One motor cortex, two different views

TO THE EDITOR—In a recent paper in *Nature Neuroscience*, Todorov[1] referred to our finding that a motor cortical representation of hand trajectory during spiral drawing precedes the hand's movement by an interval that varies with path curvature[2,3]. Although there are several possible explanations for this finding, Todorov, using a simplistic model, argued that because cortical cells share common properties with muscles, this relationship could be due to a combination of inertia, viscosity and stiffness acting on the acceleration, speed and position of the arm, respectively. Although simple, his model is flawed and cannot support this conclusion.

The author models a multijoint arm as a simple cantilever that is converted to single point-mass equation using a Jacobian transformation (web supplement A, http://www.nature.com/neuro/web_specials/). The arm's properties were derived from a simplified version of muscle whose activity is a linear combination of motor cortical activity. This model was used to reinterpret our results[2,3]. In our study, monkeys drew spirals on a vertically oriented computer touchscreen. The center of the spiral was located in front of the monkey, between its shoulders. According to Todorov's model, this location corresponded to the equilibrium point of the arm—the location where the parameters in his model would force the arm to rest. Todorov assumed that cortical activity reflects the inertia, viscosity and stiffness of the arm and showed that his model produces the same variable lags as our cortical population vectors. However, any acceleration representation in the cortical activity would actually decrease lags as a function of curvature, which is exactly opposite to our finding (web supplement B, http://www.nature.com/neuro-/web_specials/).

The increased lag with increasing curvature shown in Todorov's article is due to his positional term. The idea that extrinsic position may be a factor in motor cortical activity is not new[4–6]. However, Todorov's method of equating extrinsic position representation to muscle stiffness is incorrect. This model assumes that muscle viscoelastic properties are independent of muscle activation. Thus, even an inactivated muscle will act as a large spring pulling the arm back to some equilibrium position. In real muscle, the force–length and force–velocity relationships are modulated by muscle

activation such that at zero activation, the muscle is essentially a non-force producer. In the real world, the combination of gravity and inactive muscles will force the arm to fall to the side. In Todorov's model, the combined effect of gravity and muscle stiffness on inactive muscles would make the hand float at mid-chest level; muscle activity would be required to force the arm down below chest level. This, of course, is unrealistic. Viscoelastic models like the ones used by Todorov are only valid for perturbation studies where both posture and neural activity are assumed to be constant. Using such equations to solve for time-varying muscle activations violates the basic assumptions of perturbation models. Simple dynamic models can be useful to explain arm mechanics. However, when the models are not consistent with basic physiology, exclude important phenomena, and violate inherent assumptions, they cannot be compared to empirical data.

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TO THE EDITOR—Here we refute claims by Todorov[1] and Scott[7] that the importance of target direction as an explanatory factor for cortical activity in a regression analysis we performed[5] is an 'artifact' of a square-root transformation of neural discharge rates. Specifically, it was touted by Scott[7] that "squaring [*sic*] the discharge rate of neurons in order to stabilize the variance ... causes a dramatic increase in the percentage of neurons that appear to represent movement direction (from 17% [*sic*] to 43% in Todorov's model)." The data to which Todorov[1] referred concerned the percentages of cells for which a particular variable yielded the highest R^2 when used alone in the regression. We re-analyzed these data using the regression analysis we used previously[5] but without any transformation of the discharge rate. The results of the two analyses were practically identical, the average absolute difference being only 1.9% (http://www.nature.com/neuro/web_specials/). However, there was a statistically significant improvement of the regression fit when the square-root transformation was used. The median R^2 for the square-root transformed data was 0.5811, as compared

to 0.544 for the non-transformed data ($P <$ 0.0001, Wilcoxon's signed-rank test). This was anticipated, because the square-root transformation is expected to make the distribution of counts more symmetrical. This transformation is routinely used when analyzing counts[8–10], given the commonly highly skewed distribution of such data. Finally, we analyzed the data without any transformation or smoothing. In this case, the agreement with the original analysis was even closer, the average absolute difference being only 0.86%. We conclude that the relationship between neural activity and movement parameters found earlier[5] holds irrespective of the specific transformation and/or smoothing used. Finally, while we dealt above with the issue of square-root transformation because of the more general importance of this transformation for analyzing neuronal spike counts, there are also numerous other points raised by Todorov[1] which we also dispute, including the force direction/magnitude issue, which we cannot critically discuss due to space limitations.

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REPLY TO MORAN AND SCHWARTZ—Assuming that M1 cells control the activation of muscle groups, I have previously derived an equation[1] relating the M1 population vector (PV) to hand kinematics and kinetics. In addition to force and acceleration terms, this equation includes velocity and positional terms needed to compensate for muscle visco-elasticity. The interplay among these terms offers a simple explanation to several puzzling phenomena[1] including the curvature-dependent time-lag between PV direction and tangential velocity[2,3]. The strength of the model is that multiple phenomena are explained simultaneously, using the most basic properties of the musculoskeletal apparatus and thus avoiding the danger of curve fitting.

Moran and Schwartz claim that the fit to their data[2,3] is somehow an artifact of the approximation I used, and that the results will change if additional details are considered. It is not explained how a first-oreer approximation could produce such