

Feedback responses enforce trajectory control when required by the goal of the ongoing task

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Trajectory control models were introduced almost 30 years ago to explain our tendency to perform smooth, straight reaching movements¹. These models have led to the longstanding view that the motor system uses a pre-computed or 'desired' limb trajectory to control goal-directed movements. However, this approach cannot explain task-dependent feedback corrections that counter errors arising from motor variability or external disturbances during movement. Despite being a key feature of formal feedback control theories², task-dependent corrections have only recently been investigated³, and it is unclear whether there are circumstances where feedback responses enforce desired limb trajectories. Here we use a single-joint paradigm¹ to investigate how changes in the behavioural goal shape feedback responses during reaching. We extend this paradigm to a multijoint task where subjects reach to a stationary or moving target. We predicted that feedback responses will only enforce desired trajectories when required by the behavioural task constraints.

Single-joint reaching task: Subjects ($n = 10$) performed 50-degree elbow movements (shoulder clamped) in two conditions with different time constraints. In the time-constrained condition, subjects had to complete their reaching movements within 800-1200 ms. The target turned green if the reach was completed on time, but turned blue (too fast) or red (too slow) if the subject did not meet these time constraints. In the unconstrained time condition, the goal target always turned green after the reach was completed. We did not observe differences in peak elbow velocity ($p = 0.312$) or the elbow angle at peak velocity ($p = 0.631$) during unperturbed movements. We probed feedback responses on random trials with elbow perturbations that pushed the hand toward or away from the target (± 1 Nm, ± 2 Nm). When we perturbed the subject's hand toward the target, they performed vigorous corrections that allowed them to stop motion and avoid entering the target too quickly, resulting in behaviour that resembles trajectory control (Figure 1A, B). In contrast, subjects allowed the perturbation to carry them to the target when there were no movement time constraints, resulting in a clear reduction in movement time (Figure 1B, $p < 0.001$). We measured triceps stretch responses and found that muscle activity was reduced in the long-latency ($p < 0.01$) and voluntary time periods ($p < 0.01$) when there were no movement time constraints.

Target-tracking task: Subjects ($n = 10$) performed 15 cm movements in 800-1200 ms (Figure 2A). We probed feedback responses on random trials by applying elbow perturbations that produced left- or rightward hand motion (± 0.5 , ± 1 Nm; 10 ms ramp-up profile). Subjects completed two blocks of trials (in random order) where they were instructed either to resist the perturbation and complete the reach within the allotted time (mean reach time = 992 ± 161 ms), or track a target that moved with a bell-shaped velocity profile along a straight path from the start position to goal target (mean reach time = 1013 ± 85 ms). The motion of the moving target was adjusted for each subject's nominal (i.e., unperturbed) reaching movements. In agreement with our prediction, we found that subjects reduced their maximum hand displacements and intercepted the moving target before completing the reach (Figure 2B-D), but corrected directly to the goal target when the task did not require precise control of the movement trajectory (all p 's < 0.05).

Our results highlight goal-directed feedback corrections that selectively compensate for errors that influence performance. This key finding shows that stereotyped movement patterns are not a default property of the motor system, but are in fact a flexible form of feedback control that emerges from the behavioural constraints of the ongoing task.

¹Hogan N (1984) *J Neurosci* 4: 2745-2754.

²Todorov E, Jordan MI (2002) *Nat Neurosci* 5: 1226-1235.

³Scott SH (2012) *Trends Cogn Sci* 16:541-549.

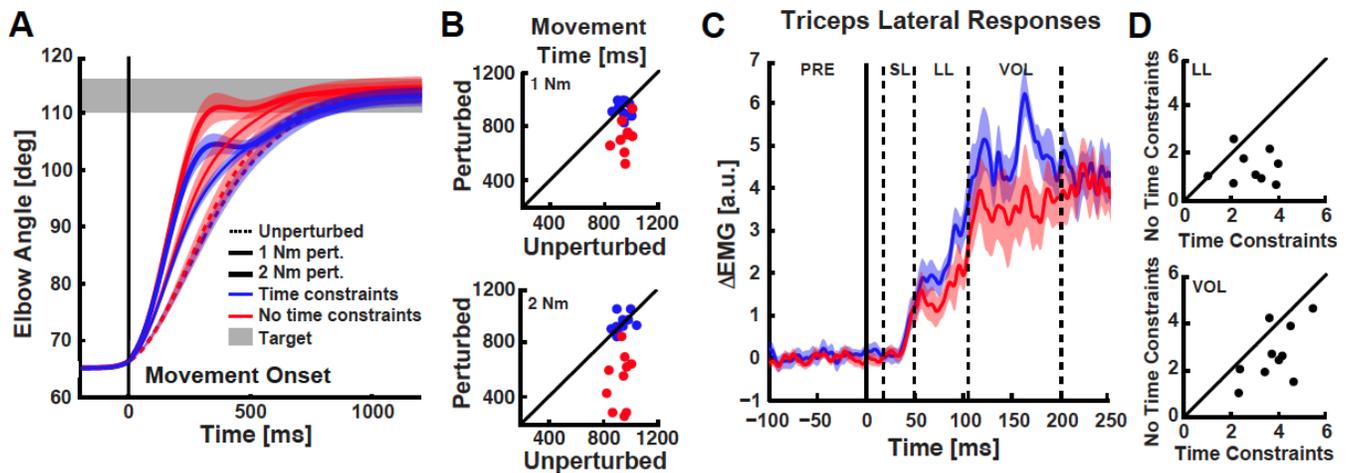


Figure 1. Single-joint reaching task. **A.** Temporal kinematics of the elbow joint (mean \pm SEM). Dashed lines are the population average ($n=10$) from unperturbed reaching movements, solid lines are perturbed reaching movements. **B.** Movement times in the 1 Nm (top panel) and 2 Nm (bottom panel) perturbation conditions. Data points represent movement times for each individual subject. **C.** Perturbation responses of the triceps lateral muscle (mean \pm SEM). Data are aligned to perturbation onset ($t = 0$ ms) and dashed vertical lines separate the different time phases of the stretch response. **D.** Average stretch responses in the long-latency (LL; top panel) and early voluntary response epochs (VOL; bottom panel).

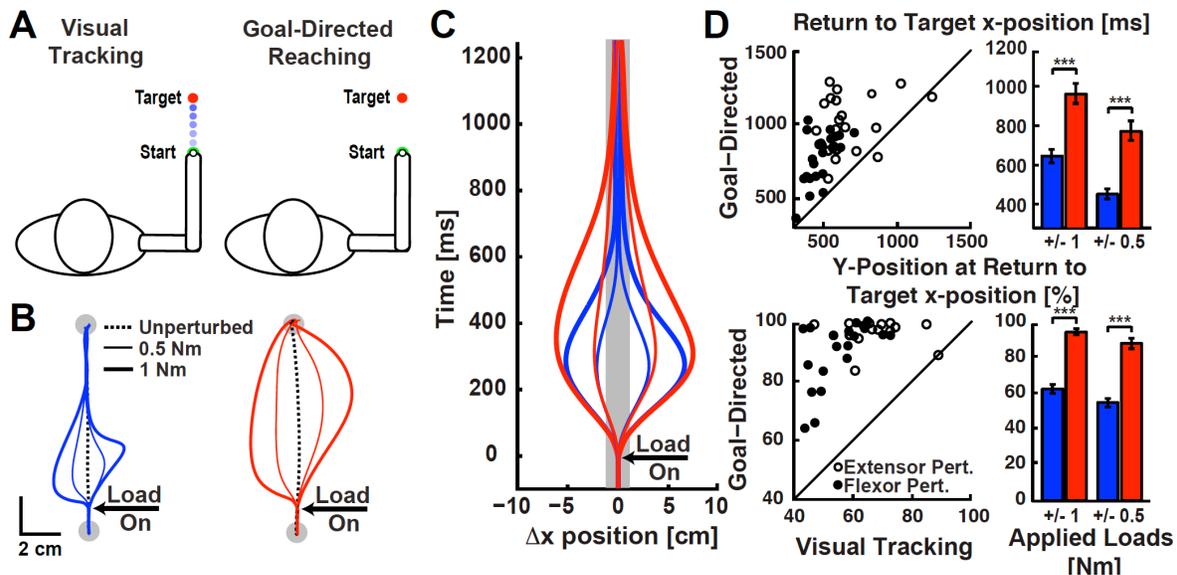


Figure 2. Multijoint reaching task. **A.** Experimental setup and target configuration. Shaded blue targets denote moving target. **B.** Representative hand paths obtained from a single subject highlighting differences in feedback corrections performed during reaching. **C.** Temporal x-axis kinematics of the hand. Data aligned to perturbation onset ($t = 0$ ms; $n = 10$). **D.** Summary statistics for perturbation-evoked hand motion (mean \pm SEM). Shaded gray region corresponds to the x-axis boundaries of the target (moving or stationary). *** $P < 0.001$.