Flexible strategies for sensory integration during motor planning

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Supplementary Note

Effects of target direction and task condition

In order to examine the effects of task parameters on reach kinematics and timing, we used a two-way ANOVA to test for effects of target direction or task condition on four kinematic and timing variables in reaches with unshifted feedback (Supplementary Table 1). The two timing variables were the reaction time (RT) and movement time (MT). RT was defined as the interval from the "go" signal until the tangential velocity exceeded 3 mm/sec. MT was defined as the interval from the end of the RT until the velocity first fell to 3 mm/sec after reaching peak velocity. This latter landmark was also used as the reach endpoint when computing the total reach distance; additional "corrective" movements were ignored. The initial direction of the reach was the same as the baseline bias ω_d in the main text.

Reaches with unshifted feedback tended to have small biases in initial direction and reach distance, and in Experiment 1 these biases depended on target direction (Supplementary Table 1, top). The most salient effect of target type was a tendency for subjects to under-reach (i.e. make hypometric movements) to proprioceptive targets: mean reach distance was 127 mm for proprioceptive targets and 138 mm for visual targets, averaged across subjects and target directions. This trend resulted in a significant main effect of target type on reach distance in 5 of 7 subjects, and a significant main effect of target type on movement time in 4 of 7 subjects.

In order to demonstrate that the effect of target type on the fit value of α_{MV} in Experiment 1 was not an artifact of this tendency to make hypometric reaches to proprioceptive targets, we fit the data with an alternative version of the model. In the new model, the target position (x^* in Equation 3) was set to the mean reach endpoint in the baseline condition. In other words, we assumed that reaches to proprioceptive targets were hypometric because of a bias in estimated target position. In this alternate analysis, we observed the same reduction in α_{MV} when reaching to proprioceptive targets as in the original analysis. The change in α_{MV} was significant in all subjects, and had a mean value of .60.

We also note that in Experiment 1 there was greater variability in reach direction for reaches to proprioceptive targets (data not shown, although see Figure 4 in the main text for an example). This trend was consistent across subjects and may have resulted from a greater uncertainty in the location of the proprioceptive target than the position of the visual target[2].

Reaches with unshifted feedback also had small biases in Experiment 2, and these biases also depended target direction (Supplementary Table 1, bottom). Although there was a main effect of feedback type on reach distance in 6 of 10 subjects, there was no consistent trend to the sign of this effect (average reach distance was greater for arm-feedback reaches

Experiment 1 (N=7)	**Initial direction (ω_d)**	**Reach distance**	**RT duration**	**MT duration**
Main effect of direction	5	7	0	3
Main effect of target type	0	5	0	4
Interaction	3	2	0	1

Experiment 2 (N=10)	**Initial direction (ω_d)**	**Reach distance**	**RT duration**	**MT duration**
Main effect of direction	9	5	0	4
Main effect of feedback type	2	6	2	0
Interaction	0	1	0	1

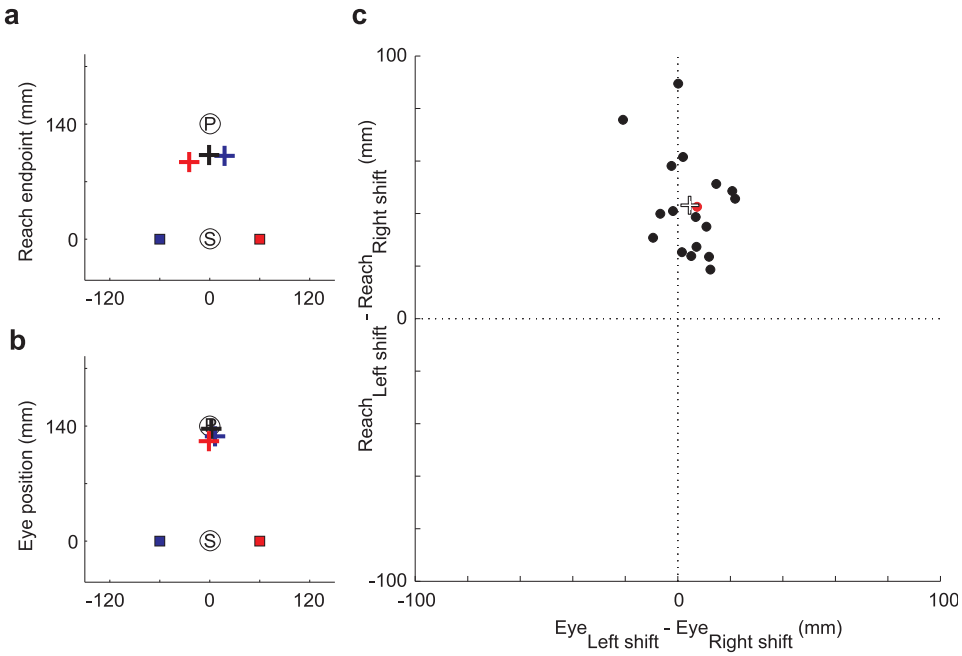
Supplementary Table 1: Analysis of movement kinematics and timing in reaches with unshifted feedback. Number of subjects for each experiment with significant ($p<.05$) effects of target direction, task condition, or interactions between direction and type on four experimental variables. For Experiment 1, task condition was target type (visual or proprioceptive). For Experiment 2, task condition was feedback type (fingertip or arm). A Bonferroni correction[1] was used to compensate for the effects of repeated testing.

in 5 of 10 subjects and greater for fingertip-feedback trials in the other 5).

Control for intermanual transfer of feedback shift effects

In Experiment 1, we observed that MV errors induced by visual shifts were smaller when subjects reached to proprioceptive (as opposed to visual) targets. In the model-based analysis, this difference was assumed to be the result of a reduced reliance on visual feedback in the proprioceptive-target condition. However, there is an alternative explanation for this observation: transfer of the feedback-shift effects to the left hand could have biased the location of the proprioceptive target. In the extreme case, if $\hat{x}_{\mathrm{MV}}$ and the felt position of the proprioceptive target were shifted by the same amount and in the same direction, then the fit value of α_{MV} would be equal to zero in proprioceptive-target reaches, since the desired movement direction would still be correct. Such an effect could potentially be responsible for the observed shift in α_{MV}.

To address this possibility, we performed an additional experiment in which six subjects used gaze direction to indicate the location of the proprioceptive target. As in Experiment 1, subjects positioned the right index fingertip at the start point using visual feedback. An arrow field then guided the left index fingertip to a target location under the tabletop. The visual feedback (a white spot of radius 5 mm) was either veridical or displaced to the left or the right by 6 cm. Unlike in Experiment 1, however, only proprioceptive targets were used. Also, the targets were located only at the 60, 90, and 120° positions, due to the constraints of the eye monitoring system. 750 ms after the right index fingertip arrived at the start position, a small green dot appeared on top of the feedback spot. When the green dot appeared, subjects moved their eyes to fixate the position on the tabletop corresponding to the felt location of the left index fingertip and then tapped the right index fingertip. An infrared eye-tracking system (ISCAN, Burlington, MA) was used to monitor gaze direction.



Supplementary Figure 1: Results of intermanual transfer experiment. Data from reaches to a single target from a representative subject are shown in (**a,b**). (**a**) Average reach endpoints for reaches made with leftward (blue crosses), zero (black crosses), and rightward (red crosses) shifts of the visual feedback. P, proprioceptive target location, S, reach start point. The blue and red squares show the location of the left- and right-shifted visual feedback, respectively. (**b**) Average gaze position used to indicate the proprioceptive target location (color conventions as in **a**). (**c**) Scatterplot of the group data. Abscissa: average left-right separation of gaze positions recorded after leftward and rightward shifts of visual feedback. Ordinate: average right-left separation of reach endpoints after leftward and rightward visual shifts. Each datapoint represents a single subject and target, the red datapoint represents the data shown in (**a,b**), and the white cross indicates the mean value across subjects and targets.

Subjects were allowed as much time as they needed to fixate the left index fingertip, and were instructed to tap their right index finger only when they were sure that they were fixating the proprioceptive target. After the subjects had tapped their right fingertip, the green dot disappeared and a small blue dot appeared in its place. After 1900-2100 msec the blue dot disappeared, signaling the subject to reach to the proprioceptive target.

Supplementary Figure 1 shows that although shifts of the visual feedback do affect reach endpoints (as in Experiments 1 and 2), they do not affect the felt location of the proprioceptive target. Leftward shifts in visual feedback lead to rightward biases in reach endpoints (blue cross in Supplementary Fig. 1a). If a leftward shift in the feedback from the right hand affected the felt location of the left hand, one would expect to see a leftward shift in the gaze position used to indicate the location of the proprioceptive target (blue cross in Supplementary Fig. 1b). However, no such pattern is seen (Supplementary Fig. 1c). This experiment demonstrates that errors in the arm position estimates induced by the visual shifts in these experiments do not transfer from the right to the left arm.

Control for eye gaze direction effects

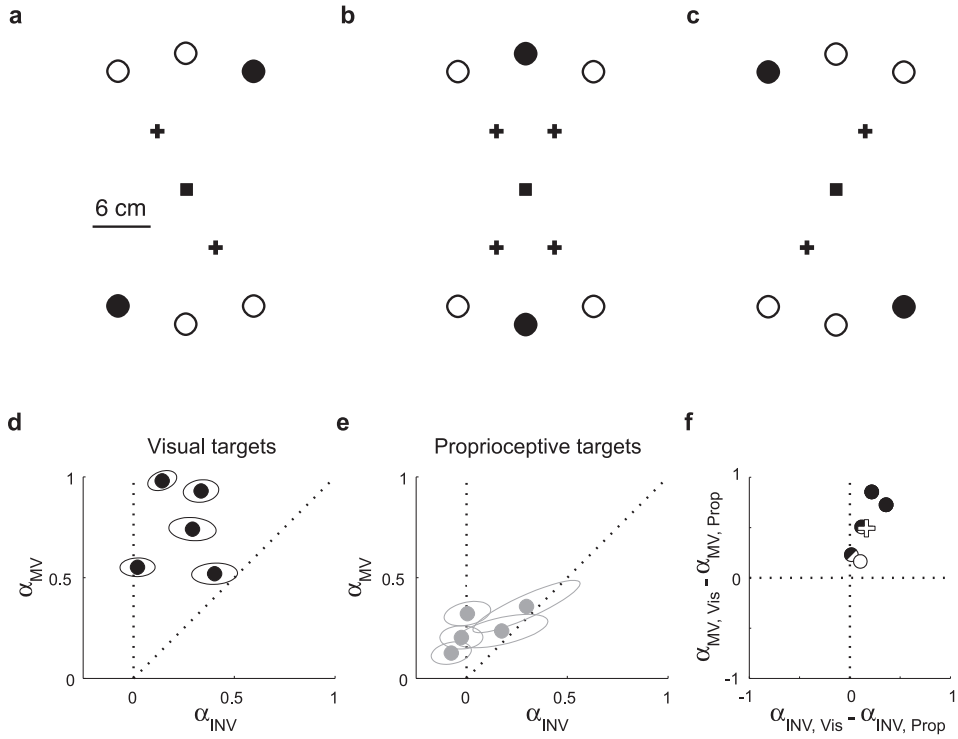
A key premise of Experiment 1 is that target information in the proprioceptive-target condition comes from the felt position of the left arm. However, in our initial experiment, gaze was neither monitored not constrained. This presents a potential confound, since gaze signals could provide additional target information or bias the planning of reaching movements. For example, in the proprioceptive-target condition, subjects might have been reaching not to the felt position of the left fingertip, but rather to a visual fixation point or to a target specified by extra-retinal signals related to gaze direction. Another potential problem is that subjects subject might have directed their gaze to different parts of the workspace in the visual-target and proprioceptive-target conditions (e.g. fixating visual targets when reaching to them, but fixating the feedback from the reaching hand when reaching to proprioceptive targets). Since gaze direction has been shown to affect the accuracy of reaching movements[3], it is therefore possible that the different patterns of motor error in the two target conditions result from different gaze behaviors.

In order to control for these effects, we ran 5 additional subjects on a modified version of Experiment 1. In each trial, a fixation cross (Supplementary Fig. 2, a-c) appeared as soon as the subject positioned the left index fingertip at the proprioceptive target. After a delay of 1400-1600 msec, the fixation cross turned either red or blue, instructing the subject to reach to the visual or proprioceptive target, respectively. Subjects were required to maintain fixation for the duration of the reaching movement.

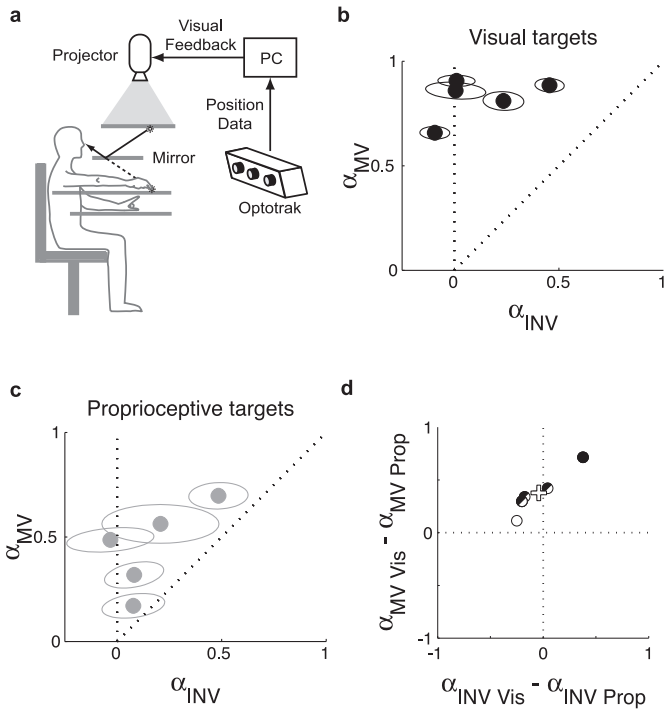
Subjects were able to maintain appropriate fixation on most trials. Trials on which the subject broke fixation before tangential fingertip velocity exceeded 40% of its peak value (see Methods) were marked as errors and excluded from analysis. Very few trials had to be excluded (average error rate 3.33%, range $2.08 - 4.51\%$).

The results of this modified experiment were similar to those of the original version. Supplementary Figure 2d shows that as before, subjects relied mostly on vision during movement vector planning when reaching to visual targets, but in every case increased their reliance on proprioception when reaching to proprioceptive targets (Supplementary Fig. 2e). The magnitude of these changes (mean change in $\alpha_{\mathrm{MV}} = .50$, mean change in $\alpha_{\mathrm{INV}} = .16$, Supplementary Figure 2f) was in very close agreement with those observed in the original version of Experiment 1 (mean change in $\alpha_{\mathrm{MV}} = .46$, mean change in $\alpha_{\mathrm{INV}} = .17$). These results show that the changes in the weighting of vision and proprioception observed in Experiment 1 are not due to a difference in gaze strategy between the two conditions, and demonstrate that our results do not change substantially when subjects are not allowed to fixate the proprioceptive target during reach planning.

Although the task-dependent *changes* in α_{MV} were nearly identical in the original and gaze-constrained versions of Experiment 1, constraining the direction of gaze appears to have affected the absolute value of α_{MV}. In reaches to both visual and proprioceptive targets, the value of α_{MV} was lower when eye position was constrained (compare Fig. 6a,b with Supplementary Fig. 2d,e). This trend, which had a magnitude of .14 in the visual-target condition and .17 in the proprioceptive-target condition, fell short of significance in both cases (t-test, p=.12 and p=.14, respectively). This effect is likely due to the fact that the fixation constraint put the visual feedback in the visual periphery at the time of reach initiation. Since peripheral visual signals are noisier than foveal ones[4;5], the finding that subjects weight proprioceptive feedback more heavily in the control study is consistent with a minimum-variance strategy (see Discussion).



Supplementary Figure 2: Methods and model fits, gaze direction control experiment. In each trial, subjects fixated a cross that appeared in the workspace. The location of the fixation cross was chosen randomly on each trial from a set of four locations (+ symbols in **a-c**), situated roughly halfway between the start point (black squares) and circle of targets (black dots). Potential fixation points were chosen based on the location of the visual and proprioceptive targets. Only two of the four fixation points were used for reaches where the targets were at 60° and 240° (**a**) and at 120° and 300° (**c**). The results of this experiment are shown in (**d-f**), using the same conventions as in Figure 6 of the main text.



Supplementary Figure 3: Methods and model fits, passive proprioceptive experiment. In this study, the left arm rested on a sled (not shown) supported by the lower table (**a**) and was passively moved to the appropriate position to serve as a proprioceptive target. The left index fingertip touched the upper table, which supported the right arm. Results are shown in (**b-d**), plotting conventions as in Figure 6.

Control for active movement of the target arm

In the original version of Experiment 1, proprioceptive targets were specified by the position of the left index fingertip. However, since subjects actively moved the left hand to the target location and supported it against gravity once it was in place, non-proprioceptive motor cues such as efference copy could have contributed to the sensed position of the left hand. We therefore tested 5 additional subjects in a second modified version of Experiment 1 aimed at minimizing non-proprioceptive cues to target location. Specifically, the left arm was passively moved to the proprioceptive target on each trial and was supported by a second tabletop (Supplementary Fig. 3a). The left forearm rested on a specially designed sled with an adjustable brace that fixed the left wrist and held the left index fingertip in a raised position against the underside of the upper table. The right arm rested on the top of the upper table. Subjects received no information about where to move the left hand. Rather, an experimenter stood to the subject's left and positioned the left index fingertip at the appropriate proprioceptive target on each trial. This positioning was done based on visual cues available to the experimenter but hidden from the subject, who was instructed to relax the left arm while the experimenter positioned it.

The results of this modified experiment are shown in Supplementary Figure 3b-d. As

in the original experiment, all subjects had a larger fit value of α_{MV} in the visual-target condition (mean difference in $\alpha_{\mathrm{MV}} = .38$, Supplementary Figure 3d). This result shows that the pattern of sensory integration during movement vector planning observed in the original experiment did not depend on the subject making active movements with the left (target) arm. The average value of α_{INV} in the modified experiment was very similar in both conditions (mean difference in $\alpha_{\mathrm{INV}} = .04$, larger for proprioceptive targets).

Supplementary Methods 1: Scoring

At the end of each trial in Experiments 1 and 2, text appeared on the feedback display which informed subjects of their current score and whether their reaching movement had been a "hit" or a "miss." If a reach ended within 2 cm of the target, the trial was judged a "hit" and subjects received 1 point. All trials that included visual feedback shifts were counted as "hits" to avoid providing error feedback and thus driving sensorimotor adaptation. If subjects missed the target by more than 2 cm on an unshifted trial, the trial was judged a "miss" and one point was deducted from the score. On trials with unshifted feedback that were scored as misses, subjects were required to make a corrective movement to the target. On reaches to visual targets, this correction was guided with re-illuminated visual feedback. On reaches to proprioceptive targets, a field of arrows directed the right fingertip to the left, in the manner described in the Methods of the main text.

In order to reduce variability in planning time and velocity profiles, subjects' score also depended on two loose timing criteria. Two time intervals were defined: interval 1 from the "go" signal until the fingertip moved 5 mm from the start point, and interval 2 from the end of interval 1 until the tangential velocity fell to 10 cm/sec. Interval 1 was required to be between 150 and 750 msec, and the Interval 2 was required to be between 250 and 650 msec. If either of these timing requirements was not met, subjects received zero points if they had hit the target on that trial and lost one point if they had missed. Text appeared at the end of each trial to inform subjects of any timing errors on that trial. Subjects committed relatively few timing errors. The average Interval 1 error rate across subjects was 3% and 2% in Experiments 1 and 2, respectively. The Interval 2 error rates were 3% and 5%, respectively.

Supplementary Methods 2: Hypothesis testing and confidence limits

We used a bootstrapping technique[6] to determine confidence limits on the fit values of α_{MV} and α_{INV}. For each subject and trial condition (e.g. visual or proprioceptive targets Experiment 1), we created 1000 bootstrap datasets in which each bootstrap trial was sampled (with replacement) from one of the eight trials with the same reach target and visual shift. The model was fit to each of these resampled datasets, resulting in a distribution of 1000 values of (α_{MV}, α_{INV}). This distribution was then used to determine a confidence ellipse for α_{MV} and α_{INV}.

To test the hypothesis that the value of α_{MV} or α_{INV} differed between two trial types, we used a permutation test against the null hypothesis that the mixing parameter in question was equal in the two conditions. For example, in order to test the hypothesis that α_{MV} differs when a subject reaches to visual versus proprioceptive targets, we tested against the null hypothesis $H_0 : \alpha_{\mathrm{MV},1} = \alpha_{\mathrm{MV},2}$, where $\alpha_{\mathrm{MV},1}$ is the value of α_{MV} in the visual-target condition and $\alpha_{\mathrm{MV},2}$ is the value of α_{MV} in the proprioceptive-target condition. This test

is derived from the following rearrangement of Equations 1 and 2 from the main text:

$$\hat{x}_{\text{MV, i}} = P_i + \alpha_{\text{MV, c(i)}} (V_i - P_i) \quad \text{(S1)}$$

$$\hat{x}_{\text{INV, i}} = P_i + \alpha_{\text{INV, c(i)}} (V_i - P_i) \quad \text{(S2)}$$

where V_i and P_i represent the visual and proprioceptive signal on the ith trial, $c(i)$=1 for visual-target trials, and $c(i)$=2 for proprioceptive-target trials. Combining Equations S1 and S2 with Equations 3-5 from the main text, we can obtain a single expression for the predicted initial velocity in all conditions:

$$\dot{x}_i = \underbrace{J\left(K^{-1}(P_i)\right) J^{-1}\left(K^{-1}\left(P_i + \alpha_{\text{INV, c(i)}}(V_i - P_i)\right)\right)}_{\Phi_i} \left(x_i^* - P_i - \alpha_{\text{MV, c(i)}}(V_i - P_i)\right).$$

This equation can be rewritten using the indicator function $\delta_{c(i)=k}$, which equals 1 if trial i is of type k and zero otherwise:

$$\dot{x}_i = \Phi_i \left[x_i^* - P_i - \left[\alpha_{\text{MV,1}}\delta_{c(i)=1} + \alpha_{\text{MV,2}}\delta_{c(i)=2}\right](V_i - P_i)\right] \quad \text{(S3)}$$

According to the null hypothesis $H_0 : \alpha_{\text{MV,1}} = \alpha_{\text{MV,2}}$, the model will produce the same predictions if the $\alpha_{\text{MV,1}}$ and $\alpha_{\text{MV,2}}$ are randomly interchanged across trials. This manipulation is achieved by permuting (randomly re-sorting) the values of $c(i)$ shown explicitly in Equation S3, leaving the un-permuted values of Φ_i. To perform the permutation test, we created 1000 artificial datasets in this manner, fit the model to each dataset, and computed the resulting R^2. If the R^2 value for the true dataset is greater than the 95th percentile of artificial R^2 values, then H_0 can be rejected. The null hypothesis $H_0' : \alpha_{\text{INV,1}} = \alpha_{\text{INV,2}}$ was tested in a similar fashion.

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