Constant effort computation as a determinant of motor behavior

Emmanuel Guigon[1], Pierre Baraduc[1], Michel Desmurget[2]

[1]INSERM U483, Université Pierre et Marie Curie, 9, quai Saint-Bernard, 75005 Paris, France
[2]INSERM U534, "Space and Action", 16 av. du Doyen Lépine, 69500 Bron, France

[guigon@ccr.jussieu.fr;Pierre.Baraduc@snv.jussieu.fr;desmurget@lyon.inserm.fr]

The nervous system controls motor behavior in a simultaneously constrained and flexible manner. On the one hand, when subjects are free to move, they automatically choose a trade-off between movement speed and accuracy, and execute longer movements in longer times (Fitts' law; 1; 2). On the other hand, they can be instructed to execute movements of prescribed amplitude, duration and accuracy (3).

Three principles are generally invoked to explain the properties of motor behavior: 1. the motor system operates according to an optimality principle. Models that select movements minimizing a criterion related to some relevant quantities reproduce many features of actual motor acts (4; 5; 6; 7; 8); 2. the motor commands are updated continuously by internal feedback loops (8; 9); 3. the motor system acts in the presence of neuromotor noise (7; 8; 10). Two models clearly illustrate the power of these principles (7; 8). Harris and Wolpert (7) proposed that the motor system chooses movements of minimal terminal variance under conditions of signal-dependent noise. The model reproduced kinematic and electromyographic properties of movements and explained the origin of Fitts' law. Todorov and Jordan (8) proposed a principled approach which states that motor behavior arises from the simultaneous minimization of an *error* cost (e.g. distance to the goal) and an *effort* cost (e.g. energy expenditure). This proposal considered cost components which can be readily measurable quantities and define a natural speed/accuracy trade-off (10), and explained the coordination of redundant degrees of freedom (8). Although successful in many aspects, these models fail to account appropriately for the control of movement accuracy. As movement accuracy covaries directly with movement cost, there is no way to explain why increased cocontraction could lead to increased stability and accuracy (3; 11) and more generally how accuracy can be controlled independent of kinematics (3).

To overcome these difficulties, we propose a five-stage description of motor control: 1. the motor system is an optimal feedback controller acting under state estimation noise (SEN; 12); 2. in this system, cocontraction level can be adjusted as an independent parameter; 3. the SEN reflects inaccuracy in estimation of position and velocity (13), is assumed to increase with movement velocity (12) and decrease with cocontraction (fusimotor control; 14); 4. all movements in a series (given instructions and cocontraction level) are performed at the same effort cost (*constant effort principle*); 5. for a given cost, the movement produced has the smallest control signal that guarantees zero estimated terminal error when compared to movements of same amplitude, duration and cocontraction level (*optimality principle*).

We show in a model of the neuromuscular system (nonlinear, multijoint version of 10; cocontraction is modeled by reciprocal inhibition between antagonist motoneurons) that these latter principles predict: 1. typical kinematic and electromyographic properties of multijoint movements (Fig. 1**ABCD**); 2. linear relationship between amplitude and movement time, peak velocity and peak acceleration, kinematic invariance, and directional variations in movement time and peak velocity (Fig. 1**EFGH**); 3. increased accuracy with cocontraction level (Fig. 1**IJK**).

Three key points must be emphasized. First, as accuracy under SEN depends on kinematics and cocontraction, the constant effort principle allows neural cost and accuracy to be dissociated. In particular, reducing the cost will not always allow to reduce movement variability. Second, the constant effort principle defines an implicit relationship between task parameters (amplitude, duration) which is modulated by cocontraction. Different costs define different amplitude/duration laws. Last, the constant effort of the constant effort principle has an ecological interpretation as the largest cost that can be alloted to a single motor act in a series (e.g. experimental session, day, race, ...) given limited total resources (e.g. energy) and expected rewards (motivation).

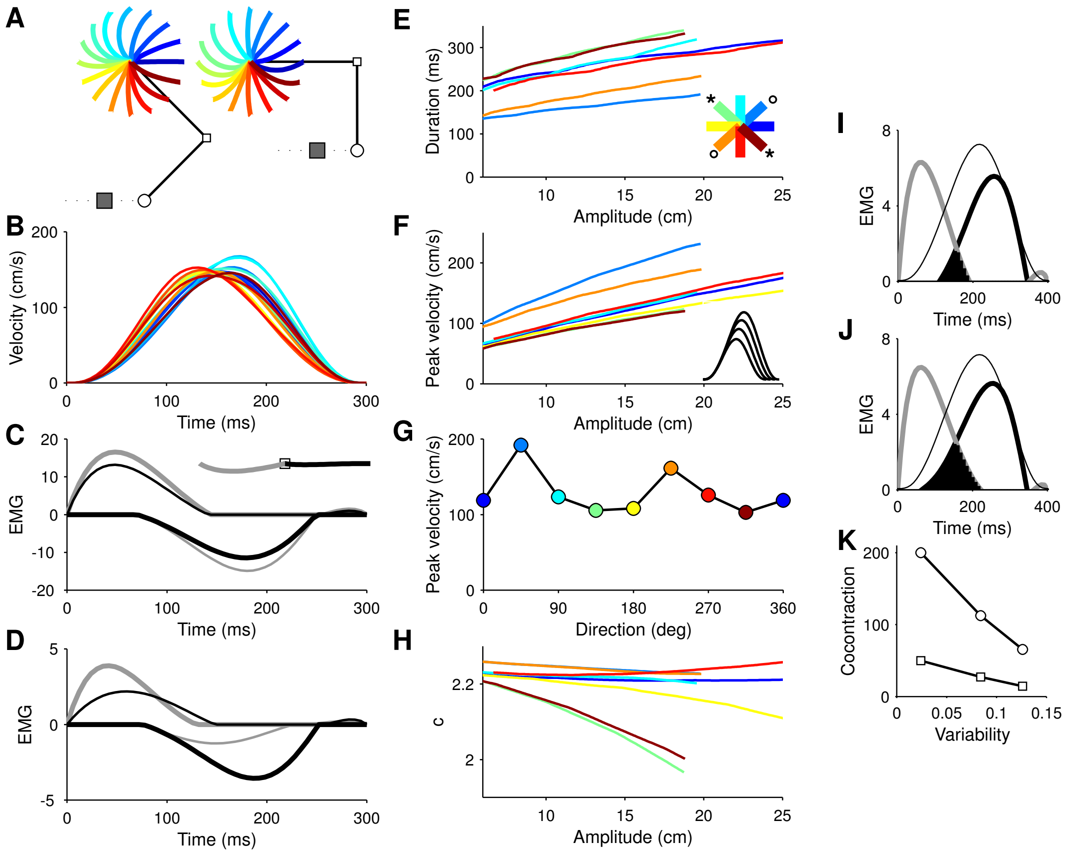

Figure 1: **A**. Simulated trajectories (20 cm, 300 ms) at two positions [(45,90) and (90,90)]. **B**. Tangential velocity profiles for the 16 movements at (45,90). **C**. Electromyographic activity for simulated movements. EMG in the shoulder flexor (thick line) and extensor (thin line) for two movement directions (black line: 0 deg; gray line: 180 deg). Antagonist activity is inverted and represented in the negative direction. **D**. Same as **C** for elbow muscles. **E**. Movement duration vs amplitude. **F**. Peak velocity vs amplitude. **G**. Peak velocity vs direction for a given amplitude (15 cm). **H**. $c = v_{\text{peak}}/v_{\text{avg}}$ vs amplitude. **I**. Shoulder EMG for a 20 cm long, rightward movement (velocity is indicated by a thin line). **J**. Same as **I** for a larger cocontraction signal. **K**. Relationship between terminal variability (determinant of the covariance matrix) and measured cocontraction (black areas in **I**,**J**) for shoulder (circle) and elbow (square). SEN was multiplicative Gaussian noise on velocity.

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