Arm trajectory and representation of movement processing in motor cortical activity

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Abstract

We review experiments in which single-cell primary motor cortical activity was recorded from Rhesus monkeys (*Macaca mulatta*) while they performed reaching and drawing tasks. The directional tuning curves generated during reaching were modulated by the speed of movement and this was reflected in the magnitude of population vectors calculated from firing rates of a large population of cells. Directional and speed representation in the firing rates of these cells is robust across both reaching and drawing. Several behavioural invariants related to the speed of drawing were represented in the time-series of population vectors. This high fidelity neural representation of velocity found in motor cortex can be used to visualize the dynamics of motor cortical activity during drawing and suggests that the cost function governing the rate of drawing is bound by neural processing.

Introduction

By recognizing movement parameters encoded in neural activity and the way they change relative to movement, we can begin to understand some of the fundamental dynamic elements underlying volitional movement. Recent movement studies have shown that multiple parameters are represented simultaneously in the activity pattern of a single neuron (Ashe & Georgopoulos, 1994; Moran & Schwartz, 1999a). Furthermore, the relative representation of each parameter in the pattern of discharge activity may vary during a task (Fu *et al.*, 1995). For instance, in the middle of a reaching task, velocity was an important factor in single cell activity; however, position was a larger factor at the end the of the reach when posture maintenance was required. Hand velocity can be subdivided into speed and direction. This is especially interesting because behavioural studies suggest that these parameters are processed separately for reaching movements (Favilla *et al.*, 1989; Soechting & Flanders, 1989; Gordon *et al.*, 1994;) and our recent work shows that these two parameters are well represented in motor cortical activity (Moran & Schwartz, 1999a).

Cells in the motor cortex have direction-related activity that can be described with a cosine function when movement direction is plotted against firing rate (Georgopoulos *et al.* 1982). This is typically determined from the 'centre→out' experiment where reaching movements are made from a central start position to a number of equally spaced targets placed circumferentially. The firing rate to each target is taken as an average, usually over the reaction and movement times, limiting the analysis to parameters such as direction that remain constant during each movement. In contrast, a general property of reaching is that speed varies during each movement with a bell-shaped profile (Georgopoulos *et al.*, 1981; Morasso, 1981; Soechting & Lacquaniti, 1981; Hollerbach, 1982). As suggested by Morasso (1981) and Hollerbach (1982) the shape of the speed profile

may be considered an invariant which is scaled in magnitude for different amplitudes or duration of reaching movements. We have carried out a series of experiments in rhesus monkeys (*Macaca mulatta*) to examine how the variation of speed within the same movement affects the ongoing discharge rate of direction-sensitive cells recorded extracellularly in the motor cortex. Furthermore, we have characterized the relation of speed and direction to motor cortical discharge in a series of drawing tasks where both direction and speed change as the hand moves. The results of these experiments support the idea that direction and speed are parameters that are processed separately. Furthermore there is a clear relation between the timing of the direction representation in cortical populations and actual movement, suggesting that large changes in direction necessitate more processing between cortex and movement.

Results

Representation of speed and direction in single cell activity

Speed and direction effects on the modulation of cell activity can be separated in the centre→out task. The targets in this task are arranged symmetrically so that each target has a partner in the opposing direction. As the response of direction-sensitive cells is characterized with a cosine function that spans all directions and is symmetrical about its mean value, collapsing the time-varying responses of a cell across movements to all targets effectively removes the direction-related response in that cell's activity (Fig. 1). The residual activity pattern matches closely the bell-shaped speed profile of the hand during the movement.

To better understand how both types of movement-related information could be incorporated in the activity of a single cell, trials were sorted by the angle between the movement and preferred directions. A regression between peak speed and mean discharge rate in each direction category relative to preferred direction showed that the height of the directional tuning was modulated by speed as shown in Fig. 2. Speed modulates both the nondirectional profile shown in Fig. 1 (as is evident by the overall positive bias of speed on the tuning

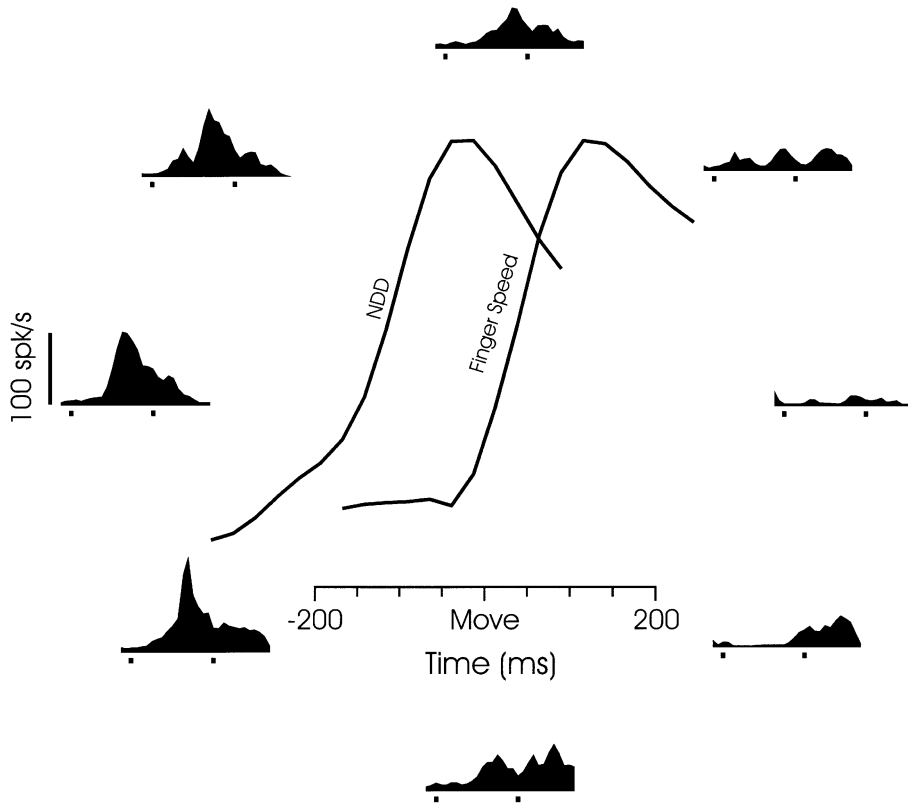*Correspondence*: Dr A. B. Schwartz, as above.
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FIG. 1. Single cell encoding of arm speed. The time-varying response to each of the eight targets (peripheral histograms) are summed after subtracting prereaction time activity from the profile. The marks under each profile mark the beginning of the reaction time and the end of the movement. The traces in the middle are the mean speed profile across targets and the nondirectional discharge component (NDD) from the subtraction procedure. Modified from Moran & Schwartz (1999a).

curve) as well as the directional component (as is evident by the larger shifts in activity when moving in the cell's preferred direction). Combining these velocity-based results with those found for position by Kettner *et al*. (1988), an overall equation for the discharge rate of a generic primary motor cortical cell can be written as:

$$D(t-\tau) = b_0 + b_n \|\hat{V}(t)\| + \hat{B} \cdot [\hat{V}(t) + b_p \hat{P}(t)] \qquad (1)$$

where the symbol ^ indicates vectors, D is the discharge rate of the cell, t is time, τ is the time lag between cortical activity and arm kinematics, b_0, b_n and b_p are scaling factors, B is preferred direction vector (e.g. b_x, b_y, b_z), V is hand velocity vector, P is hand position vector.

The first term on the right hand side of Eqn 1 is the tonic activity of the cell, the second term represents the nondirectional activity shown in Fig. 1, and finally the last term shows the interrelation between a cell's preferred direction and the vector kinematics of hand position and velocity. As stated earlier, the relative weighting of position and velocity information in cortical activity can vary during a task such that the position term only becomes significant during low speeds. The exact formulation of this relationship has not been fully determined yet; thus, the b_p term is subject to future modelling refinements.

Speed is represented as population vector length

Speed-modulated direction representation has consequences when building population vectors. An activity-weighted vector contribution in each cell's preferred direction is combined with other contributions from a large population of units recorded as the animal repeated the same task. These contributions are averaged, resulting in a single, 'population vector'. Due to the nature of the population vector algorithm and assuming a uniform distribution of preferred direc-
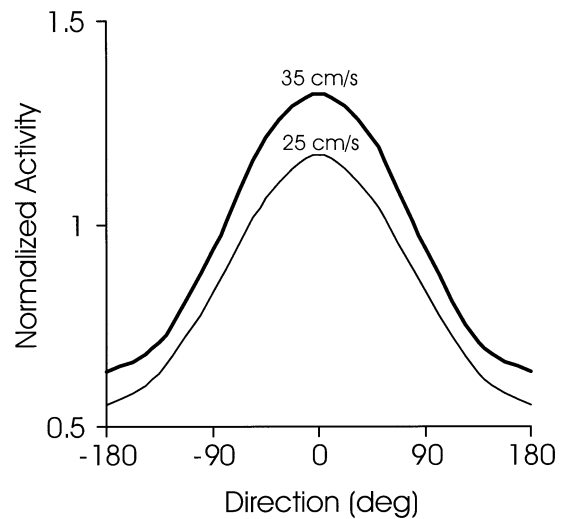

FIG. 2. Effect of speed on motor cortical directional tuning. Tuning curves were derived by regressing discharge rate against speed. The tuning curve derived for faster speeds (heavy line) had higher discharge rates, especially in the preferred direction, compared with slower movements (lighter line). Modified from Moran & Schwartz (1999a).

tions, the tonic and nondirectional activity represented by the first two terms of Eqn 1 are eliminated mathematically (Moran & Schwartz, 1999a). Thus, only the third term in Eqn 1 survives in the construction of population vectors. Assuming that position effects are small in comparison with velocity during the movement, it can be shown that the length of the population vector is directly proportional to movement speed. Binning each cell's activity consistently during a
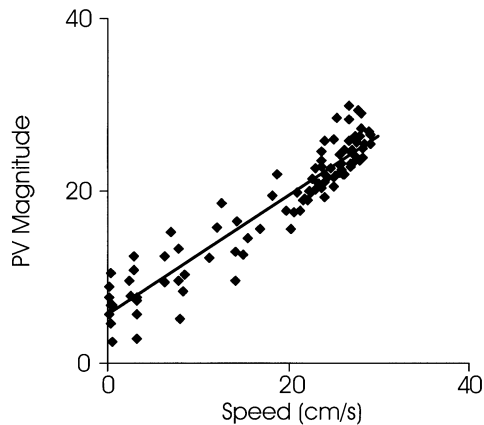
FIG. 3. Population vector magnitude matches hand speed. The magnitude of each vector during each bin of all reaches to each of the eight centre→out targets is plotted against the corresponding speed of the hand (averaged across trials and shifted by 145 ms). Modified from Moran & Schwartz (1999a).

reaching movement and calculating a population vector for each bin results in a time series of population vectors whose lengths match the bell-shaped speed profile of the movement (Fig. 3). The finding that the population vector represents both the direction and speed of movement can be summarized with a single vector quantity, velocity.

Drawing tasks can be used to study the interaction of speed and direction because both parameters can change continuously within a movement. In our experiment, monkeys first performed the centre→out task (on the surface of a touch-sensitive computer monitor) and then while isolation of the same unit was maintained, traced different shapes. Initially we found that the tuning function for a cell recorded in the centre→out task was also valid during drawing (Schwartz, 1992). However, residual activity in the drawing task unrelated to direction was also evident when the hand moved rapidly in the cell's preferred direction. This residual activity was correlated with movement speed. This speed coding was also evident in population vectors calculated throughout the task as a modulation of the vector's length that was proportional to movement speed. Results from our drawing experiments (Schwartz, 1993; Schwartz, 1994; Schwartz & Moran, 1999) show that the instantaneous velocity of the hand is represented continuously in the motor cortex.

Drawing invariants

One of the more characteristic properties of drawing is the inverse relation between speed and curvature (Viviani & Terzuolo, 1982). A more precise formulation of this 'power law' (Viviani & Flash, 1995) is:

$$\|\hat{V}(s)\| = K(s)\{R(s)/1 + \alpha R(s)\}^{\beta} \quad \alpha \geqslant 0,\ K(s) \geqslant 0 \tag{2}$$

where $\|\hat{V}\|$ is the speed at spatial coordinate s, and R is the radius of curvature. K is the 'velocity gain factor' dependent on the trajectory's length, α is a constant between 0 and 1 depending on the average velocity and β is an exponent typically equal to 1/3.

There may be several reasons for this relation including mechanical properties of the limbs, acceleration constraints, smoothness constraints and noise constraints. Nevertheless, this relation develops as children age, is found for isometric force pulses, is present when perceiving movements and has been found in the motor cortical representation of drawing movements (Viviani & Stucchi, 1989; Viviani & Schneider, 1991; Fagg *et al.*, 1992; Massey *et al.*,
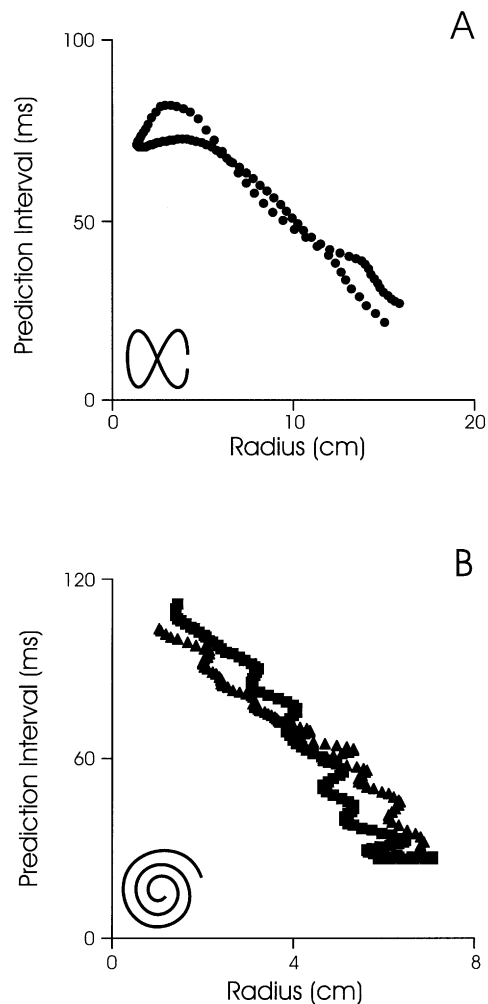

FIG. 4. The prediction interval is linearly related to the radius of curvature. (A) Curvature and prediction intervals were averaged by segment and plotted here as a scatter plot for one of the figure eight drawing experiments. (B) Prediction intervals for spiral drawings. Squares are for outside→in spirals and triangles for spirals drawn in the opposite direction. Modified from Moran & Schwartz (1999b) and Schwartz & Moran (1999).

1992; Schwartz, 1994; Schwartz & Moran, 1999) suggesting that at least some aspects of this relation are manifest in the planning portion of the drawing behaviour. This relation might be considered in the same light as Fitts' law (Fitts & Peterson, 1964). Instead of a constraint between speed and accuracy, the power law suggests a tradeoff between speed and curvature. Pellizzer (1997) proposed that during continuous trajectories, the speed of movement is determined by two factors; the length of time it took the hand to move along an increment of the trajectory and the change in direction between segments. This formulation differs slightly from that of the power law, but both fit the data nearly as well. Our experimental findings show that the power law fits the neural trajectories derived from motor cortical activity during drawing (Schwartz, 1994; Schwartz & Moran, 1999) showing that direction-induced processing delays are present at this level. However, we found an additional direction-dependent delay between the motor cortical representation and movement by matching vector directions between each population vector and its corresponding movement vector. The time increment between the matched members of each pair has been termed the 'prediction interval.' This was first shown to vary inversely with the radius of curvature in a spiral-drawing task (Fig. 4B) showing that the
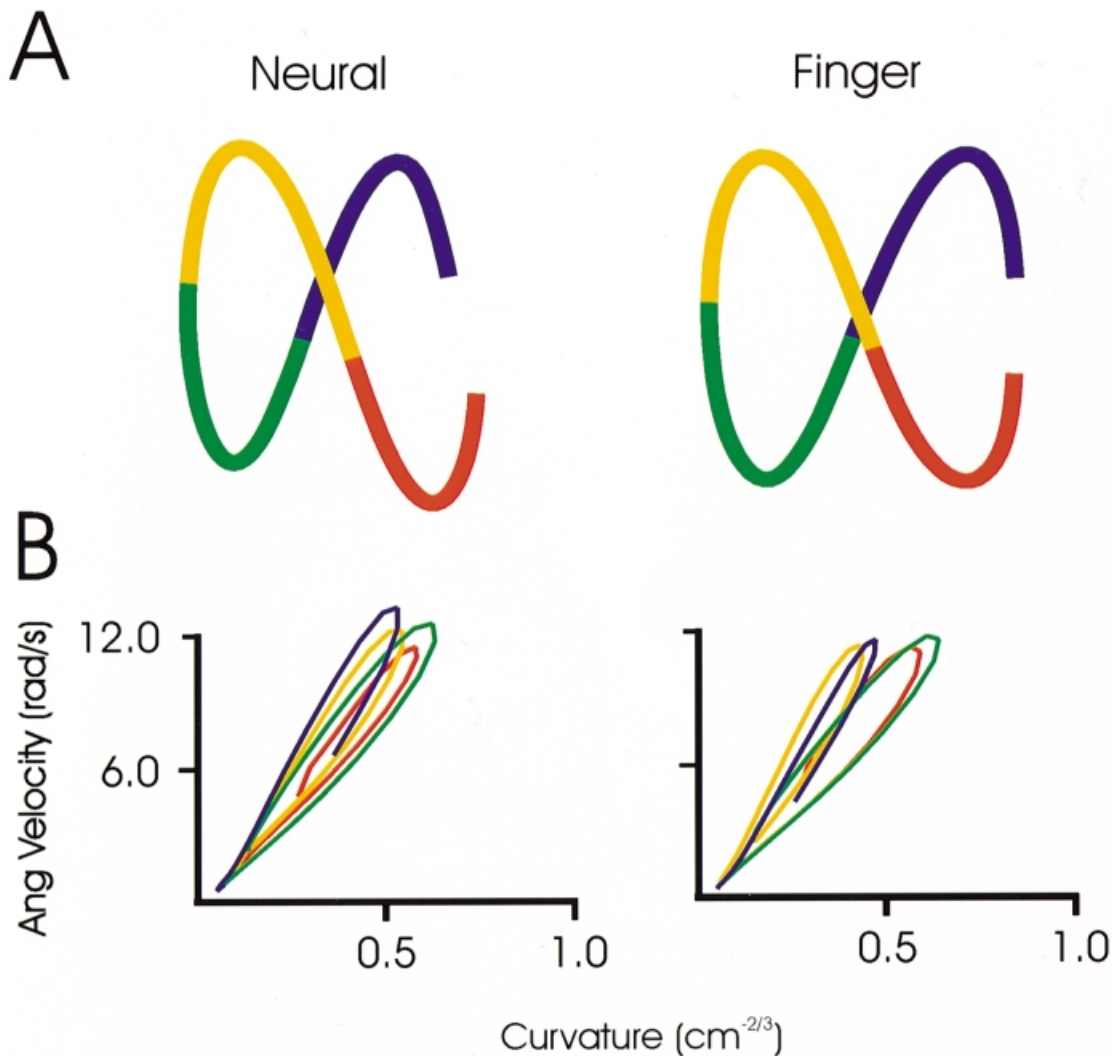
FIG. 5. (A) Neural and finger trajectories during a figure eight drawing task. A time series of population vectors calculated during the task was temporally integrated to yield the neural trajectory. Individual movement segments are colour coded. (B) Two-thirds power law representation in the actual hand kinematics and those predicted by population vectors. The two-thirds power law is quite evident in the neural data. Modified from Schwartz & Moran, 1999.

direction represented in the motor cortex takes longer to be implemented with larger incremental changes in direction along the drawn path. This finding is robust, as it also occurs when drawing figure eights (Fig. 4A). As curvature and speed are related inversely, it is expected that the prediction interval is also correlated with speed. Although this relation is present, the correlation to radius of curvature is slightly stronger (with spirals $r = 0.98$ for curvature, vs. 0.92 for speed). Interestingly, the time lag between population vector and movement in a reaching task is fairly constant (≈ 120 ms). This fixed time lag is also present during drawing initiation but then becomes elastic as the task proceeds (Moran & Schwartz, 1999b).

Segmentation is another feature of drawing (Viviani & Cenzato, 1985; Soechting & Terzuolo, 1987a). Segment boundaries are defined kinematically as places in the trajectory where speed is maximal. There are several reasons for defining segments this way. Speed is continuously modulated during drawing so finding maxima is reasonable. Curvature varies inversely with speed and is minimal at speed maxima; also curvature inflections (clockwise to anticlockwise or the reverse) will occur at these points. Finally, the k (velocity gain factor) in the power law relation changes instantaneously at the segment boundaries (Viviani, 1986). Interestingly, figures drawn in

free space are confined to planes delineated by segment boundaries and subjects are unable to draw figures in free space with a continuously changing plane of motion. (Soechting & Terzuolo, 1987b).

The representation of segmentation in a pattern of motor cortical activity was measured with the population vector algorithm as monkeys drew figure eights (Schwartz & Moran, 1999). Neural trajectories, composed of temporally integrated population vectors, closely matched those of the hand's trajectory and had the same pattern of segmentation (Fig. 5). Within each segment (segment boundaries were defined as zero-crossings in angular acceleration and corresponded to maxima of tangential velocity), curvature was highest in the middle where tangential velocity was smallest. The prediction interval between corresponding directions was largest in the middle of each segment, as would be expected from the spiral data. An analogous measure for magnitudes between corresponding vectors in the neural and movement data was only slightly modulated within each segment and could be approximated with a constant, suggesting that the lag between neural and movement speeds was almost fixed throughout the task. In addition to the kinematic details reflective of psychophysical segmentation studies (Viviani &

Cenzato, 1985; Soechting & Terzuolo, 1987a; Pellizzer *et al.*, 1992), these neuronal data, based on the prediction intervals and population sums, show that neuronal activity involved in the specification of the arm movement is structured in a segment-like manner.

Conclusion

Our results suggest that these behavioural invariants have their origins in neural processing and are consistent with the idea that motor control is constrained by the properties of the system itself, in particular the neural processing that underlies movement specification. This is not a new idea and was the basis of early psychophysical work (Woodworth, 1899; Bernstein, 1967) and later work on reaching (Paillard, 1960; Fitts & Peterson, 1964; Soechting & Lacquaniti, 1981; Georgopoulos & Massey, 1988; Georgopoulos, 1991). In the work of Fitts for instance, information content determined by the target size and movement amplitude was transmitted at a maximal rate (channel capacity), so that with smaller target size and/or larger amplitudes movements were slower. In a study designed to measure information capacity, Massey and Georgopoulos found that a large number of directions could be distinguished and moved toward, corresponding to a relatively high information capability both in terms of performance and motor cortical output. Based on our findings of the power law representation in motor cortical activity and the prediction interval, we suggest that the channel for directional information is limited so that the rate of information transmission is constrained, slowing the arm when direction changes rapidly. This constraint is evident in each segment and is characterized by a consistent temporal relation between neural activity and extrinsic hand velocity. The variable time lag we observed could not be reconciled using other arm kinematics (e.g. joint angular velocity) or arm kinetics (e.g. EMG; Moran & Schwartz, 1999b). There are undoubtedly time lags between other central structures and movement. Further study of these temporal relations within a variety of movements could lead to a better understanding of the neural organization underlying motor processing.

How does this idea relate to other movement strategies for arm movement?

Segmentation, the power law and 'isochrony' (movements of the same form with differing extents tend to have the same duration) suggest that at least portions of volitional arm movements are specified before they take place (Viviani & Flash, 1995). In contrast, strategies conforming to a global constraint or cost function do not require a prespecified plan. Flash & Hogan (1985) proposed the idea that movements were optimally smooth and constrained by minimizing mean squared jerk (the time derivative of acceleration). They showed that given a starting, intermediate and terminal point that there was a single set of parametric equations (one equation for each coordinate axis) that would minimize jerk. With the appropriate initial conditions, trajectories predicted with these equations were shown to accurately fit experimental data. This theory requires only the prespecification of the initial conditions and not the spatial coordinates of the movement. These two ideas have a mutual relationship (Viviani & Flash, 1995). It can be shown analytically that the power law gives an optimally smooth trajectory. Conversely, applying the minimum-jerk algorithm gives trajectories that conform to the power law with $\beta = 1/3$ and show segmentation. Furthermore, the minimum-jerk algorithm model generates smooth transitions between segments by ensuring continuity in speed and acceleration. These two viewpoints, preplanning and optimal constraint, can be further fused by allowing the smoothness criterion to be applied in a

planning stage before the movement is produced. This could take place in a continuous manner so that the plan and the movement stay at some fixed or variable time increment apart as suggested by our data. In fact it is quite likely that the planning stage is constrained by all of the operations that take place at later stages as suggested by the high correlations between kinematic trajectory, joint angular velocity and EMG (Schwartz & Moran, 1999).

Harris & Wolpert (1998) suggest that the motor system is constrained by noise. By assuming that within the motor system, noise and signal increased proportionally, they were able to generate both bell-shaped velocity profiles from simulations of point-to-point movements and the power law for modelled movements of curved trajectories. The output of their simulation was optimally smooth. This is another example of how constraints within neural activity of the motor system are manifest in global characteristics of motor behaviour. All of these observations are consistent with the central idea that the motor system relies on an accurate execution of motor commands that are formed in advance of the movement (Massey *et al.*, 1986).

Acknowledgements

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