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Sensitivity to Hand Path Curvature During Reaching

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Abstract: People optimize reaching to make straight and smooth movements. We performed experiments characterizing human sensitivity to hand path deviations from a straight reach. Vision of the arm was blocked. Subjects either moved the hand along paths of constrained curvature, or a robot moved the relaxed limb along similar trajectories (active and passive conditions, respectively). Subjects responded after each trial whether or not they thought the movement curved convex right. In a series of three experiments, we tested the effects of modifying visual feedback of hand position to suppress curvature, isotonic muscle activation, and a distracter task on subjects ability to detect curvature during reaching. We found that both active reaching and artificial minimization of visual hand path deviations significantly decreased proprioceptive curvature sensitivity. Specifically, isotonic contraction of muscles antagonistic to the movement decreased sensitivity to curvature while agonistic contraction had no effect. The distracter task did not significantly affect proprioceptive sensitivity, though it did interfere with the detrimental effect of minimizing visual error feedback. These findings demonstrate that: 1) "antagonist" muscle activation decreases efficacy of proprioceptive feedback during hand path curvature estimation, and 2) vision's dominance over proprioception can be manipulated by altering the attentional demands of the task.

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Introduction

Feedforward control of limb movement relies on a properly tuned internal model (IM) of environmental dynamics to guide the selection of motor commands for a given task.[1,2] People use feedback of hand path errors from previous movements to update this IM, allowing us to make straight and smooth movements[6] in a variety of mechanical environments. While both visual and proprioceptive information clearly can be used to update the internal model[3,4] it is unknown how these feedback sources combine to detect hand path deviations from a straight line. We performed a set of human psychophysical studies designed to explore the interaction of visual and proprioceptive feedback in their contribution to hand-path curvature detection during reaching. We also investigated the influence of muscle activation and the diversion of attention on curvature detection sensitivity.

Methodology

Experimental Protocol

Twenty human subjects with no known neurological disorders gave informed consent to participate in this study in accord with the policies and guidelines established by Marquette University's Office of Research Compliance. Subjects wore "blinders", glasses that prevented direct view of their hand and arm at all times. Subjects made 0.8 second, 15-cm reaching movements with their dominant arm in the horizontal plane while grasping the handle of a two-joint, robotic manipulator (Fig. 1). The robot forced the handle through trajectories of varying curvature under stiff PID control. Subjects were instructed to indicate via a 2-button forced-choice response box whether or not they felt their most recent hand movement was curved to the right (convex right). Position, force, and acceleration data were collected at 1000 samples per second.

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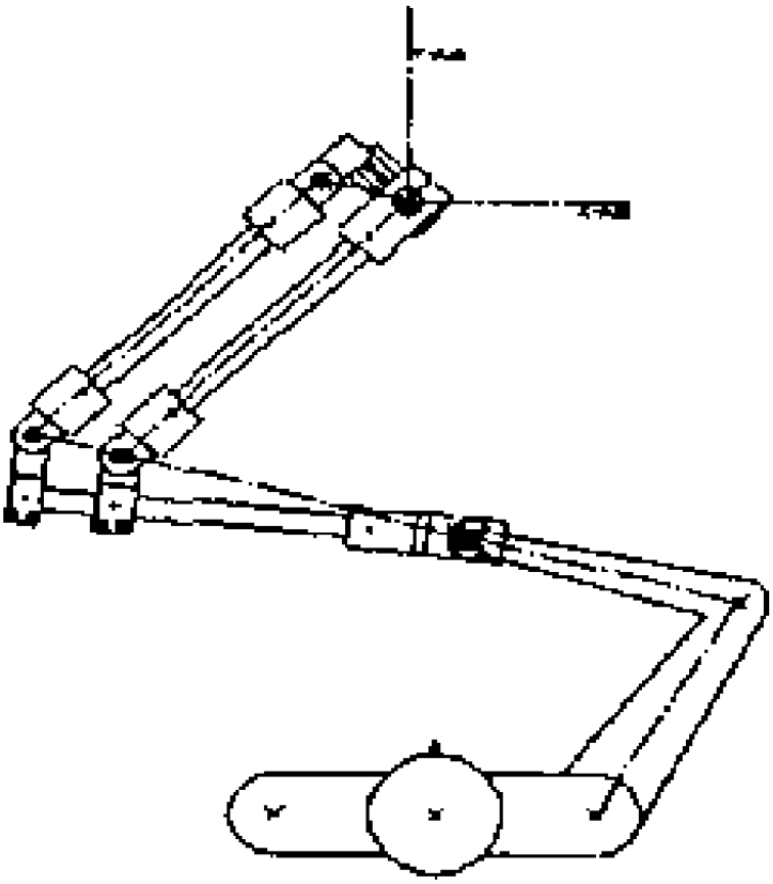

Fig. 1: Orientation of subject with respect to the two-joint robot manipulandum. The subject wore "blinders", glasses that block direct view of the arm and hand at all times. The subject used a forced-choice response box to indicate whether they were confident the movement was convex right or not.

Experiment 1

In the first experiment, 20 subjects were required to assess the right convexity in their hand paths during 16 blocks of reaching movements: four blocks each of four different trial types. The: four trial types were the possible combinations of two experimental variables: 1) MOVE-MENT TYPE - subjects were instructed to either relax passively while the robot moved their hand through paths of varying curvature; or actively attempt a straight movement (but be forced along a path of pre-defined curvature) and 2) VISION TYPE - subjects were provided with either no visual feedback of hand position during movement; or visual feedback constrained to the Y-axis only (i.e. all movements looked straight),

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Experiment 2

The second experiment examined the effects of isotonic force generation on curvature sensitivity in order to explore the effects of muscle activation on this sensitivity. 6 subjects were required to assess the right convexity of movements in nine blocks of trials: 3 each of Passive, Assist, and Resist trial types. Subjects had no visual feedback of hand position while the robot moved them through trajectories of controlled curvature. A gauge provided information about the forces being produced at the handle. The gauge consisted of a ball providing feedback of forces generated at the handle, and target regions indicating the magnitude and direction of desired hand forces. The y-position of a ball corresponded to the forces along the y-axis, while the size of the ball corresponded to forces along the z-axis (the ball grew bigger when forces were generated toward the ceiling and smaller for forces towards the floor). Subjects were instructed to hold the ball in the center of the gauge while keeping the ball at a certain size. The center of the gauge corresponded to zero force along the y-axis for Passive trials, $\sim$10N for Assist trials and $\sim -10N$ for Resist trials.

A

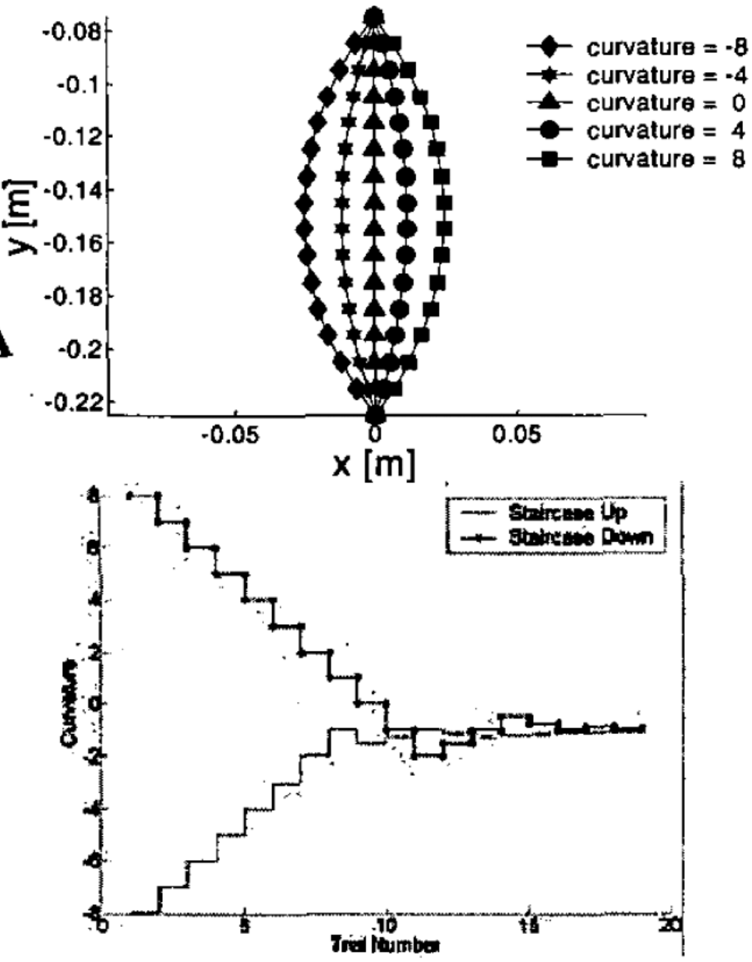

Fig. 2: A) Hand path trajectories showing the range of curvatures tested. B) Example of the dual staircase technique for one block of trials.

Experiment 3

The third experiment explored the role of attention during our curvature detection task. 6 subjects assessed the right convexity of movements in 12 blocks of trials: 3 each of 4 different trial types. The four trial types were the possible combinations of two binary experimental variables; 1) DISTRACTER TYPE - subjects were instructed to either relax while the robot moved their hand through paths of varying curvature; or perform a sequence of finger movements with the contralateral hand while the robot moved their hand through paths of varying curvature, and 2) VISION TYPE - subjects were provided with either *no visual feedback* of hand position during movement; or visual feedback *constrained* to the Y-axis only (i.e. all movements looked straight). When subjects were required to perform the distracter task, they were instructed to play a sequence of keys (fingers 5–3-4–2) on an electronic piano keyboard with the contralateral hand.

Curvature Generation

The x-component of the trajectory (for all trial types) followed a constant-curvature are along the perimeter of a circle whose perimeter passed through the "beginning" and "end" targets and whose radius varied from trial to trial. Curvatures for each staircase began at $-8 \text{and} 8 m^{-1}$ respectively (Fig. 2A) and were adjusted using the dual-staircase technique for threshold detection (Fig. 2B;[5]). On a given trial in a block subjects were randomly presented with either a "*staircase up" trial* or a "*staircase down*" trial. This technique provided a range of hand path curvatures between $-8 \text{and} 8 m^{-1}$ with dense sampling near the threshold.

Data Analysis

A logit response function (Fig. 3; Equation 1) was fit to the response data by optimizing two parameters (a and ß). The curvature threshold $\kappa_{threshold}$ for each block was taken as the 50% likelihood value of this function (Equation 2)

$$P(\text{Response} = yes) = e^{\alpha+\beta^{*}\kappa}/(1+e^{\alpha+\beta^{*}\kappa})(1)$$

$$\kappa_{threshold} = \kappa|_{P(+)=0.5}(2)$$

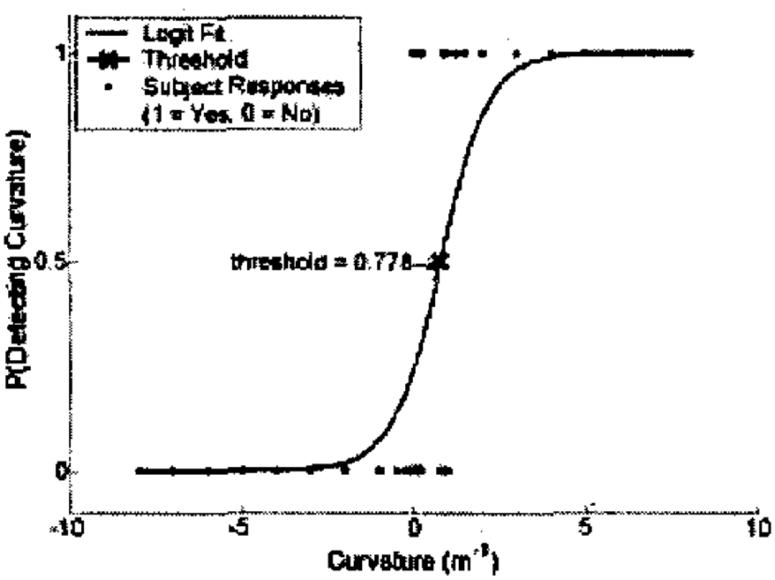

Fig. 3: The curvature detection threshold was the point where the logit response function crossed 0.5.

General linear model ANCOVAs were performed to evaluate the effect of experimental treatment on hand path curvature detection thresholds. Since the range of

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curvature sensitivities varied widely between subjects, a measure of subject sensitivity was needed as a covariate in the ANCO-V As. Passive Movement No Vision blocks were common to all three experiments and provide a common basis for comparison across subjects and experimental conditions. The mean of the Passive Movement No Vision thresholds for each subject was used for the "sensitivity" covariate measurement An initial ANCOVA was performed with experimental variables (e.g. Movement and Vision) as independent variables, each subject's mean threshold for each block type as the dependent variable, and subject sensitivity as a covariate. A second ANCOVA explored the influence of muscle activation on curvature sensitivity. In experiment 3, instead of averaging each subject's threshold by block type, block number was included as an independent variable for those analyses examining distracter task effects since the finger sequence task often became "easier" with practice.

Results

Experiment 1

An ANCOVA revealed that proprioceptive sensitivity to curvature was significantly decreased (detection thresholds increased) by both active movement ($F = 5.18$; $p < 0.05$; $N = 19$) and constrained visual feedback ($F = 16.39$; $p < 0.05$; N = i9). Fig. 4 shows average subject performance for each trial type. Statistical significance is not immediately apparent from these figures because of inter-subject differences, which were accounted for in the ANCOVA.

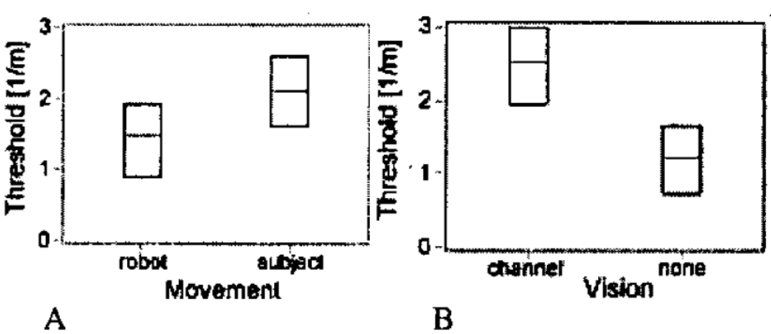

Fig. 4: Main effects plot summarizes the effects of A) Movement and B) Vision. The middle line represents the median threshold, while the boxes show the 95% confidence intervals. While the confidence intervals may overlap, the ANCOVA (which takes into account inter-subject differences) revealed that both active movement and constrained visual feedback significantly increased subject thresholds for detecting curvature.

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Experiment 2

A second ANCOVA found that the "Resist" trial curvature detection thresholds were significantly higher than "Passive" trial thresholds (Fig. 5; $F = 20.17$; $p < 0.05$; $N = 6$). However, no significant difference between the Passive and Assist curvature detection thresholds was observed ($F = 0.51$; $p > 0.05$; $N = 6$).

Experiment 3

A final ANCOVA revealed that there were significant interaction effects between making a sequence of contralateral finger movements and receiving constrained visual feedback of hand position ($F = 9.04$; $p < 0.005$; $N = 72$). Contralateral finger movements eliminated the desensitizing effect of visual feedback of hand position projected onto a straight line, though it did not affect curvature detection by itself (Fig. 6).

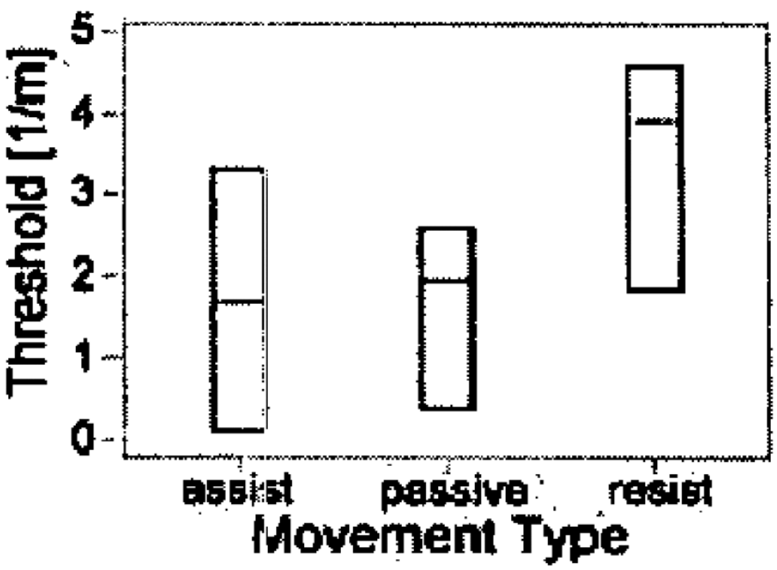

Fig. 5: Summary of experiment 2 results. The middle line represents the median threshold, while the boxes show the 95% confidence intervals. Although the 95% confidence intervals overlap, an ANCOVA, which accounts for inter-subject sensitivity differences revealed that resist thresholds were significantly higher than either passive or assist trial thresholds.

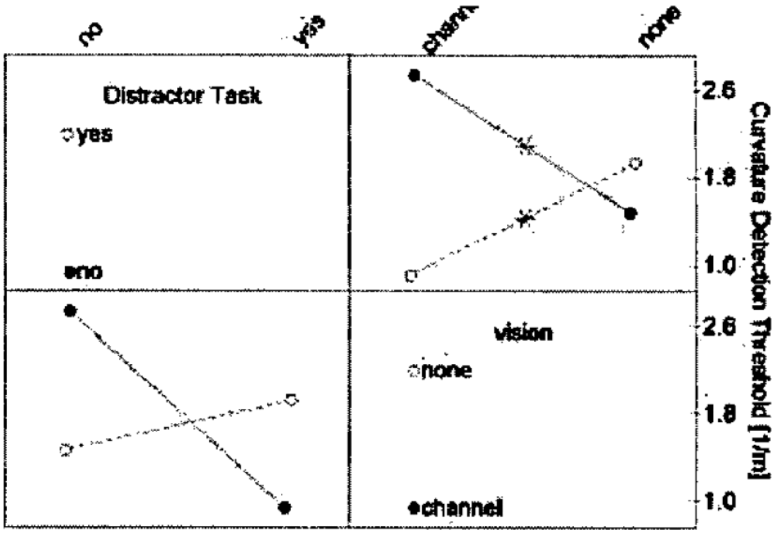

Fig. 6: The interaction effects between playing the keyboard and visual feedback of hand position. Significant effects are labeled with an asterisk (∗). The constrained visual feedback only significantly increased curvature detection thresholds when the subjects were not making a sequence of contralateral finger movements.

Discussion and Conclusion

Humans are extremely good at making reaching movements of the arm and they use feedback of prior kinematic performances (specifically, hand path errors) to guide corrective changes in motor commands on subsequent movements[6] This ability, called motor adaptation, allows us to generate accurate movements in a variety of different mechanical environments and is crucial for making movements in an unpredictable environments, In the current study, we use curvature detection as a proxy for kinematic error detection, and investigate factors that influence how we detect and perceive such errors during movement. The results offer insight into sensorimotor integration during reaching, and therefore, may offer insight into the neuromotor control mechanisms mediating an important form of motor learning: motor adaptation.

Hand path curvature sensitivity decreases during active movement

Stereotypical (triphasic) patterns of electromyographic activity often arise during single- and multi-joint reaching of the arm.[7] This pattern starts with an initial agonist burst which acts to accelerate the limb. Next, an antagonist burst decelerates the limb. Finally, a second agonist burst provides co-contraction and increased stability about the final posture, It is frequently observed that the antagonist burst is progressively delayed as subjects learn such movements (cf.[8]). Our findings suggest why that may be so. Specifically, we observed that isotonic pulling (activation of muscles "antagonistic" to the limb's motion) decreased curvature detection sensitivity, while isotonic pushing (agonist activation) had no effect. This finding is anticipated by studies showing that muscle spindle output is more consistently related to muscle length during stretch[9] and by the finding that the variability of nervous signals increases with signal intensity.[10] Our results clearly reveal that subjects are better able to utilize proprioceptive feedback if the muscles being stretched during movement are inactive (Fig. 5). It is possible that the nervous system optimizes muscular control such that the joint position feedback information available from proprioceptors is maximized. One way this could be done is to delay firing of muscles antagonist to the motion (i.e. those muscles being stretched) as long as possible.

The role of attention in visuoproprioceptive integration

Previous experimental studies have shown that the degree to which a subject attends to a motor task does not necessarily impact on their proprioceptive sensitivity during the task.[11] For example, Collins et al. (1998) demonstrated that neither counting backwards from 100 by 3's nor contralateral reaching decreased proprioceptive sensitivity to artificially induced muscle twitch. Similarly, experiment 3 of the current study finds that executing a sequence of contralateral finger movements did not increase subjects' thresholds for detecting curvature during reaching. However, the current study also demonstrated that a distracter task shifts the relative weighting of sensory integration from the visual input toward the proprioceptive input. Consequently, it is likely that the mechanisms mediating sensorimotor integration combine visual and proprioceptive sensory signals in a non-linear and/or time-varying way in order to estimate limb state during movement These weights are not just dependent on where the limb is in extrapersonal space.[12] Rather, they must also depend on attentional focus and the level of muscle activation.

Neurobiological basis of visuoproprioceptive integration

Proprioceptive feedback of limb state ascends along two pathways in the spinal cord. The dorsal column-medial lem-niscal tract projects to the somatic sensory cortex of the cerebrum and conveys information pertaining to discriminative touch, vibration and joint position. The spinocerebellar tract is thought to convey unconscious proprioceptive information to the cerebellum, and also conveys information of body segments relative to one another.[13] Since there are two potential pathways for proprioceptive information to influence central activity, it remains somewhat unclear whether the proprioceptive information used for declarative estimation of hand path curvature travels along the same

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pathways used for motor adaptation of reaching. Further-more, unconscious detection of hand path errors for motor adaptation may not involve the same central mechanisms as conscious perception of limb state as explored here. However, by manipulating the attentional demands of a reaching task, and by manipulating visual feedback of hand path errors, it should be possible to elucidate the role of visual and proprioceptive feedback in the adaptive control of reaching.

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