Uncovering representation from trial-to-trial changes in performance during adaptation

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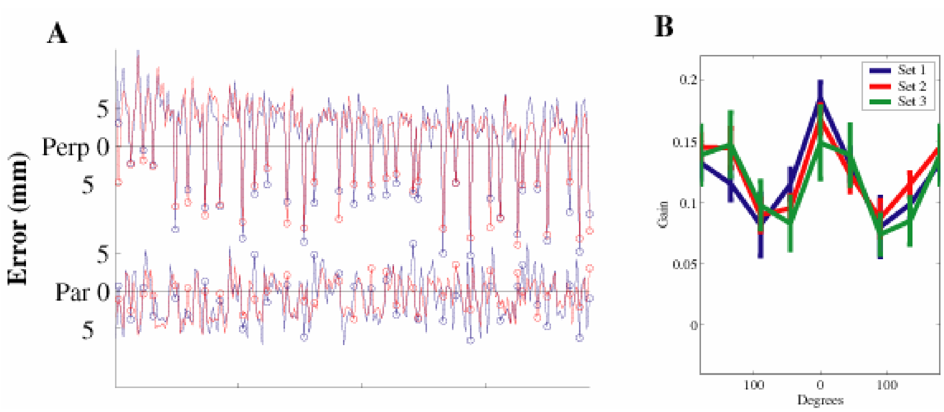
In a number of neural systems, understanding representation has been key for understanding the system. Unfortunately, in voluntary motor control, an understanding of representation has proven elusive. Plasticity is one reason for this difficulty. The motor system constantly adapts to a changing environment, and probing the system inevitably changes it and its representation. We show how to leverage plasticity in order to probe representation, turning difficulty into strength.

Our theory is based on a biophysically realistic simulation of reaching movements adapting to a velocity-dependent curl field. Using a series of approximations, we derived a simple dynamical system that described the affect of error in one movement on performance in another. In the dynamical system, error ($y^{(n)}$) on a given movement (*n*) performed in direction $k^{(n)}$ affects the internal state of the system ($z_l^{(n)}$) in all of the other directions (*l*). The relationship is described by a generalization function that relates any two directions ($B_{l,k^{(n)}}$) and measures overlap of representation for two movements. The original error is a discrepancy between the expectation of force and the actual force experienced ($F^{(n)}$). This leads to the following dynamical system:

$$\begin{cases} y^{(n)} = DF^{(n)} - z_{k^{(n)}}^{(n)} \\ z_l^{(n+1)} = z_l^{(n)} + B_{l,k^{(n)}} y^{(n)} \end{cases}$$

The system has two multi-valued parameters: a generalization matrix, *B*, that gives the effect of errors in each direction of movement on other directions of movement and a compliance matrix, *D*, that relates perturbation force to actual displacement. The sequence of errors made by the simulation in an arbitrarily long succession of reaching movements can be captured using these 2 parameters with only 12 values.

Strikingly, the same dynamical system fits errors in subjects performing sequences of perturbed reaching movements. Figure 1A shows the error (averaged across subjects) in a sequence of 192 movements and the fit of the dynamical system. The r^2 of the fit is 0.77. Figure 1B shows the generalization function that produced the best fit and also generalization functions that fit successive sets of data. The consistent shape of the generalization function indicates that subjects generalize force from one direction of movement more strongly to movements in the opposite direction than to movements separated from them by 45º. We reproduced this finding by fitting the model to different fields, including fields that induce parallel as well as perpendicular error. We also found the same result when we allowed the field to vary randomly from one movement to the next. We could not reproduce this bimodal generalization function using our original simulation based on a Gaussian representation of space. However, by using basis elements that were a sum of two Gaussians, we were able to reproduce the generalization function with the simulation. Thus, our approach allows us to use psychophysics to glean information about the underlying representation with which movements are represented.



(A) The sequence of parallel (Par) and perpendicular (Perp) errors on successive movements during exposure to a viscous curl field and when the field was removed (circles). Blue trace shows subject data; red trace shows fit of dynamical model. (B) Generalization functions. X-axis shows difference between direction where error was experienced and other directions; y-axis shows gain (see equation above). Error bars are bootstrapped confidence limits. Blue trace shows generalization function that produced fit in A. Red and green traces are for other data sets.

We also used this approach to explore representation of position. Subjects made movements beginning in one of the three spatially separated positions. Movements beginning on the right were perturbed to the right; movements beginning on the left were perturbed to the left; in the middle, there was no perturbation. Learning of this task improved with increased distance between starting positions up to 10 cm. This challenged earlier results in the lab where a field learned in one position readily generalized across space. How could we explain lack of interference across 10 cm despite generalization across 80 cm? We hypothesized that representation of position uses piecewise-linear basis elements, leading to broad generalization but local interference. This is consistent with the neurophysiological findings of broad, linear position representation and localized gaussian-like representation of veloccity. Using a simulation whose basis elements combined piecewise-linear representation of space with gaussian velocity representation, we reproduced the earlier generalization results and our current interference results. We noticed that a piecewise-linear representation would only be able to represent a sequence of fields that was linear in position space. We tested this prediction by training subjects on a sequence of fields that were not linear in position space and found, in fact, that they were unable to learn them. This lent credibility to our hypothesis of piecewise-linear representation of space and bimodal gaussian representation of velocity.