Combined intrinsic and extrinsic representation for visuomotor rotation learning

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The coordinate frame in which the central nervous system (CNS) represents movement planning is a key issue in motor control. In the context of learning novel physical dynamics it has been suggested this frame is defined intrinsically (I) with respect to the body, specifically depending on the limb configuration associated with the trained movement [1]. In contrast, in visuomotor rotation (VMR) learning it appears that the coordinate frame is based on position or motion in extrinsic (E) space [2]. These findings suggest that motor adaptations are based on entirely different types of reference frames for VMR and movement dynamics adaptation. Here we hypothesize that the representation of VMR learning is instead based on a combination of intrinsic and extrinsic coordinates.

Previous work has looked closely at this issue (see Figure 8 in Krakauer et al., 2000). That experiment looked at the transfer of adaptation across arm configurations for a single target direction and concluded extrinsic adaptation since a large amount of transfer was found in extrinsic coordinates. Because generalization across multiple target directions was not studied, the target direction eliciting maximal transfer could not be determined. A second issue with this study is that the comparison between intrinsic and extrinsic representations relied on a version of intrinsic representation in which intrinsic adaptation was associated with extrinsic representation of the initial movement vector – this would result in untenable predictions for small adaptations.

We therefore took the approach of studying transfer to a second arm configuration to a range of movement directions. In Experiment 1 (Exp. 1), 6 subjects adapted to a 30° VMR while reaching for a single target in the Training workspace (Panel A). After 120 training trials, we measured the directional generalization function (GF) in the training workspace to 13 targets (every 15° between -90° and +90°) w.r.t. the direction of the trained target with 39 no-feedback trials. Subjects were then studied in the Testing workspace (Panel B), by imposing a -45° (45°clockwise) shoulder rotation, where the GF was once again probed. In the testing workspace extrinsic versus intrinsic movement-vector representations differed from one another by 45° compared to the training workspace as illustrated in Panel B. Therefore, if adaptation was based entirely on extrinsic coordinates, we would expect no shift in the GF (w.r.t. extrinsically-labeled target positions) and if it was based entirely on intrinsic coordinates we would expect a -45° shift. We measured a shift of -25° w.r.t. the GF in the training workspace and -20° w.r.t. the training direction (Panel C). Both measurements were approximately halfway between 0° and -45° and significantly different from both 0° and -45° (p<0.001). This result suggests that the learned VMR is represented in a combination of extrinsic and intrinsic coordinate frames.

We propose two models (Panel D) which could allow for the implementation of a combined intrinsic-extrinsic coordinate frame. Model 1 postulates that the CNS maintains parallel representations in intrinsic and extrinsic space and each representation adapts independently so that the overall adaptation is the sum of the two. Model 2 postulates the existence of a combined, higher-order, intrinsic-extrinsic representation. In Model 2, generalization depends (in a Gaussian fashion) on total distance (d) across intrinsic and extrinsic coordinates between training and testing: 

\[ d = \sqrt{dI^2 + dE^2} \] 

and 

\[ GF = \exp\left(-\frac{d^2}{(2\sigma^2)}\right) \]

The complete generalization patterns predicted by these models are illustrated in Panel E. Model 1 generates a plus-sign-shaped GF and Model 2 generates a hill-shaped GF. Here the X and Y axes represent angular distances from the training direction in extrinsic and intrinsic space, respectively. Note that each workspace that we study represents a diagonal slice through these 2D GFs as illustrated. Importantly, rotation of the arm configuration by 45° introduces a 45° shift in the correspondence between intrinsic and extrinsic representations. Note that both models predict identical GFs in the training workspace (Panel F). The \( \sigma \) for both models was set so as to produce generalization in the training workspace with a width of 27.5°; our best estimate for the width of the training workspace GF based on a more complete dataset (\( \sigma_{\text{MODEL1}} = 27.5° \) \( \sigma_{\text{MODEL2}} = 27.5° \sqrt{2} \)). Model 1, therefore, had 3 free parameters: the magnitudes of the intrinsic and extrinsic functions and an offset. Model 2 had 2 free parameters: the magnitude of the combined function and an offset. Note that for Model 2 the illustrations in Panel E and our model fitting assume equal weightings for distances in extrinsic versus intrinsic space but differential weightings are, of course, possible.

Fitting both models to the data from the testing workspace in Experiment 1 (Panel G) showed that they can both explain our results well (\( R^2=96.6% \) vs. \( R^2=94.7% \)). Therefore Exp1 shows VMR learning depends on both intrinsic and extrinsic representations, but fails to show how. Thus we devised a 2nd experiment to distinguish between them. We noticed that with larger changes in arm configuration between training and testing workspaces, Model 2 would continue to predict a unimodal Gaussian-shaped GF (although its height would decrease), whereas Model one would predict a bimodal GF with separate peaks for the intrinsic and extrinsic components of adaptation (see the +90° lower diagonal (dotted) slices in Panel E).

In Experiment 2 (Exp. 2) 11 subjects adapted to a 30° VMR to a single target for 120 trials (Panel H) and generalization was measured at 19 different target directions in both the training and testing workspaces as illustrated in Panels H and I. We found that the GF in the testing workspace was unimodal and its peak was shifted to 47°, approximately halfway between 0° and 90° and significantly different from both (Panel I, \( p<0.001 \)). Model 2 (\( R^2=84.3% \)) explains this data set much better than Model 1 (\( R^2=27.1% \)), \( p<0.001 \) as shown is Panel K when the widths of the Gaussians are held fixed as in the fitting of Experiment 1 data. Note that if the widths of the Gaussians are allowed to vary, the quality of fit for Model 1 improves (\( R^2=64% \)) but is still significantly worse than the Model 2 fit. Furthermore, the Gaussian widths expand from 27.5° to an average of 83° and are grossly incompatible with the Experiment 1 data.

These results indicate that both intrinsic and extrinsic reference frames contribute to VMR learning and the CNS generalizes this type of adaptation as a combined function of these two reference frames rather than as independent intrinsic and extrinsic adaptations.
References: