

Discrete Corrective Submovements in the Monkey: Predictive Control under Uncertainty

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Two macaque monkeys were trained to turn a knob rapidly and accurately to align a cursor to a target on a computer screen for juice reward. The position and velocity traces were recorded while the monkey was performing the behavioral task. Visual perturbations of the target were randomly introduced at movement onset. Target perturbations toward the cursor (“near perturbation”), target perturbations away from the cursor (“far perturbation”), and no-perturbation trials were randomly presented in equal proportion.

We introduce an algorithm for automatic decomposition of the movements into an initial primary plus one or more corrective submovements even when the latter overlap the former. The algorithm is based on the principles laid down by Novak et al. [3]. Our main results are:

1. The amplitude of primary and corrective submovements tend to have a constant coefficient of variation (SD/Mean). Similar linear scaling of the noise SD with the signal mean has been reported for human isometric force production [2].
2. Primary movements and corrective submovements tend to undershoot the target. The undershoot bias was noise dependent; the undershoot size for the unperturbed trials significantly increased after target perturbations were introduced to the experimental procedure. A similar phenomenon has been demonstrated in human subjects and is consistent with stochastic optimal control theory [1].
3. The primary movement relative error is defined as the ratio of the error at the end of the primary movement over the initial distance to the target. We show for the unperturbed trials that

the onset of error correction is correlated with the expected value of the primary movement relative error. The greater the expected relative error of the primary movement the shorter the latency of the ensuing corrective submovement. Since in most of the cases the correction starts well before the primary movement ends, these findings support a stochastic predictive control mechanism.

4. We show that visual feedback from the perturbed target had a significant impact on the corrections the monkeys made only at latencies greater than 176 ms in one monkey and 220 ms for the second monkey.

5. Initial results from single cell recordings from the basal ganglia and motor cortex of our behaving monkeys [4] suggest a possible role for the basal ganglia in the process of corrective submovement initiation. Taken together, these results set the stage for single unit studies of optimal predictive control in the monkey.

References

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- [2] K.E. Jones, A.F. Hamilton and D.M. Wolpert, Sources of signal-dependent noise during isometric force production, *J. Neurophysiol.* 88 (2002) 1533-1544.
- [3] K.E. Novak, L.E. Miller and J.C. Houk, Kinematic properties of rapid hand movements in a knob turning task. *Exp. Brain Res.* 132 (2000) 419-433.
- [4] S.A. Roy, A. Fishbach, C. Bastianen, E. Neonene, L.E. Miller and J.C. Houk, Neural correlates of corrective submovement formation in the basal ganglia and motor cortex, to be submitted to the workshop on Theoretical approaches to basal ganglia function, the Annual Computational Neuroscience Meeting (2004).

Figure Captions

Figure 1: Amplitude dependent noise: Primary movements (Pr), overlapping submovements (OSM) and delayed submovements (DSM) were sorted according to their distance to the target before the movement started and divided into equal size groups. The amplitude mean and SD were then calculated for each group and plotted on a log scale. Regression line for the primary movements is given by $\log_{10}(\text{SD}) = 0.964 \cdot \log_{10}(\text{Mean}) - 0.559$ and the regression line for the corrective submovements (OSM and DSM) is given by $\log_{10}(\text{SD}) = 0.936 \cdot \log_{10}(\text{Mean}) - 0.313$. This implies that while corrective submovements tend to be noisier than primary movements, for both types of movements the amplitude SD scales linearly with the amplitude mean. This result is consistent with the results of Jones et al. [2] showing that the SD of isometric force production scales linearly with the mean force.

Figure 2: Onset of corrective movement as a function of the relative error of the primary movement. Relative error of zero implies an accurate primary movement which ended at the target center, while relative error of 1 signifies the extreme case of 0 amplitude primary movement. The relative error of the primary movement is negatively correlated with the latency of the correction ($r_{1568} = -0.49$, $p < 0.05$). Data is shown for overlapping submovements for unperturbed trials only.

Figure 3: In order to measure the earliest point at which a visual perturbation of the target had a significant effect on the performed correction (T_{visual}) we used the following analysis. Trials were sorted according to the duration of their primary movements and divided into equal sized groups. For each such group we calculated the percentage of trials that included overlapping submovements (OSM) for each of the perturbation types (near, far or none). For a group of trials with primary movement duration which is shorter than T_{visual} , the occurrence of overlapping submovement should be independent of the perturbation type. However, for a group of trials with

primary movement durations that exceed T_{visual} , the occurrence of overlapping submovements should depend on the perturbation type. Panel *A* plots the percentage of OSM trials for the no-perturbation and near perturbation conditions for monkey L. and demonstrates that for trials with primary movement duration greater than 160 ms the occurrence of OSM corrections is suppressed under the near-perturbation condition. The significance of the dependence of the OSM occurrence on the perturbation type is calculated using a chi-square test. The X-marks in panel B plots the significance level for each group of trials. For illustrative purposes we also plot the filtered significance using the black curve. The red line marks a significance level of 0.05. For monkey L. the perturbed target had a significant impact on the corrections monkey L. made after 176 ms, as marked by the dashed line. For monkey V. the visual perturbation had a significant effect only after 220 ms.

Figure 1

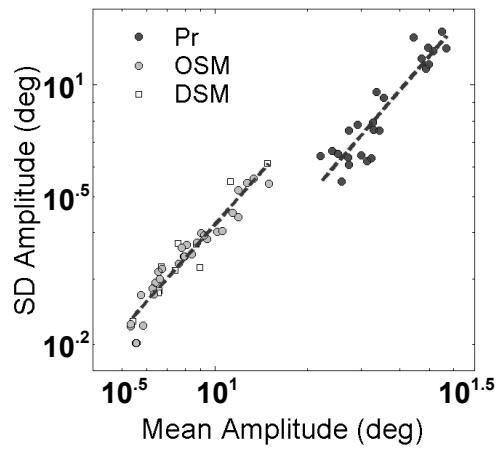


Figure 2

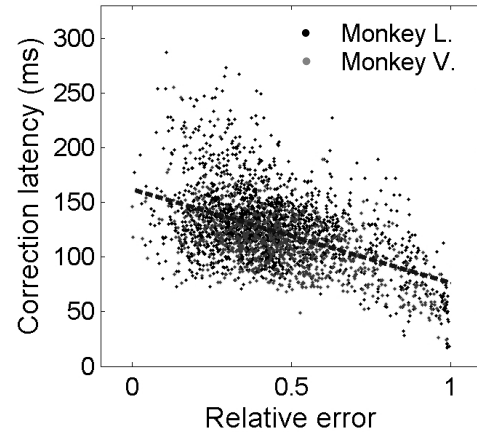
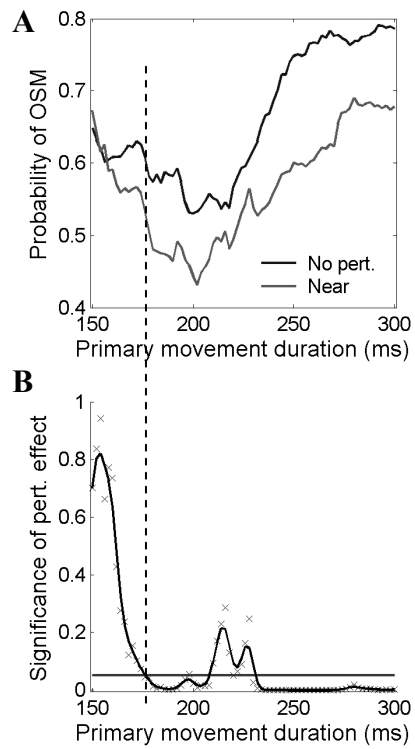


Figure 3



Biosketch:

Alon Fishbach studied computer science at Tel-Aviv University, where he received his Ph.D. in 2000 for his work on “The Auditory Edge: Psychophysical, Neurophysiological and Computational Aspects”. He is currently a research fellow in James Houk’s group at Northwestern University, studying motor control in behaving monkeys.