (35 to each target and in each visual feedback condition in total).

5. Data Analyses

All data was post-processed in MATLAB. Reach metrics were computed using the portion of the reach between the onset of movement and time of the trigger state. Trials with false starts, aimed at the wrong target, or that took longer than 10 seconds were not included in the analysis. Perpendicular error was measured as the maximum deviation from straight line between the reach starting location and its location at the trigger state. Angular error was defined as the unsigned angle created by a straight line from the movement's initial location to the center of the target, and a straight line from the initial location to the point on the reach where speed was at a maximum. Path Length was calculated by numerically integrating the reach's path up to the trigger state. For comparisons across reaches, path length was normalized by the straight line distance between the starting finger position and its position at the trigger state (thus the minimum path length for any reach was 1.0).

In order to ensure that no condition was too difficult, we analyzed the score rate every 2 blocks. In each condition, we report the average number of blocks it took for subjects to achieve a success rate of 50%. The minimum block number was chosen when the 95% confidence interval of the mean subject score rate first exceeded a 50% success rate. Concretely, when the mean subject score rate was 2 standard deviations above 50%.

5.1.Statistical Analyses

To provide a quantitative comparison of reach curvature, unpaired t-tests were calculated between reaches and groups. Also, a one-way ANOVA and post-hoc Tukey-Kramer tests determined if there was an effect of reach number within each group. To determine the overall effect of visual feedback on the curvature of reaches, a two-way ANOVA (groups and reaches) and post-hoc Tukey-Kramer tests were performed across groups. Significance levels for all tests were set to 0.05.

In order to determine if the observed curvature could be an effect of task difficulty, we analyzed the relationship between the average score and perpendicular error in each condition. Average scores and perpendicular errors were calculated for the 8 reach numbers for every subject (total of 88 in each condition). The correlation coefficient between these two variables was calculated and tested for significance (chosen significance level $\alpha=0.05$).

In addition to the one-way ANOVA and post-hoc Tukey-Kramer tests, Experiment 2 also compared the metrics against each visual feedback condition within groups using two way ANOVA's and also compared the metrics across experiments. The change in metrics from the first and second halves of the experiment were also checked for significance from 0 with the help of t-test.

6. Results

6.1. Experiment 1

In order to examine the potential for a visually-induced bias, we conducted a reaching experiment that manipulated the extent of visual feedback; each condition progressively eliminated visual cues representing the hand and target locations. Subjects made a repeated sequence of eight reaches under three visual feedback conditions. Changes in reach curvature were compared in terms of perpendicular error, angular error and path length (Figure 3.1 C). We found that all metrics significantly increased as visual feedback was extinguished, suggesting visual feedback may bias how individuals control their movements. We present our results in more detail below.

6.1.1. Group 1: Full Visual Feedback or Cursor condition

In this Group the standard visual feedback for the subject's cursor and target was provided. On an otherwise black screen, a small solid circle displayed hand location and another displayed the target location. With continuous visual feedback, subjects scored the highest of the three conditions. On average, subjects were able to achieve a 50% success rate by the 1st block of the experiment (~8th trial) and had an average score of 92.34% over the last half of the experiment. As is often found, subject's reaches were typically straight with bell-shaped velocity profiles. Reaches were consistent both within and across subjects (compare Figures 7.1 A-C and 7.1 D). The results from this standard condition were used as a point of reference to compare against the two following groups.

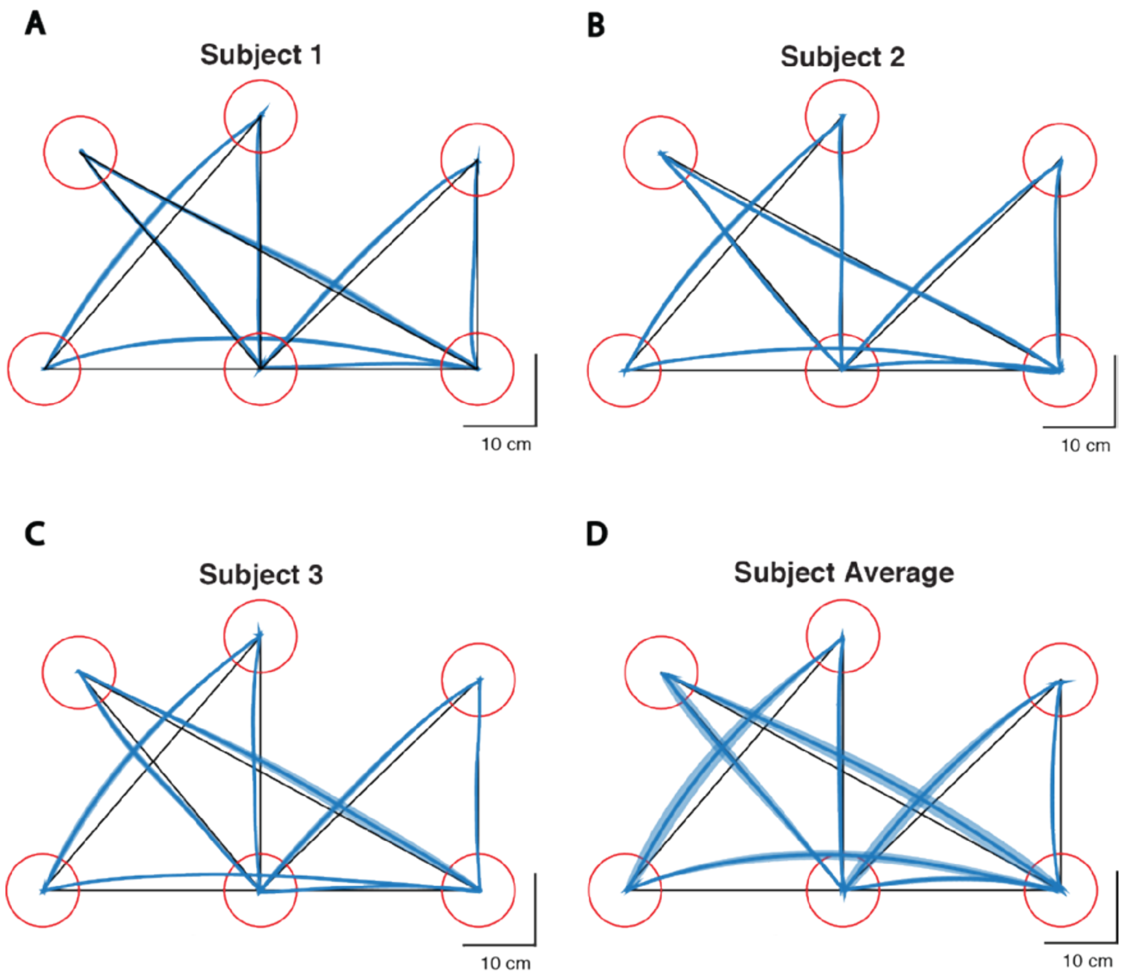

Figure 7.1. **Average trajectories from Group 1: *Full Visual Feedback.*** Subjects in this group received the standard visual feedback, which consisted of a small circular cursor marking the location of the hand and a stationary circle marking the target position. (a) (b) and (c) Trajectories of individual subjects. It is important to note that all of the trajectories are relatively similar and straight. (d) An average of all 11 subjects' mean trajectories.

It is worth noting that reaches made in certain directions exhibited relatively large curvature. In particular, across body, transverse reaches (Figure 7.1 ; reaches 3 and 7) had more curvature than in and out reaches (Figure 7.1; reaches 1 and 4). More specifically, for reach 3, the across-subject average perpendicular error was 50.24 ± 5.42, the angular error was 11.68 ± 1.15, and the path length was 1.029 ± 0.005. For comparison, reach 1 had perpendicular error of 10.77 ± 0.93, angular error of 3.78 ± 0.45, and a path length of 1.009 ± 0.001. ANOVAs quantified these comparisons, finding an effect for reach number for the perpendicular and angular error ($F(7,80) = 18.2$; $p = 2.96e-14$, $F(7,80)$

= 6.4; p = 5.45e-06). A post-hoc Tukey-Kramer test revealed that the perpendicular error of reach 3 was significantly larger than that of all of the other reach numbers. Similarly, the mean angular error for reach 3 was significantly larger for all but reaches 2 and 8. An ANOVA performed on path length did not find a significant effect for reach number ($F(7,80) = 1.2$; $p = 0.32$). Thus the across body reaches, requiring relatively large angular excursions to achieve straight hand paths, were generally more curved than other movements when full visual feedback was provided.

6.1.2. Group 2: Partial Visual Feedback of Hand or Ring condition

This was our first test for whether removing visual feedback could uncover a bias for straight reaches. In this group the targets were continuously visible, as in Group 1, but the exact hand location was not provided. Instead, a ring centered on the target, whose radius was equal to the hand's distance from it, was displayed. Subjects took slightly longer to become familiar with reaching under this feedback condition and achieved a 50% success rate by the 2nd block (~16 trials). By the end of the experiment the average score over the last half of the experiment was 80.90%. In contrast with Group 1, reaches made under this feedback condition were visibly curved and variable across subjects (see typical subjects Figure 7.2 A-C). Interestingly, deviations from the typically observed straight trajectories resulted from merely a partial elimination of the standard visual feedback of hand location. Note, however, that the variability in curvature was lost when averaging across subjects' hand paths (Figure 7.2).

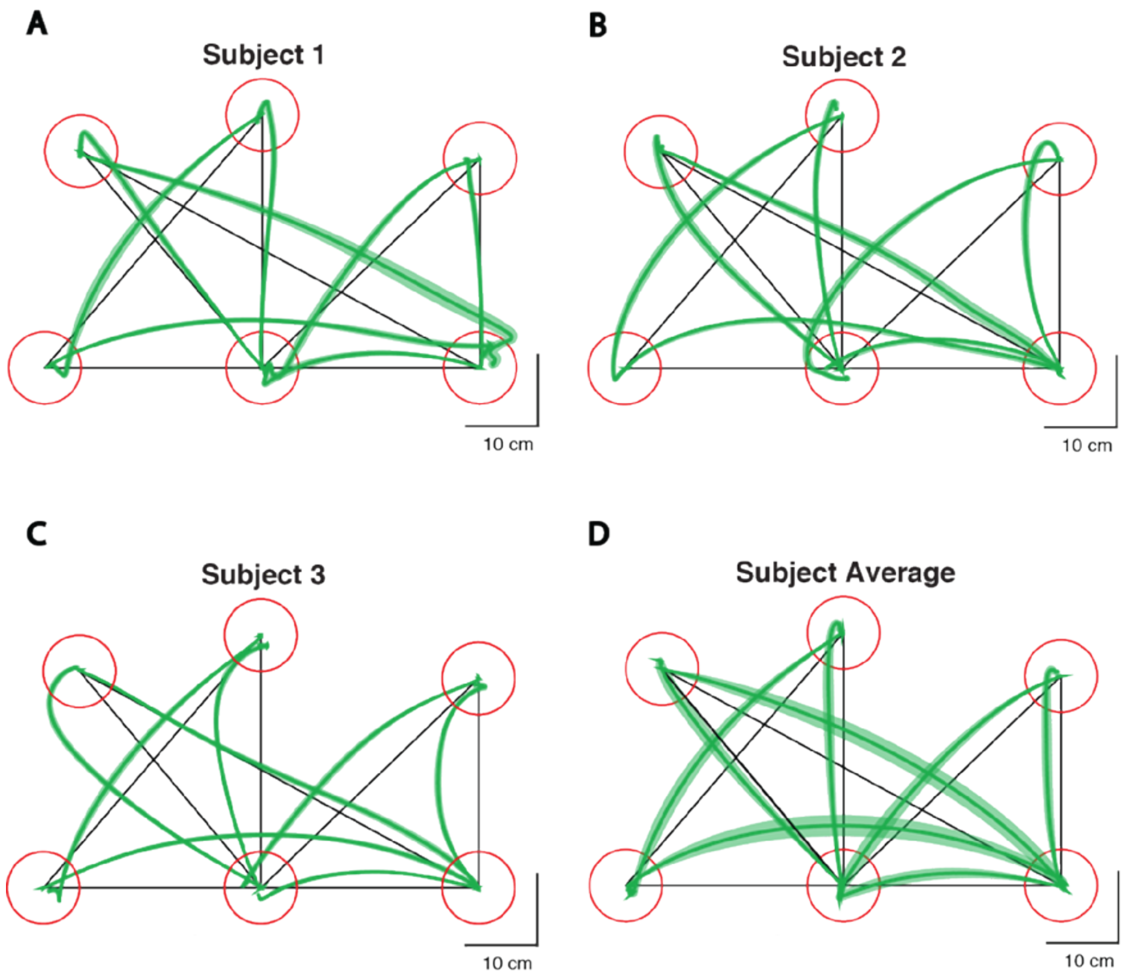

Figure 7.2 ***Average trajectories from Group 2.*** **Partial Visual Feedback** of Hand. *Subjects in this condition experienced a reduced extent of visual feedback. A ring centered on the target, whose radius was equal to the hand's distance from it, replaced the full visual feedback of the hand. The target's visual feedback remained the same. (a) (b) and (c) Trajectories of individual subjects. In this condition, we observe more variable and curved reaches. (d) An average of all 11 subjects' mean trajectories. Since subjects curve on either side of the straight line trajectory, the average resembles a relatively straight line.*

Similar to Group 1, the across-body movement reach 3 exhibited a relatively large curvature: 83.70 ± 12.85, 18.93 ± 3.03, and 1.088 ± 0.022 for the across-subject average perpendicular error, angular error and normalized path length, respectively. Again, for comparison reach 1 had an average perpendicular error of 23.35 ± 5.54, angular error of 7.62 ± 1.56, and the path length of 1.051 ± 0.016. As before, a significant effect was found for reach number for both perpendicular and angular errors

(F(7,80) = 7.23; p = 1.06e-06, F(7,80) = 2.85; p = 0.010) and no effect was found for path length (F(7,80) = 0.76; p = 0.624). Post hoc tests revealed the perpendicular error of reach 3 was significantly greater than all but reach 7, and the angular error was significantly greater than only three other reaches. The curvature of reach 3 was not as distinct in this condition since the curvature of all reaches grew relative to Group 1 (see Comparison Across Groups below).

6.1.3. Group 3: No Visual Feedback of Hand and Target or Bar condition

This group's condition further reduced the extent of visual feedback provided to remove any potential visually-induced bias for straight reaches. Feedback of both the target and hand location was extinguished. A rectangle, whose length represented the subject's distance to the target center, was displayed along with the target number. Thus only information concerning the subject's distance to an unspecified target location was displayed. Subjects relied on proprioception and remembered target locations to make successful reaches. This condition was relatively difficult, but a success rate of 50% was achieved after 26 blocks (~208th trial) and the average score over the last half of the experiment was 67.48%. As in Group 2, the reduction in extent of visual feedback led to a qualitative increase in reach curvature. Reaches exhibited a wide range of trajectories, curving on either side of a straight line to the target (see Figure 7.3 A-C for typical subjects). And similar to Group 2, this variability in curvature was lost when averaging across subjects (Figure 7.3 D).

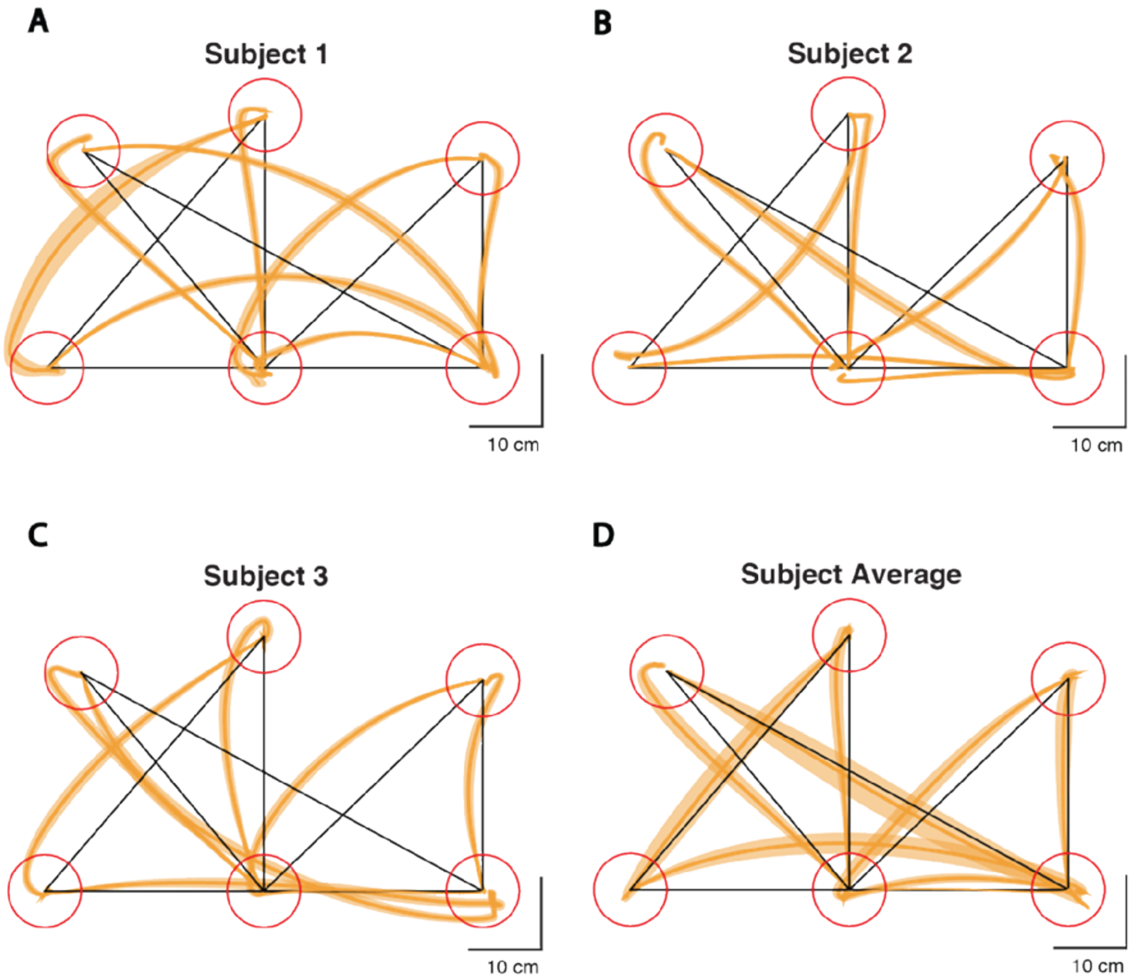

Figure 7.3 ***Average trajectories from Group 3.*** No Visual Feedback of Hand and Target. *Subjects in this group did not receive visual feedback of the hand and target locations. Target numbers and a displayed rectangle, whose length represented the distance between the hand and target center, allowed subjects to find and memorize target locations. (a) (b) and (c) Trajectories of individual subjects. It is qualitatively apparent that the trajectories in this condition are severely curved and variable. (d) An average of all 11 subjects' mean trajectories. Since subjects curve on either side of the straight line trajectory, the average resembles a relatively straight line.*

In contrast with the previous groups, reach 3 did not stand out: 75.77 ± 12.05, 14.68 ± 2.49, and 1.082 ± 0.018 for the across-subject average perpendicular error, angular error and normalized path length. For comparison, reach 1 had an average perpendicular error of 41.26 ± 7.61, angular error of 7.85 ± 0.80, and the path length of 1.130 ± 0.034. In this group, the mean normalized path length of reach 1 surpassed that of reach 3. Again, a significant effect was found for reach number for perpendicular error and angular error ($F(7,80) = 4.2$; $p = 0.0005$, $F(7,80) = 2.19$; $p = 0.0437$) and no effect was found for path length ($F(7,80) = 1.47$; $p = 0.1904$). Here, the post-hoc tests showed that the perpendicular error for reach 3 was significantly different from only reach 8, whereas angular error and path length contained no differences between reach 3 and other reaches. As with Group 2, this reduction in the number of significantly different reaches reflects a general increase in curvature for all reaches (as seen in Comparison Across Groups).

6.1.4. Comparison Across Groups

Next we quantified how reaches varied across different visual feedback conditions, comparing reach curvature with changes in extent of visual feedback. The across subject averages for each reach in each group revealed an obvious trend; as the extent of visual feedback was reduced the curvature metrics increased (see Figure 7.4 and Figure 7.5). To quantify this finding, two-way ANOVAs tested for the effects of extent of visual feedback and reach number. We found a significant effect for reach number in perpendicular error and angular error ($F(7,254) = 16.28$, $p = 1.14e-17$; $F(7,254) = 7.23$, $p = 6.70e-8$); however, no effect was found in path length ($F(7,254) = 1.03$, $p = 0.4112$). This finding is consistent with our analyses within groups, emphasizing that not all reaches are equally straight, especially as visual feedback is removed. We can speculate that this may be due to the biomechanics of the limb.

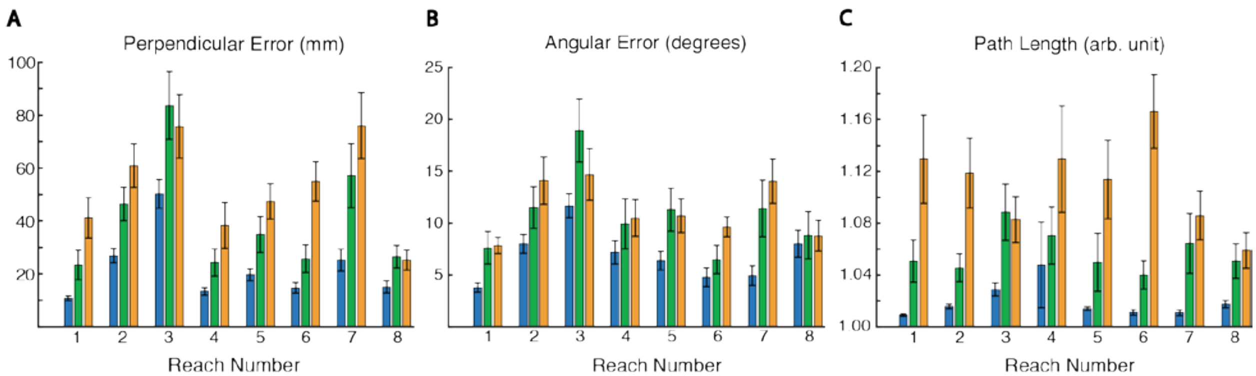

Figure 7.4 ***Average metrics across groups:*** *For each of the 8 reaches, the mean and standard error of the mean for perpendicular error, angular error and path length curvature metrics are shown (A,B, and C respectively). In each plot, Groups 1, 2, and 3 are represented by blue, green, and orange bars, respectively. For most metrics and reaches, there is a gradual increase in curvature as the extent of visual feedback is reduced. There are a few reaches where Group 2 exceeded Group 3, but both of these groups with reduced extent of feedback are larger than the group with full visual feedback.*

Table 7-1 ***Post-Hoc Tukey-Kramer Test Across Groups.*** *For each curvature metric, three post-hoc comparisons were conducted between the Groups (one for every combination). The significance levels for all test were 0.05. All comparisons were significantly different except the comparison of angular error between Group 2 and 3.*

Groups of Comparison	*p*-value Perpendicular Error	*p*-value Angular Error	*p*-value Path Length
1 & 2	7.500E-07	2.208E-05	6.369E-04
1 & 3	9.560E-10	1.056E-06	9.561E-10
2 & 3	1.655E-03	8.139E-01	7.289E-07

We also found a significant effect for extent of visual feedback for perpendicular error, angular error and path length ($F(2,254) = 37.49$, $p = 5.42e-15$; $F(2,254) = 15.46$, $p = 4.59e-7$; $F(2,254) = 39.61$, $p < 1e-17$, respectively). Indeed, this was the positive response to our studies main question: does removing visual feedback of the hand and target locations eliminate a visually-induced bias for straight reaches. Post-hoc tests revealed that all three groups were statistically different from each other when comparing perpendicular error and path length (Table 7.1). When comparing angular error, Groups 2 and 3 (with reduced visual feedback) were not significantly different from each other, yet both were significantly different from Group 1. Thus, the elimination of visual feedback had a clear effect on the curvature of reaches.

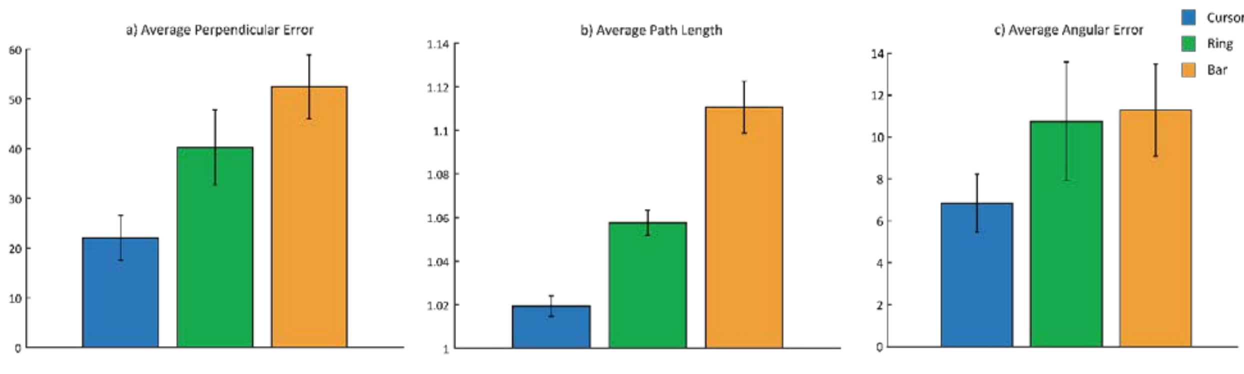

Figure 7.5 ***Average Metric for each visual feedback condition.*** *This figure shows the average metrics (a. Perpendicular error b.Path length c. Angular error) for each visual feedback condition (blue-cursor, green – ring, orange – bar) calculated from the average of average metric for each of eight reaches of all the subjects. A clear increase in reach metrics, and thus an increase in curvature can be seen with the reduction of extent of visual feedback.*

6.1.5. Curvature Was Not a Result of Task Difficulty

It could be that path curvature was a result of task difficulty. If this were so, then subjects with relatively high scores should have had relatively straight reaches. To test this, we examined the correlation between the successful score rate over each eight consecutive reaches (see Materials and Methods) and the average perpendicular error over the same period within each condition. No significant correlations were obtained (ρ=-0.180, p=0.094; ρ =-0.172, p=0.092; and ρ =-0.0287, p=0.791 for Groups 1-3 respectively). Thus we found that successful performance of the task did not influence reach curvature.

6.2. Experiment 2

In Experiment 1 we were able to observe how reduced extent of visual feedback was able to elicit curved trajectories opposed to the straight line reaches made in complete visual feedback condition. Though this result is a clear indication of a possible bias induced by the full visual feedback masking the reaching behavior, it is necessary to address an important question. Are the curved trajectories observed in the no visual feedback condition the result of the control strategy or simply random trajectories that people happened upon by chance? It is essential to test whether the trajectories we observe in the absence of visual feedback is not a consequence of subject's unclear picture of the exact target location but rather a choice that the subject preferred to do.

In order to answer this question, we performed another experiment where subjects reach for the same targets but the visual feedback switched halfway through the experiment. Using this setup, we can observe how a subject performs the same reach in the absence and presence of complete visual feedback. Additionally, if there exists a bias due to the complete visual feedback condition, then it is also critical to understand the number of trials it took this bias takes to wear off. As we hypothesize a strong influence, we also believed that the order in which the subject gets the complete visual feedback could affect the curvature even after it is removed. Thus, this experiment was divided into two groups and each received the complete visual feedback at different halves of the experiment.

The experimental setup, the visual feedback condition, data analysis and statistical analyses are same as the previous experiment (Refer Methods section). The 35 blocks (280 reaches) regime is chosen for this experiment because it took an average of 26 blocks for people in the Experiment 1 to achieve a success rate of 50% and also to have consistent trajectories as discussed before. Following are the results of the second experiment and the observations made.

6.2.1. Group 1: Bar-to-Cursor (B2C)

The subjects in this first group performed the reaches in the 'No visual feedback' condition for the first half of the experiment and in the 'Full visual feedback' condition for the second half. As in the previous experiment, the bar representing the subject's distance to the target center was provided along with the target number for the first 280 trials and they were shown the exact location of their hand and the target location for the remaining trials.

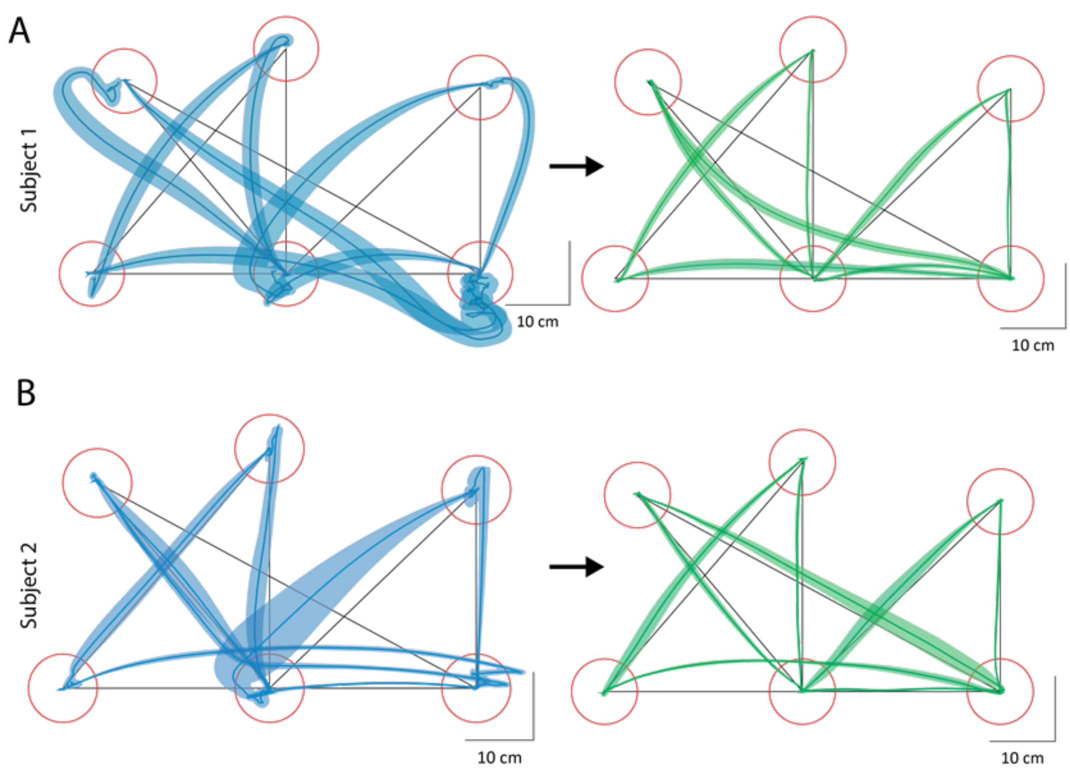

Figure 7.6 ***Experiment 2, Average trajectories from Bar-to-Cursor Group:*** *Subjects in this group received the bar visual feedback for the first half of the experiment and for the rest of the experiment, the visual feedback of the hand and target locations. (A) and (B) shows Trajectories of individual subjects. It is qualitatively apparent that the trajectories in this condition are severely curved and variable for the initial Bar visual feedback condition (blue) and became straight when the standard visual feedback was presented.*

The performance as well as the trajectories in the first half were very similar to those in the Bar Group in Experiment 1. The reaches were highly curved and variable across subjects (Figure 7.5). In contrast, when the complete visual feedback was provided in the latter half, the trajectories immediately became straight and consistent. This switch from highly curved trajectories to straight trajectories happened very quickly within a span of 8 blocks and remained straight for the rest of the experiment. This clearly indicates the possibility of the standard full visual feedback being a strong bias, as hypothesized.

The metrics for the trajectories for the final 6 blocks (~50 trials) for both the visual feedback condition were calculated. An apparent decrease can be seen from the metrics plotted (Figure 7.7). We found a significant difference between both in perpendicular error as well as the path length of the trajectories at the end of the two visual feedback conditions through ANOVA and a post hoc Tuckey-Kramer test. (P.E. $F(1,175) = 19.66$, $p < 1e-4$, P.L. $F(1,175) = 27.37$, $p < 1e-4$). A one sample t-test performed on both the metrics also showed that the decrease in perpendicular error was significantly larger than zero (P.E. $p=3.36e-5$, P.L. $p=1.35e-5$). This result strongly suggests that with the introduction of the standard visual feedback, the trajectory became more straight similarity in trajectories from either experiments.

6.2.2. Group 2: Cursor-to- Bar (C2B)

The subjects in this first group performed the reaches in the 'Full visual feedback' condition for the first half of the experiment and in the 'No visual feedback' condition in the second half. As expected, the trajectories in the first half of the experiment were very similar to experiment 1. It is characterized by higher success rate and highly straight trajectories, even from the beginning. The first 280 trials of practice in the Full visual feedback condition helped the subjects to locate the targets and also the sequence in which the targets appear too. This made the reaching in the second half easier, where the targets and hand location was replaced by the error bar.

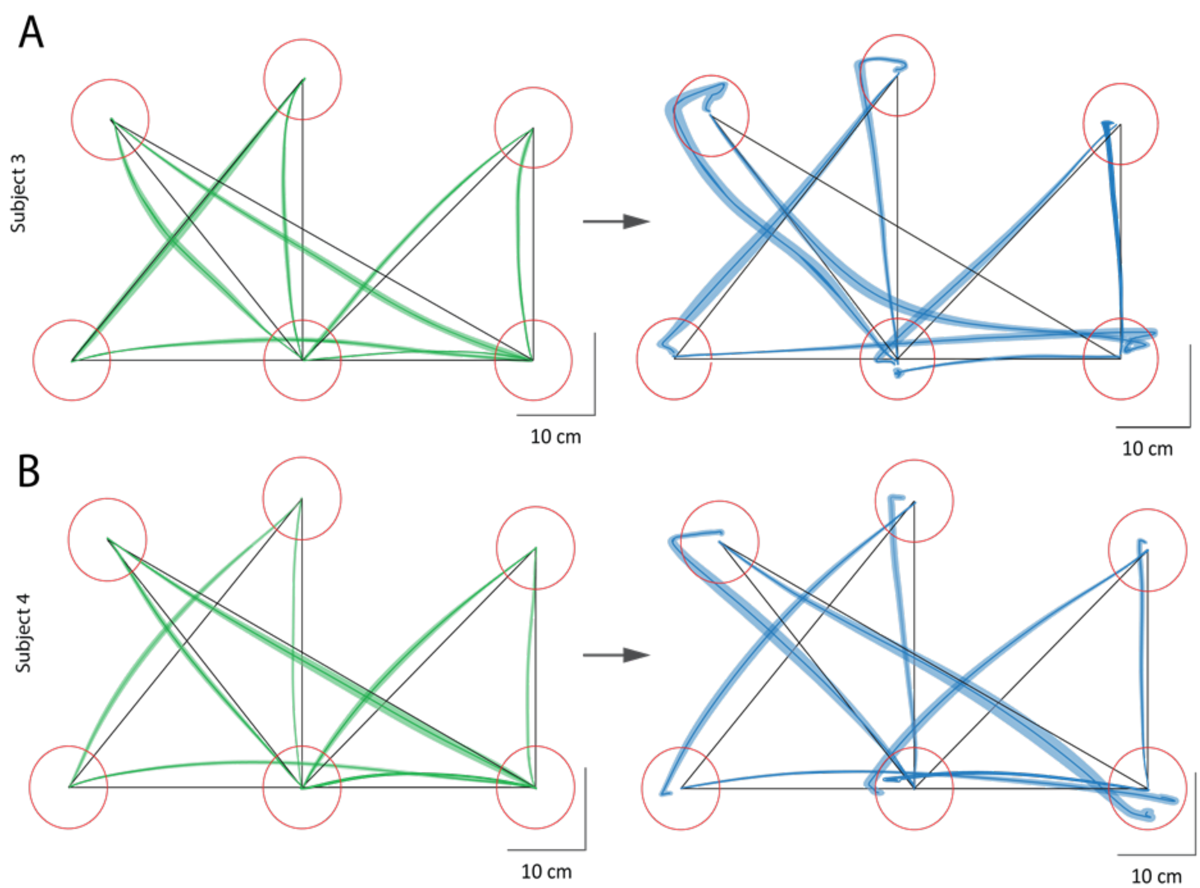

Figure 7.7 ***Experiment 2, Average trajectories from Cursor-to-Bar Group:*** *Subjects in this group received the standard visual feedback for the first half of the experiment and Bar visual feedback of the second half. (A) and (B) shows Trajectories of individual subjects. It is qualitatively apparent that the trajectories in this condition are severely curved and variable for the initial Bar visual feedback condition (blue) and became straight when the standard visual feedback was presented.*

As soon as the visual feedback was removed in the latter half, interestingly, the trajectories' curvature increased. By the end of the experiment the curvatures had increased visibly comparable to the ones that were made in the end of the first half. Though this increase was not distinguishable in the perpendicular error, this change was captured by a significant rise in path length (P.E. $F(1,175) = 3.13$, $p = 0.0788$, P.L. $F(1,175) = 19.16$, $p < 1e-5$). This increase can also be appreciated from the one sample t-test showing an increase significantly more than zero (P.E $p=0.0174$, P.L $p<1e-4$). This suggests that the subjects prefer to abandon the straight line trajectories to follow an arced path even after thorough practice with complete visual feedback.

6.2.3. Comparison across Groups

The two groups differ only in the order in which the subjects practiced in the standard visual feedback of a cursor. Comparing these two groups can help us understand how the previous exposure in one visual feedback can affect the other. In addition to the trends in curvature, the amount of change in both the experiments also revealed more insights. A two way ANOVA on comparing the reach metrics of the same visual feedback condition across groups showed that the curvatures of the two Cursor conditions were highly similar (P.E. $F(1,175) = 2.9$, $p^* = 0.0902$, P.L. $F(1,175) = 2.39$, $p^* =0.1237$), while the Bar condition had significant difference (P.E. $F(1,175) = 7.56$, $p = 6e-3$, P.L. $F(1,175) = 12.92$, $p =4e-4$).

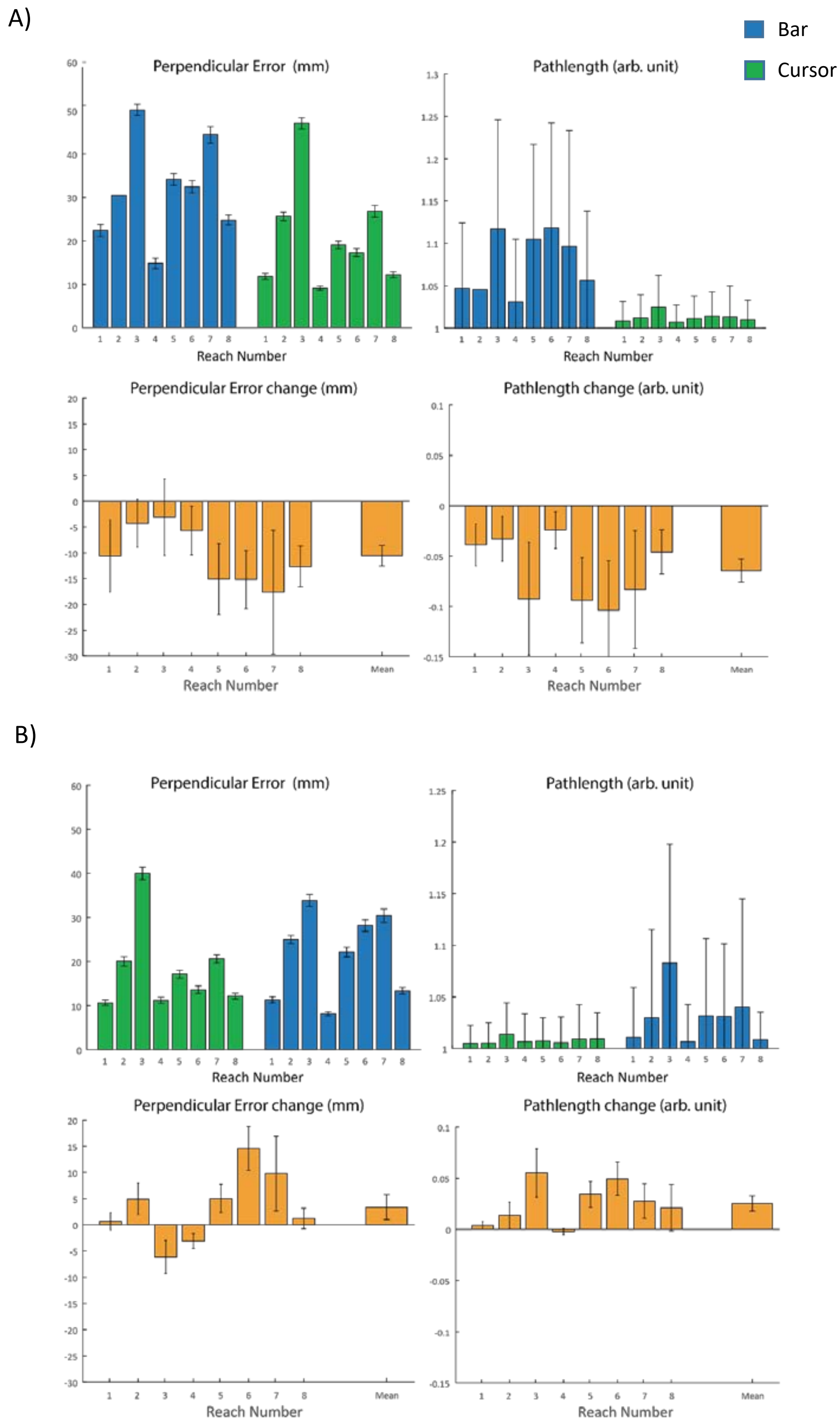

Figure 7.8 ***Experiment 2, Comparison of metrics between groups:*** *Here we see (A) Bar-to-Cursor (B) Cursor-to-Bar Group showing the average metric for the last 6 blocks in each condition for 8 reaches and change in metrics from the first block to the second (green-Cursor, blue-Bar, orange-change in metrics). The thick bar in the bottom panels*

also show the mean change in metrics in each group for perpendicular error and path length. A clear decrease in curvature can be seen in the Bar-to-Cursor group, whereas, significant yet only a slight increase in the curvature in the Cursor-to-Bar group. This hints at the bias that is induced by the prolonged exposure to the standard visual feedback in the first half of the Cursor-to-Bar group.

This dissimilarity is consistent with our hypothesis that the standard visual feedback has a strong influence on the reaching behavior. Thus, this is a clear indication that prior exposure to the standard visual feedback has an effect on the reaching behavior even after the visual feedback is removed.

In order to understand the nature of this influence the reach curvature was analyzed across time. The error metrics averaged over every block across the entire experiment not only showed the change in reach curvature after the removal of visual feedback, but also revealed that the reach metrics did not plateau at the end of the second half of C2B experiment. This suggests that the effect of having straight reaches due to the prolonged exposure to the standard visual feedback could diminish over time.

7. Discussion

We investigated whether or not visual feedback may bias movements to be straight. As the extent of visual feedback was reduced, there was a general increase in the curvature of all reaches. This increase in curvature was both qualitatively and quantitatively evident across conditions. Importantly, reach curvature progressively increased as visual cues were systematically eliminated, and these changes could not be attributed to increases in task difficulty. We suggest that the straight reaches often observed in experimental settings may be the result of a bias to move the displayed feedback along a straight path.

Observing the changes in curvature from one visual feedback condition to another also evidently portrayed the strong bias the standard visual feedback has and how it could influence reaching behavior even long after it is removed. More importantly, the fact that the subjects didn't have a straight trajectory in the absence of visual feedback even after enough practice in the complete visual feedback condition, alone is a strong evidence suggesting that the subjects prefer to move on a curved hand path. Experiment 2 is a clear indication that the curved trajectories are not a ramification of imprecise perceiving of targets or mere confusion due to lack of visual feedback, but preference to move curved and possibly even optimal.

Knowing the time it takes for the cursor to bias the movements (approximately 8 blocks), a potential study to further extend this study, he same experimental paradigm can be extended to have a Bar-Cursor-Bar experiment to have a short exposure to Cursor visual feedback. Also, in our experiments, the Bar condition sought to completely minimize visual feedback and cues to eliminate any potential visually-induced bias. While all visual cues of the hand and target were extinguished, some information was conveyed visually (the target number, target error, and score). It is possible that even these relatively benign cues may influence how subjects interpret the task. Future studies could explore reaches made in the complete absence of visual information. For example, target number and error could be presented with audio cues. It would be interesting to see if such a "blinded" experiment revealed similar, or perhaps increased, curvature.

With this initial study we can only speculate as to why the conventional visual feedback biases movements to be straight. One possibility is that by replacing the normal view of the limb, with artificial feedback of the hand's location, the goals for reaching are converted to an abstract task. In particular, reducing the distance between two points in space may take priority over an efficient reach. Indeed, a recent study found that a subject's familiarity with similar visual cues (i.e. a computer mouse) may significantly alter that subject's motor behavior (Wei et al. 2014). In a somewhat related study, subjects made curved, energy-optimal reaches, when the visual and haptic feedback of an object they interacted with was realistically rendered, but made straight, inefficient reaches, when only a cursor was displayed (Farshchiansadegh et al. 2016). Together these studies make it clear that the visual feedback can affect a subject's interpretation of the task and the resulting motor behaviors.

We considered the possibility that the relatively large curvature and variations across individuals might be due to a use-dependent effect: subjects may have merely adopted the first successful reaches as their overall strategy. To examine this possibility, we compared the average reach metrics during the first 5 successful reaches with those of the final 5 reaches. No correlations could be found, however, suggesting reach paths were not influenced by the happenstance of initial success, but rather were the result of an intentional plan.

Many experimental and theoretical considerations of reaches suggest movements should be efficient (Alexander 1997; Hatze and Buys 1977; Huang et al. 2012; Kang et al. 2005; Selinger et al. 2015; Uno et al. 1989). For any limb with rotating joints, efficient reaches move the hand along curved trajectories. Therefore, the curved reaches we observe in our experiment may not be surprising. Furthermore, an efficient reach is uniquely determined by limb properties (e.g. size and mass). As such, variations in these properties across individuals should result in different efficient trajectories. Thus, increases in curvature and variability may both be the result of efficient reaches.

If there is an inherent preference for curved reaches, then perhaps a neural correlate of this phenomenon should exist. Evidence suggests that the dorsal premotor cortex (PMd) may encode trajectory specific information such as target location, initial reach direction, and curvature (Hocherman and Wise 1991). Curiously, a higher proportion of neurons in the PMd exhibited a selectivity for curved rather than straight reaches, possibly revealing a preference for curved reaches. In parallel, other researchers have found that the PMd is active during a delay period before making curved reaches around obstacles to a target (Pearce and Moran 2012). It has also been found that lesions of the PMd in primates cause an inability to curve the hand's path, but preserve the ability to reach straight to a target (Moll and Kuypers 1977). Collectively, these studies point to a neural preference for curved trajectories.

That point-to-point reaches are controlled to be straight is nearly an axiom in the field of motor control. At the same time, straight reaches stand in contrast with a great deal of work that suggest movements should be efficient and curved. If there is an unintentional, experimentally-introduced bias for reaches to be straight, it may help to explain this apparent contradiction, and it will have important ramifications for the interpretation of past motor behavior studies and the design of future ones.

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