Interpreting motor adaptation results within the framework of optimal feedback control

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While motor adaptation experiments provide valuable and potentially very informative data, the interpretation of that data is often more challenging than its gathering. This is because, by definition, adaptation is a change in the state of the underlying sensori-motor control mechanisms. Therefore we cannot talk about adaptation without assuming – either explicitly or implicitly – a model of how those underlying mechanisms function in their "steady state", irrespective of adaptation.

Presently, the most common assumption is that motor control is based on the execution of detailed desired trajectories. Whenever a systematic perturbation is introduced experimentally, the motor system is thought to oppose the perturbation so that the resulting trajectories return to baseline. This is not always the case, but, in the absence of a clear alterative, inconsistencies are usually dealt with by patching the desired trajectory hypothesis with hypothetical internal limitations.

We have recently argued that desired trajectory tracking is inappropriate as a general framework of motor control, because it contradicts a wide range of phenomena related to the coordination of redundant actuators, and furthermore results in suboptimal performance. The alternative theory we have proposed is based on stochastic optimal control[1]. The purpose of this talk is to extend our theory to the process of motor adaptation, and apply it to the task of reaching. We propose that the baseline feedback control law is being adapted so as to become optimal for the new dynamic environment. While complete re-optimization may be impossible within a single training session, and approximatons may be unavoidable, such an idealized model should predict the "direction" of behavioral change (if not its magnitude).

Our underlying model of reaching, derived from[1], will be introduced first. That model continuously estimates the state of the plant (by optimally integrating delayed noisy feedback, prior control signals, and knowledge of plant dynamics), and maps the instantaneous state estimate into a vector of control signals using the optimal time-varying feedback gains. The feedback gains are optimal for a behaviorally relevant cost, that includes endpoint error and effort terms but does not specify any preferred movement pattern. To validate this underlying model, we will briefly show that it gives rise to the following empirical phenomena: a) bell-shaped speed profiles, that become heavily skewed when target size decreases; b) smooth corrections for target perturbations, that are incomplete when the perturbation occurs late in the movement; c) elongated covariance ellipses, whose shape varies with movement extent. Then we will present models of four adaptation results.

1. Adaptation to curl-viscous force fields has been found to be overcomplete: subjects initiate a movement in a direction opposite to the perturbation, and later the force field pushes the hand back towards the target[2]. We will show that such overcompensation is indeed the optimal strategy in the presence of curl-viscous forces. This is because subjects have to push against the forces at some point in time, and the earlier that is done, the more time the feedback loop has to cancel the signal-dependent noise that pushing against the forces produces. Incidentally, skewed speed profiles in reaching to small targets have the same explanation: although such a pattern is energetically suboptimal, it allows more accurate control of the final hand position because most of the signal-dependent noise is injected early, and the feedback loop has time to cancel it.

2. Adaptation to unstable elastic forces increases impedance selectively in the unstable direction, and produces "aftereffects" that are more straight than normal reaching movements[3]. Therefore, under normal circumstances, the motor system is not primarily concerned with producing straight movements. Our model shows the same direction-specific increase in feedback gains, and a corresponding decrease in path variability (in aftereffects, compared to baseline conditions).

3. Local visual distortions, that make the perceived path curved but do not affect the endpoint, might appear to distinguish between desired trajectory tracking and optimal control[4]. The results (about 25% adaptation) have been interpreted as supporting evidence for desired trajectories. However, these results are equally consistent with optimal control, as follows. The motor system is likely to interpret this unusual perturbation, at least in part, as some change in dynamics that causes the physical movements to become curved. Such a change does not affect the average endpoint location, but in general will affect the expected variance and effort, and therefore trigger a change in the optimal control law. We have designed two different dynamic force fields which can account for the perceived curvature, and trigger partial adaptation in agreement with the experimental results. A more systematic approach to identifying what the motor system might learn from this perturbation would be to use system identification methods, which we are in the process of incorporating into the model.

4. Adaptation to inertial force fields is known to be far from complete, while adaptation to viscous and elastic force fields is normally complete[5]. We have found that this pattern can be reversed by emphasizing temporal rather than spatial accuracy. It is essential to understand the effect of these force fields, because they are the ones experienced most often in the real world, and therefore are likely to cause "perfect" adaptation. Our explanation is the following. When the task allows some freedom in either the duration or extent of the movement, that freedom can be exploited to reduce both variance and effort. It turns out that movements with added inertia benefit more from slowing down than from reducing extent; on the contrary, movements with added visco-elasticity benefit more from reducing extent than from slowing down.

1. E. Todorov and M. I. Jordan, *Nature Neuroscience*, in press (2002). Available at http://cogsci.ucsd.edu/~todorov
2. K. A. Thoroughman and R. Shadmehr, *Nature* 407, 742-747 (2000).
3. E. Burdet, R. Osu, D. W. Franklin, T. E. Milner, M. Kawato, *Nature* 414, 446-449 (2001).
4. D. M. Wolpert, Z. Ghahramani, M. I. Jordan, *Experimental Brain Research* 103, 460-470 (1995).
5. G. L. Gottlieb, *Journal of Neurophysiology* 76, 3207-3228 (1996).