

Rhythmic muscular activation pattern for fast figure-eight movement

A. Bengoetxea^{a,*}, B. Dan^{a,d}, F. Leurs^a, A.M. Cebolla^a, C. De Saedeleer^a, P. Gillis^c, G. Cheron^{a,b}

^aLaboratory of Neurophysiology and Movement Biomechanics, Université Libre de Bruxelles, Belgium

^bLaboratory of Electrophysiology, Université de Mons-Hainaut, Belgium

^cBiological Physics Department, Université de Mons-Hainaut, Belgium

^dDepartment of Neurology, Hôpital Universitaire des Enfants reine Fabiola, Université Libre de Bruxelles, Belgium

ARTICLE INFO

Article history:

Accepted 16 December 2009

Available online 13 January 2010

Keywords:

Muscle synergy
Temporal modulation
Electromyography
Figure-eight
Rhythmic movement
Fast movement

ABSTRACT

Objective: To address the question of how the CNS generates muscle activation patterns for complex gestures, we have chosen to study a figure-eight movement. We hypothesized that the well defined rhythmic aspect of this figure will provide further insights into the temporal features of multi-muscular commands.

Methods: Subjects performed, as fast as possible, figure-eights initiated in the center of the figure with 4 different initial directions and 2 positions of the shoulder. We extracted the temporal modulation of the EMG patterns by calculating conjugate cross-correlation functions.

Results: (1) The muscular command was tuned with respect to the rotational direction of the figure-eight, (2) two sets of synergistic muscles acted in a reciprocal mode, and (3) these reciprocal commands presented an invariant temporal correlation with the spatial component of the velocity having the highest frequency.

Conclusion: Our results suggest that the rhythmic features of certain drawing movements favor the partitioning of the muscles into synergistic groups acting in a reciprocal mode. The inclusion of an individual muscle in one group or the other takes into account the expected number of changes of direction in the movement as a whole.

Significance: Muscular temporal synergies may depend on the rhythmic features of the trajectory.

© 2009 International Federation of Clinical Neurophysiology. Published by Elsevier Ireland Ltd. All rights reserved.

1. Introduction

A central problem in motor control research has been to understand the different processes that link the planning and execution of goal-directed movements. For any such movement at least two main processes must be carried out by the CNS: (1) coordinate transformation of sensorimotor information (Soechting et al., 1986; Flanders and Soechting, 1992; McIntyre et al., 2000) and (2) serial ordering of motor sequences (Lashley, 1951; Carpenter et al., 1999; Averbeck et al., 2002). Sensorimotor coordination begins with the integration of multiple sensory signals conveying information about the spatial field of action, represented in an extrinsic coordinate frame, and ends in the building of muscle activation patterns expressed in an intrinsic coordinate frame. In addition, when the movement consists of producing an integrated motor sequence, such as when manipulating a tool or drawing a learned shape, a serial ordering of motor sequences is organized

even before the action begins (Averbeck et al., 2002, 2003). Given the complexity of such processes, a remarkable feature of human motor control is the ability to rapidly reproduce the same gesture in different directions and in different regions of external space, without the apparent need for extensive reprogramming or adaptation. This performance requires the selective mapping and sequencing of the central command, taking into account the dynamic behavior of the musculoskeletal system (d'Avella et al., 2006; Buneo et al., 1997).

Insight has been gained into the processes of sensorimotor transformations by examining the coordinate frames that are represented at different levels of the motor system. In motor cortex (M1), neurons involved in extrinsic (Georgopoulos et al., 1982, 1986; Georgopoulos, 1999; Schwartz, 1992; Fu et al., 1993; Moran and Schwartz, 1999) and intrinsic encoding coexist (Evarts, 1968; Kalaska and Crammond, 1992; Kalaska et al., 1997; Kakei et al., 1999; Wu and Hatsopoulos, 2006). The transformation from extrinsic to intrinsic coordinates can also be produced by spinal mechanisms, like those described in the frog (Saltiel et al., 1998; Tresch et al., 1999, 2002), or in the cat (Poppele and Bosco, 2003). Finally, at the muscular level, both intrinsic and extrinsic coordinates of the movement modulate

* Corresponding author. Address: Laboratoire de Neurophysiologie et Biomécanique du Mouvement, ISM C.P. 640, Université Libre de Bruxelles, 808, route de Lennik, 1070 Brussels, Belgium. Tel.: +32 555 34 74.

E-mail address: abengoec@ulb.ac.be (A. Bengoetxea).

the patterns of muscle activity, reflecting processing carried out at each of these levels.

Spatial and temporal aspects of a muscle's activation depend heavily on its mechanical action, which depends directly on joint position (Buneo et al., 1997; Hogan, 1985) while electromyographic (EMG) patterns are also known to be modulated by movement direction in 3D space. Two fundamental types of EMG burst modulations have been described: namely amplitude grading in step tracking (Hoffman and Strick, 1999) and shifted timing in reaching movements (Flanders, 1991; Flanders et al., 1994, 1996). It has been proposed that the CNS generates the appropriate muscle patterns through the organization of muscle synergies because such a mechanism does not require an analytical control of the musculoskeletal system (d'Avella et al., 2003, 2006). Indeed, d'Avella et al. (2006) showed that combinations of a small number of time-varying muscle synergies capture the organization of the muscle patterns observed during fast-reaching movements. The synergistic organization is flexible, however, such that a single muscle may be a member of more than one synergy (Tresch et al., 1999; Weiss and Flanders, 2004).

In this context, it is interesting to study the muscular activation patterns for more complex movements like handwriting or geometrical drawing (Accornero et al., 1984; Lacquaniti, 1989; Viviani and McCollum, 1983; Viviani and Flash, 1995), for which these pioneering studies and others (see below) have revealed some simplification rules based on kinematics. According to these simplifying principles, complex movements are organized into segments with bell-shaped velocity profiles (Atkenson and Hollerbach, 1985; Plamondon, 1995a,b) reflecting the Isochrony Principle (Viviani and Terzuolo, 1982; Viviani and Cenzato, 1985) and presenting stable covariation between tangential velocity and curvature of the path (i.e., the 2/3 power law) (Lacquaniti et al., 1983; Soechting et al., 1986). To address the question of how the CNS generates the appropriate multi-muscular activation pattern in such complex movements, we chose to study the drawing of a figure-eight. This figure is of particular interest because: (1) this drawing movement implies the displacement of the end-effector segment in all directions within the drawing plane and (2) the vertical and horizontal frequency components are in an exact ratio of two (Buchanan et al., 1996), as is the case for a Lissajous curve. We hypothesized that the well defined rhythmic aspect of this figure will allow further insights into the temporal features of multi-muscular commands. Overall, we ask the question: how is the temporal multi-muscular command organized specifically for the figure-eight movement?

2. Experimental procedures

2.1. Subjects and experimental conditions

Data were collected from four right-handed subjects aged between 21 and 40 years. They were in good health, free from neurological disease, and had given informed consent to take part in the study, which was approved by the local ethics committee. They were asked to draw, as fast as possible, 2 series of figure-eight movements with the right arm extended in free space (Fig. 1). Movements were initiated in the center of the figure with an initial up-right (UR), down-right (DR), up-left (UL) or down-left (DL) direction with respect to external coordinates. The task was performed in the frontal (Fig. 1A) or in the sagittal (Fig. 1B) workspace depending of the flexion or the abduction posture of the shoulder. In a control experiment, one subject was asked to perform up-down and right-left cyclic movements in the frontal workspace. Each series of cyclic movements was repeated three times.

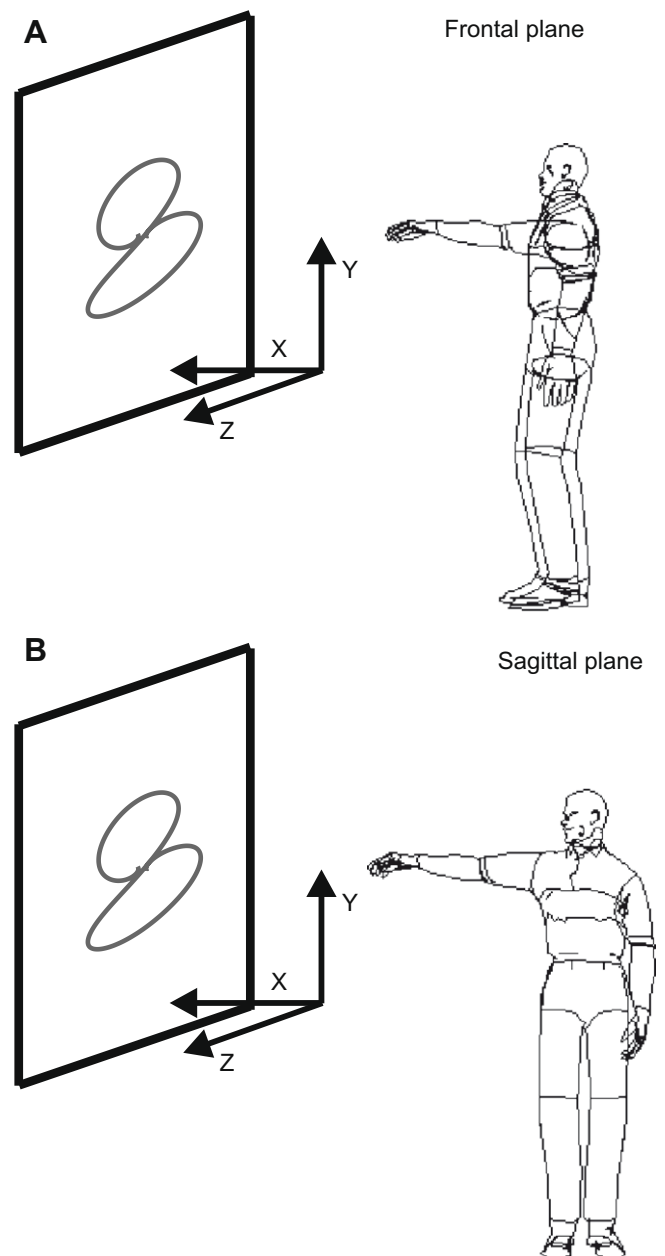


Fig. 1. Dissociation of muscle action from either an extrinsic or joint frame of reference. Subjects performed figure-eight movement in two shoulder positions, with the arm flexed at 90° (frontal workspace, upper panel) and with the arm abducted at 90° (sagittal workspace, lower panel). In each workspace, subject performed the figure-eight with 4 different initial directions, starting from the central point. The figure-eight were drawn without following a visual model.

2.2. Data acquisition

The movements of the arm were recorded and analyzed using the optoelectronic ELITE system (BTS, Milan) (Ferrigno and Pedotti, 1985). This system consists of 2 CCD-cameras detecting retro-reflective markers at a sampling rate of 100 Hz. The cameras were placed 4 m apart from each other and 4 m from the subject. Four markers were attached to the arm (on the acromion, the lateral condyle of the humerus, the radial apophysis of the wrist and the index finger). Velocity signals were obtained by digitally differentiating position signals using a fifth-order polynomial approximation. As the movements were performed with the extended limb, the information from the 4 markers is partly redundant. The reconstruction of the arm movement by the ELITE system

using the trajectories of the 4 markers confirmed the visual observation that the upper arm, forearm, hand and index finger acted as a rigid link (Cheron et al., 1996). Thus, we analyzed here only the index-finger marker, which was the one with the best definition related to the representation of the figure-eight.

Surface electromyographic activity (EMG) was recorded with the TELEM system (BTS, Milan) synchronized with the kinematic data. Silver–silver chloride electrode pairs (inter-electrodes distance of 1 cm) were placed over the belly of the following 6 muscles: posterior deltoid (PD), anterior deltoid (AD), median deltoid (MD), pectoralis major superior and inferior (PMS and PMI), and latissimus dorsi (LD). Raw EMG signals (differential detection) were amplified 1000 times and transmitted to the main unit with a telemetry system (Telemg, BTS). A functional resistance test that isolated specific muscles was made in order to verify the absence of cross-talk between adjacent muscles. Thereafter, EMGs were bandpass filtered (10–500 Hz) digitized at 1 kHz, full-wave rectified and smoothed by means of a third-order averaging filter with a time constant of 20 ms (Hof and Van Den Berg, 1981).

2.3. Cross-correlation analysis

In order to compare the temporal modulation of the EMG patterns between the different initial directions, conjugate cross-correlation functions (CCF) were calculated. The cross-correlation coefficient represents the correlation between two series, d_1 and d_2 , for different amounts of time-lag τ between the two signals. The CCF between two signals, e.g., d_1 and d_2 (EMG1 and EMG2), was defined as:

$$CCF_{d_1 d_2}(\tau) = \frac{1}{T\sigma_1\sigma_2} \int_0^T (d_1(t) - \mu_1)(d_2(t + \tau) - \mu_2) dt$$

where μ_1 and σ_1 are the mean value and the variance of d_1 and τ is the lag between the two functions, expressed in ms. Note that the cross-correlation function is not symmetrical about the lag of 0 that is, different correlations will emerge depending on whether d_2 is shifted forward or backward in time with respect to d_1 . Positive values of τ denote a time lead of $d_1(t)$ relative to $d_2(t)$, whereas negative values denote a time lag. The time window (T) represents the total shift (lead and lag) for which the correlation between all the duration of the two signals is calculated.

The CCF can provide valuable information concerning the kind of modulation, depending on the sign of the cross-correlation, ranging from -1 to $+1$. When the signals $d_1(t)$ and $d_2(t)$ are statistically correlated for a given time shift their CCF displays a peak (a significant CCF maximum) or a trough (a significant CCF minimum) at the corresponding value of τ (abscissa). A significant CCF peak at τ (ms), corresponding to a $p < 0.05$ (StatSoft, Inc.), means that the two signals present the same temporal sequence with a shift of τ (ms). Conversely, a significant CCF trough at τ (ms) means that they present an opposing temporal pattern with a shift of τ (ms).

Our interest in the first part of this study was to analyze the modulation of the temporal command of each recorded muscle across different movements. To this end we computed CCFs between EMG signals for each pair muscles and each pair of differing movements. To establish a baseline for the stability of the measurements across trials, we computed the CCF between signals from the same muscle for each of the two repetitions of the same movement condition (initial direction and workspace). To look for differences between commands of the same and different initial directions, we used ANOVA analyses. These statistical analyses were performed using Statistica (StatSoft, Inc.).

In the second part of our study we look for the invariance in the temporal relationship between the multi-muscular command and the velocity components of the figure-eight. In order to better char-

acterize the temporal relationships between muscles, we computed the difference between activities of 2 different muscles by subtracting one rectified EMG signal from the other. This was made without any anatomical *a priori* and gave rise to a compound signal for all the possible pairs of muscles. This procedure allowed us to accentuate the command type (reciprocal or co-activation) received by each pair of muscles. Before subtracting the EMG signals, we normalized each signal. For each EMG signal (i.e., for each of the 6 channels), the maximum value over each entire figure-eight was used to normalize the peak. This resulted in signals ranging from 0 to 1 for each muscle. This type of normalization enhanced the temporal aspect of the command. In a second step, we analyzed the temporal relationships between these compound signals and the velocity profile of the movement. In this part of the analyses the first function for the CCF analyses is the vertical or the horizontal component of the velocity index and the second function is the EMG compound signal. Finally, we compared the resulting CCF profiles two-by-two across the different initial directions. In order to quantify the likeness of the obtained CCF curves, we calculated a similarity index (SI) using the following equation:

$$SI = \frac{\int f_1(t)f_2(t)dt}{\left[\left(\int f_1(t)^2 dt\right)\left(\int f_2(t)^2 dt\right)\right]^{\frac{1}{2}}}$$

If $f_1(t) = f_2(t)$, then $SI = 1$.

3. Results

Fig. 2A and B show the superposition of two figure-eights drawn by 4 different subjects (columns) for the four different initial directions (rows). As the task requirement was to perform the movement as fast as possible, emphasis was not placed on the precise shape of the figure-eight and so the path followed by the hand varied considerably across subjects and initial directions. However, the shape of the figure remained relatively constant between the first and the second repetition. Average vertical size of the figure across subjects and conditions was 752.48 ± 158.6 mm for the first repetition and 735.81 ± 151.01 mm for the second. Measures of the horizontal size of the first loop (mean and sd 418.89 ± 91.71 mm and 409.34 ± 101.57 mm, for the first and second repetition, respectively) and the second loop (mean and sd 360.95 ± 111.56 mm and 349.49 ± 118.43 mm) were similarly constant between repetitions. An ANOVA with repeated measures analysis on these three values with initial direction, workspace and repetition as within subjects factors revealed no main effect of the repetition factor and no cross effects, consistent with the observation that subjects produced more-or-less the same shape from one repetition to the other within the same condition. ($p > 0.2$).

In order to define a baseline for similarity between EMG signals from different movements, we first verified the reproducibility of the EMG patterns for two repeated movements performed with the same initial direction and in the same workspace. Fig. 2C and D show the reproducibility of CCF profiles across subjects and initial movement directions for each muscle. Comparisons between EMG recordings from the same muscle for two trials having the same initial direction all showed significant CCF values ($p < 0.05$) and their lag distributions were in a range of values centered around 0 ms (see Table 1). The variability of CCF values for the same muscle on different trials (peak and associated lag) is an indicator of the reproducibility of the timing of the global activation command. These lag values will be considered as the reference for statistical analyses when comparing CCFs for movements with two different initial directions. Given the fact that for a lag or lead of 150 ms the temporal relation of our signals reverses, we chose for the subsequent CCF analyses a time window (T) of 300 ms.

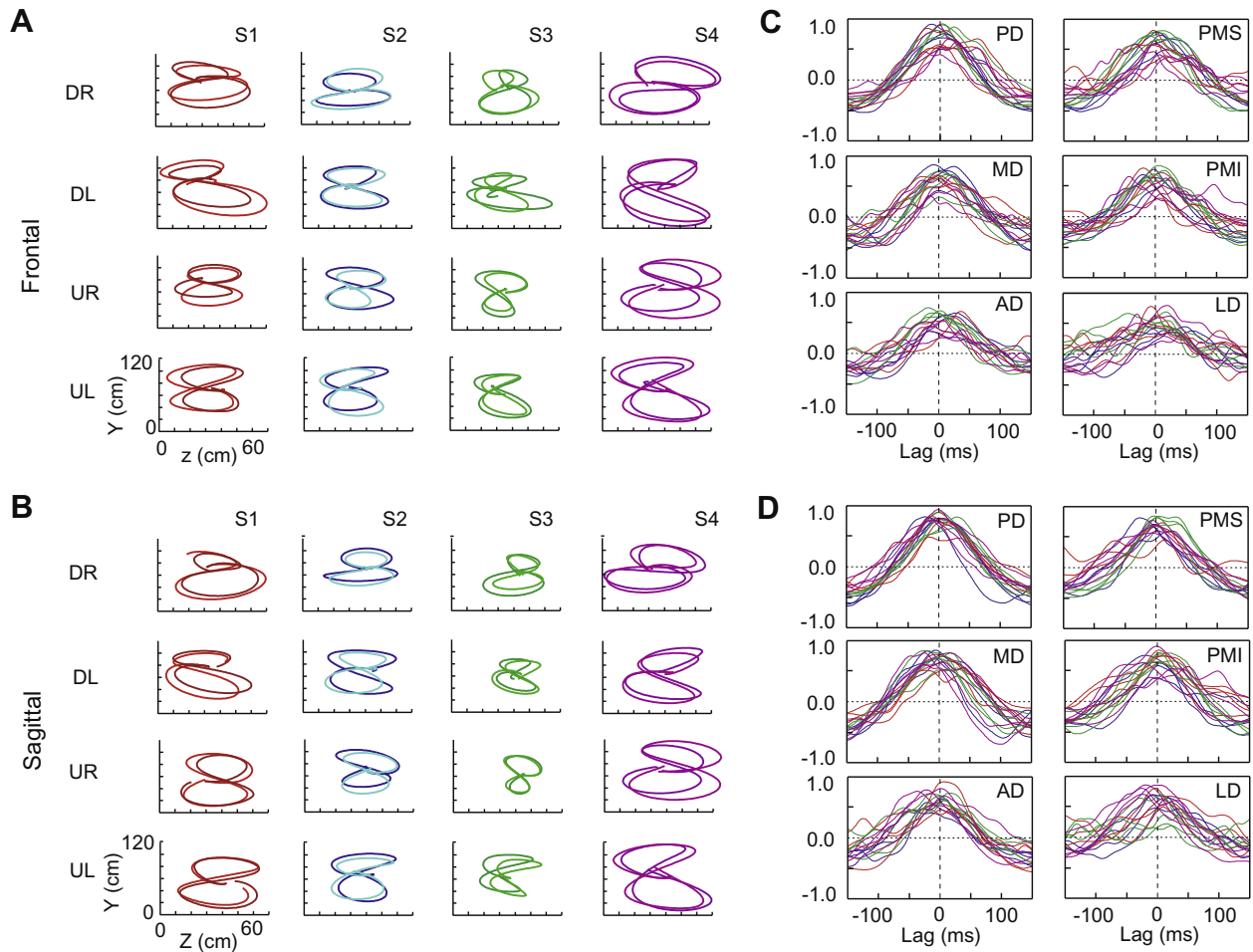


Fig. 2. Superimposition of movement trajectories initiated with the same initial direction, in the frontal (A) and sagittal (B) planes. Each column corresponds to one of the 4 subjects. Each line corresponds to one of the 4 initial directions. Reproducibility of the temporal sequence of the command (C and D). Each graph shows the CCF curves for each muscle (PD: posterior deltoid, PMS: pectoralis major superior, MD: median deltoid, PMI: pectoralis major inferior, AD: anterior deltoid, LD: latissimus dorsi). In each graph, there are 16 curves. For a given muscle, each CCF curve corresponds to the correlation between the EMG from the two repetitions of the same movement. The 4 colors correspond to the 4 subjects (S1, S2, S3 and S4) and for each subject there are 4 different initial direction movements (DR: down-right; DL: down-left; UR: up-right; UL: up-left).

3.1. In-phase and anti-phase temporal activation commands

The figure-eight movements were characterized by complex combinations of EMG activities (Fig. 3). Despite the different directions of the drawings (see the corresponding trajectories in the squares), the durations of the 4 movements were approximately the same (all the movements across subjects lasted on average 980 ± 90.4 ms). The multiple EMG patterns differed according to the initial direction of movement. For example, movements initiated toward the right were consistently associated with an initial burst in PD and MD (Fig. 3A and B), whereas movements initiated toward the left started with a burst in PMS and PMI followed

shortly by a burst of AD activity (Fig. 3C and D). For most muscles clear bursts were recognized, albeit with variations in intensity and duration, while LD showed variable tonic activities.

To test how the temporal pattern changed for a given muscle as a function of direction of the figure-eight movement, we performed a CCF analysis on pairs of EMG traces for the same muscle from movements with different initial directions. All such temporal comparisons are illustrated in Fig. 4 for the PD muscle and for one subject. In the upper-right corner of the figure, the CCF curves for all the combinations from movements realized in the frontal plane are illustrated. Amongst the 6 CCF profiles for movements in this workspace region, only single peak or trough shapes (categories 1 and 3, according to McKiernan et al., 2000) appear. CCF peaks (positive values) were seen when the horizontal component of the initial direction was the same (e.g., up-right and down-right, Fig. 4B), while CCF troughs (negative values) occurred when the horizontal component differed (e.g., down-left and down-right, Fig. 4A). Thus, instead of a complex temporal tuning used to produce all figure-eights for this muscle, the relative timings seem to fall into two classes, in-phase or anti-phase. The same results were obtained for the movements realized in the sagittal plane (bottom-left corner of the figure).

A total of 96 CCF comparisons were made in this part of the analysis (4 subjects * 2 series per subject * 6 initial direction combinations * 2 workspaces). We counted how many of these 96

Table 1
CCF and lags for the reproduction of the same movement.

	Frontal		Sagittal	
	CCF	Lag (ms)	CCF	Lag (ms)
MD	0.62 ± 0.16	5.0 ± 15.0	0.72 ± 0.11	1.3 ± 19.6
PD	0.72 ± 0.16	7.5 ± 23.8	0.78 ± 0.11	1.3 ± 12.6
PMS	0.63 ± 0.15	7.5 ± 21.8	0.70 ± 0.11	2.0 ± 13.7
PMI	0.64 ± 0.13	3.1 ± 21.8	0.68 ± 0.13	6.3 ± 17.8
AD	0.57 ± 0.14	6.9 ± 18.9	0.65 ± 0.13	-3.1 ± 20.2
LD	0.54 ± 0.15	5.0 ± 29.2	0.60 ± 0.21	3.1 ± 19.6

Values are means \pm SD, $n = 16$.

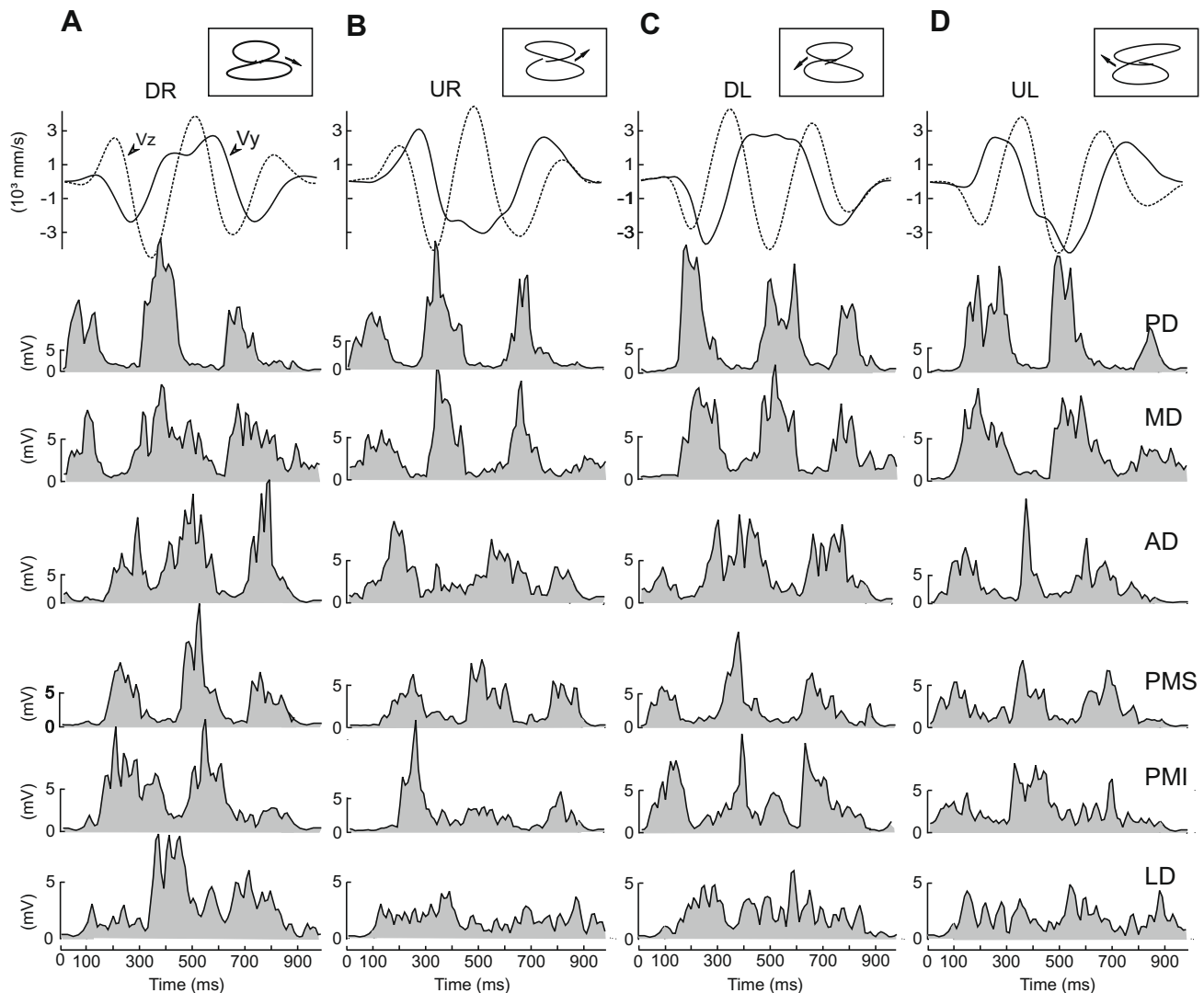


Fig. 3. EMG activity during figure-eight movements with different initial directions. From top to bottom: hand trajectory (inset), velocity profile of the finger in the vertical (v_y) and horizontal (v_z) directions; filtered (20 ms) and rectified EMG activities for each of 6 muscles: posterior deltoid (PD), median deltoid (MD), anterior deltoid (AD), pectoralis major superior and inferior (PMS and PMI), and latissimus dorsi (LD). Columns correspond to the figure-eight realized with different initial directions: down-right (A), down-left (B), up-right (C) and up-left (D).

comparisons obeyed the empirically observed rule of two opposing CCF patterns noted above, that is, a CCF peak for the movements with an initial direction where the horizontal component is conserved and a CCF trough for the other combinations. The number of comparisons respecting this trend was 91 for PD (95%), 94 for PMS (98.1%), 76 for DM (79.3%), 86 for PMI (90%), 68 for DA (71.2%) and 63 for LD (65.6%).

For each muscle, the distributions of lag values were not statistically different with respect to the reference ranges (Table 2), indicating that the observed variability reflects random fluctuation linked to movement reproduction without any effect of the motor command. The amplitudes of the obtained CCF peaks were significantly smaller when the initial movement directions were different (0.41 ± 0.04 , in absolute values) versus when they were the same (0.62 ± 0.06), but the CCF values for pairs of movements with different initial directions were nevertheless statistically significant ($p < 0.05$). The sign of the CCF peak depended on the combination of initial directions for the pair of movements. A total of 96 CCFs were between movements having the same initial horizontal direction (UR–DR, UL–DL) within a given workspace (2 movements having the same horizontal initial directions * 4 subjects * 2 series per

subject * 6 muscles). Of these 96 comparisons, 66.3% and 78.1% of the CCFs performed had the same sequence of activation whether they were performed in the frontal or sagittal field, respectively. Only 13.5% and 3.1% had the opposite sequence of activation whereas 20.2% and 18.2% of the CCFs were non-significant for the frontal and sagittal field, respectively. Conversely, for movements initiated in a direction where the horizontal component was different (DL–DR, UL–DR, UR–DL, UL–UR), 61.5% and 69.3% of the 192 CCFs (4 combinations of different horizontal initial directions * 4 subjects * 2 series per subject * 6 muscles) had opposing sequences of activation for the frontal and sagittal workspace, respectively. Only 16.7% and 10.9% had the same sequence of activation whereas 21.8% and 19.8% of the CCF were non-significant for the frontal and sagittal field, respectively.

3.2. Muscle grouping based on the horizontal component

In the preceding analysis we saw that for each muscle only two types of temporal modulation of the command could be observed despite the four different initial directions and the two workspaces. But a new question emerges concerning the multi-muscular tempo-

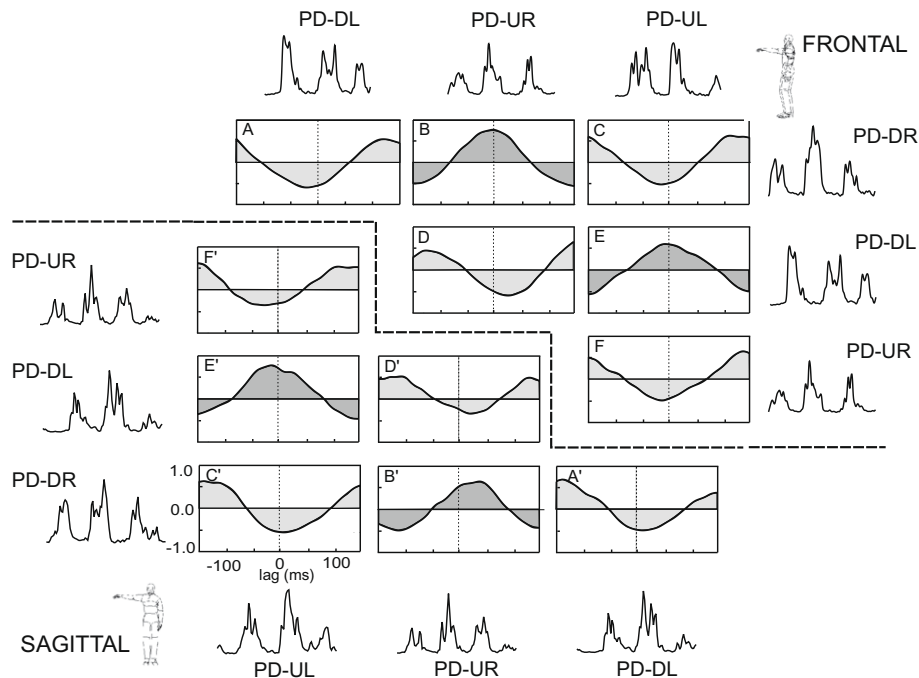


Fig. 4. Temporal modulation of the PD muscle for all different initial directions of movement. The upper-right corner shows the 6 CCF curves obtained from the combination of all the different initial directions in the frontal workspace. For example, graph A represents the CCF for PD activations between figure-eights initiated down and to the left (PD-DL) and down and to the right (PD-DR). The lower-left corner illustrates the same combinations for the sagittal workspace.

ral modulation: Is the temporal activation of the set of 6 muscles recorded here organized in a simple global mode of activation (reciprocal or synergistic) or in a more complex pattern? In order to study the relative timing between the different muscles, we analyzed the relationship between the activations of pairs of different muscles for figure-eight movements initiated in different directions. Extending the analysis to all possible muscle combinations, two groups of muscles emerged. Combinations between AD, PMS and PMI showed in-phase CCF patterns, as do combinations between MD, PD and LD. The cross-correlations between these two groups showed anti-phase CCF patterns. When the movement was initiated with the same horizontal component, intra-group combinations showed significant positive CCF signs (78.8% (frontal workspace) and 87.8% (sagittal workspace)). In contrast, for the same condition 75% and 78% of the CCF signs obtained for inter-group combinations were negative. Conversely, when the initial horizontal components were not conserved 59.2% and 70.6% of the CCF signs were negative for the intra-group and 79% and 80% of the CCF signs were positive for the inter-group combinations, respectively.

3.2.1. Choice of in-phase or anti-phase CCF configuration

The presence of muscle pairs activated only in-phase or anti-phase point to the prevalence of a dual mode of activation: recipro-

cal or synergistic. However, the shoulder muscles have different lines of action and a given muscle can potentially contribute to both horizontal and vertical components of the movement. To better understand what determined the reciprocal or synergistic relationship between two muscles for a given figure, we compared activation patterns and the CCF type for movements performed only along the horizontal or vertical axis and compared these to those observed for the more complex figure-eight movements.

When the arm was rapidly displaced along the horizontal axis (Z) (left–right oscillation) (Fig. 5A), PD and MD were activated synergistically (see positive CCF in Fig. 5C), while PMS was reciprocally activated (Fig. 5B) with respect to these two muscles (see negative CCF in Fig. 5C). In contrast, when the same type of movements were performed along the vertical axis (Y) (up–down oscillation) (Fig. 5D), PMS was synergistically activated with respect to MD and PD (Fig. 5E) (see positive CCF for PD–PMS in Fig. 5F). This in-phase or anti-phase behavior of the muscular sequence that depended on the horizontal or vertical direction of the movement raises the problem of “choice”. When the drawing movement includes both horizontal and vertical components, which pattern will be observed? We showed that in the case of figure-eight movements, PMS was reciprocally activated with respect to the PD and MD muscles (anti-phase CCF) (Fig. 5G) as was the case for left–right oscillations along the horizontal axis.

3.3. Temporal relationship between the reciprocal command and the horizontal and vertical velocity components

To further characterize the reciprocal relationship between muscles, we constructed compound signals by subtracting rectified EMG activities two-by-two for different pairs of muscles. This was made systematically for all possible pairings, without any *a priori* assumption based on anatomy. With this procedure, we obtained EMG profiles for which alternative bursting in positive and negative values reflected a reciprocal command of the two muscles (e.g., the ad–pd signal in the Fig. 6). Conversely, the absence of such

Table 2
CCF and lags for movements with different initial directions.

	Frontal		Sagittal	
	CCF	Lag (ms)	CCF	Lag (ms)
MD	0.39 ± 0.13 (n = 39)	−6.9 ± 37.4	0.38 ± 0.11 (n = 39)	9.2 ± 36.4
PD	0.46 ± 0.15 (n = 44)	1.1 ± 32.9	0.48 ± 0.15 (n = 48)	7.3 ± 21.3
PMS	0.46 ± 0.14 (n = 42)	7.1 ± 24.4	0.44 ± 0.15 (n = 46)	6.1 ± 29.6
PMI	0.40 ± 0.14 (n = 36)	13.9 ± 27.5	0.38 ± 0.14 (n = 39)	−1.3 ± 33.3
AD	0.38 ± 0.12 (n = 30)	−2.7 ± 41.6	0.37 ± 0.12 (n = 32)	7.2 ± 34.1
LD	0.37 ± 0.10 (n = 31)	2.6 ± 33.1	0.33 ± 0.08 (n = 30)	−14.0 ± 34.0

Values are means (expressed in absolute values) ± SD.

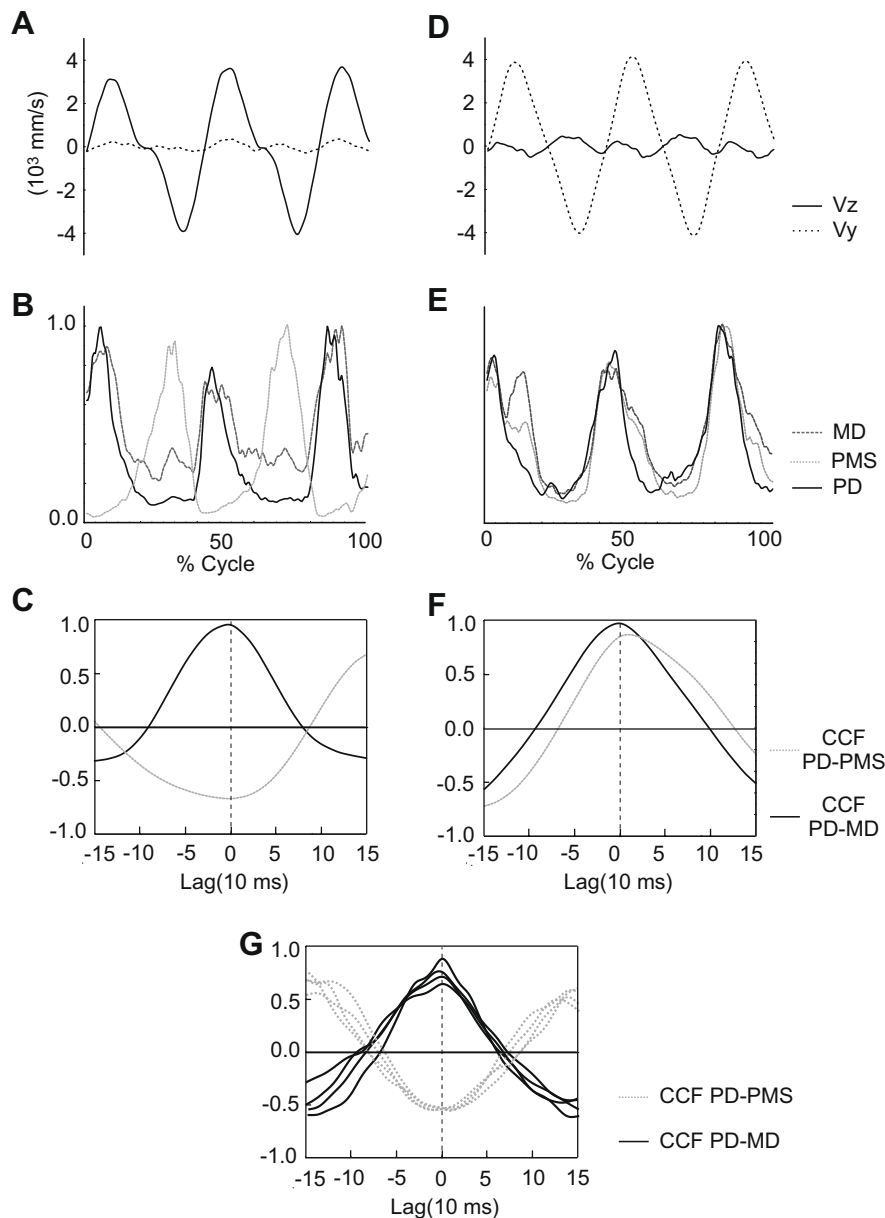


Fig. 5. Modulation of synergistic and antagonistic muscles for unidimensional cyclic movements performed in the frontal plane. Left column corresponds to the data of a cyclic up–down movement and the right column shows the data of a right–left cyclic movement. The traces correspond to the mean curves of three movements. (A) Velocity profile of the finger in the vertical (v_y) and horizontal (v_z) directions, presenting the same number of directional changes as the horizontal velocity component of an up–right figure-eight. (B and E) EMG activities for each of 3 muscles: posterior deltoid (PD), median deltoid (MD), pectoralis major superior (PMS). (C and F) CCF profiles for PD and MD (black solid line), and PD and PMS (grey dotted line). (G) CCF profiles for the same pairs of muscles of the four figure-eights in the frontal plane.

alternating bursts indicates co-activation or the presence of synergist bursts (ad–pms signal in Fig. 6). In order to analyze the temporal relationship between activation of muscle pairs and movement velocity, we calculated the CCF of compound EMG signals for a given pair versus the horizontal and vertical components of the velocity. For the muscle pairs showing reciprocal activation between them, the CCF profiles for the compound signal versus horizontal velocity (e.g., V_z versus ad–pd), were very similar (Fig. 6D, D', D'' and D''') whatever the initial direction of movement, whereas the CCF between compound signals (ad–pms) of co-active muscle pairs against horizontal velocity showed different profiles even when the CCF peaks were significant (Fig. 6C, C', C'' and C'''). CCF profiles of muscle pairs (both reciprocal and co-activated) against vertical velocity (V_y) were different for the different initial directions (6B, B', B'' and B''' and 6A, A', A'' and A''').

Fig. 7 summarizes for all subjects, these CCF analyses performed for all compound muscles versus the vertical (below the diagonal) and horizontal (above the diagonal) velocity, for the sagittal workspace. Each graph presents the superposition of 4 curves, each corresponding to the mean CCF ($n = 8$; 2 movements * 4 subjects) for a given initial direction. For example, graph A (Fig. 7) shows the CCF between the horizontal velocity component and the compound EMG signal obtained from the subtraction of the PMS activity (column label) from the AD activity (row label).

We quantified the reproducibility of the CCF curves throughout the movements by a similarity index. In each of these graphs the background is filled with color tiles, one for each subject and movement performed. Each tile reflects the value of the similarity index for a given trial; the higher the similarity index, the redder the color. Tiles were sorted in an increasing order, from left to right

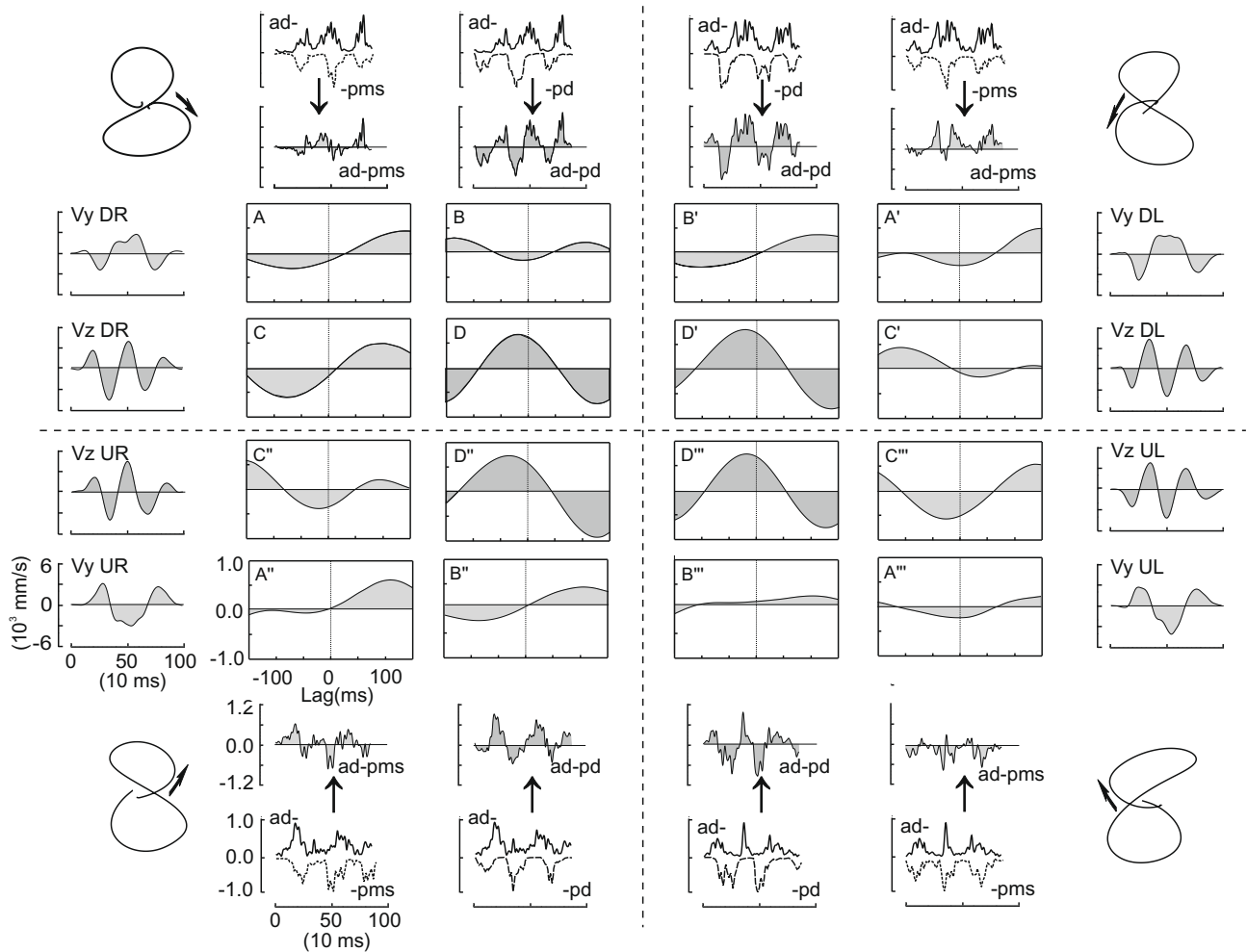


Fig. 6. Temporal invariance of the reciprocal command with respect to the horizontal component of the finger velocity. In each quadrant, a grid of 4 CCF patterns is illustrated. For instance, in the upper left quadrant the two composite signals ad-pms and ad-pd are distributed along the columns of the 2 × 2 grid with the two velocity components are presented in each of the two rows. In this case, Panel A shows the CCF between ad-pms and Vy for the initial movement downward and to the right. (B: ad-pd versus Vy; C: ad-pms versus Vz; D: ad-pd versus Vz). A similar presentation in each quadrant corresponds to the initial movement direction indicated by the arrow in the corresponding figure-eight graph.

and bottom to top, across all trials. The color of the background therefore gives a global view of the reproducibility between trials.

It is evident that green dominates the graphs of the bottom part of Fig. 7, indicating weak reproducibility of the correlation between the vertical velocity profile and each of the 15 compound muscle activities. We observe this result for both planes of action. Few pairs of muscles showed a constant temporal relationship with the vertical component of the velocity across the 4 different initial directions. This is the case of the pairs formed by MD-PD (graph M'), AD-PMI (graph B'). Their mean CCF peak values were significant (0.45 ± 0.05) with a lag of 110 ± 10 ms. For the other combinations summarized in the bottom part of Fig. 7 one can observe large variations in mean CCF profiles (and low similarity indices).

In contrast, the backgrounds of the top part of Fig. 7 are predominantly red, indicating the greater similitude between the compound EMG signals and the horizontal velocity component. In fact, the muscle pairs receiving a reciprocal command (AD-MD, AD-PD, AD-LD, PMS-MD, PMS-PD, PMS-LD, PMI-MD, PMI-PD and PMI-LD) showed an invariant relationship with the horizontal component of the velocity (color close to red in the graphs C, D, E, G, H, I, J, K, and L); whereas, the muscles pairs receiving a synergistic command (AD-PMS, AD-PMI, PMS-PMI, MD-PD and MD-LD) showed smaller indices of similarity (predominant green color in the graphs A, B, F, M, and N). Even if the muscles pairs

formed with the LD (DA-LD, PMS-LD and PMI-LD) showed similarity indices lower than the pairs formed with AD, PMS, PMI and MD, PD; their invariability was greater than the muscles receiving a synergistic command (AD, PMS and PMI, and DM, DP, LD) (Table 3). This was true for all muscle compounds, except for AD-LD and PD-LD, which showed similar SIs in the frontal plane. Globally, the temporal relation between the compound EMG, showing a reciprocal activation, and the horizontal velocity presented similarity indices that were bigger, in a highly significant way, than the same compound EMG with respect to the vertical component of the velocity (0.4 ± 0.21 versus 0.06 ± 0.09 for the frontal workspace, and 0.46 ± 0.18 versus 0.06 ± 0.09 for the sagittal workspace), and than a synergistic compound EMG versus either velocity component (0.08 ± 0.13 and 0.07 ± 0.11 for the horizontal velocity component and 0.11 ± 0.11 and 0.10 ± 0.10 for the vertical velocity component, for the frontal and the sagittal workspaces, respectively) ($F(3,1436) = 455,44$; $p < 0.0001$) for the frontal plane and $F(3,1436) = 856,03$; $p < 0.0001$ for the sagittal plane).

4. Discussion

Three main findings emerge from the present results: (1) the temporal activation of the muscular command for a figure-eight

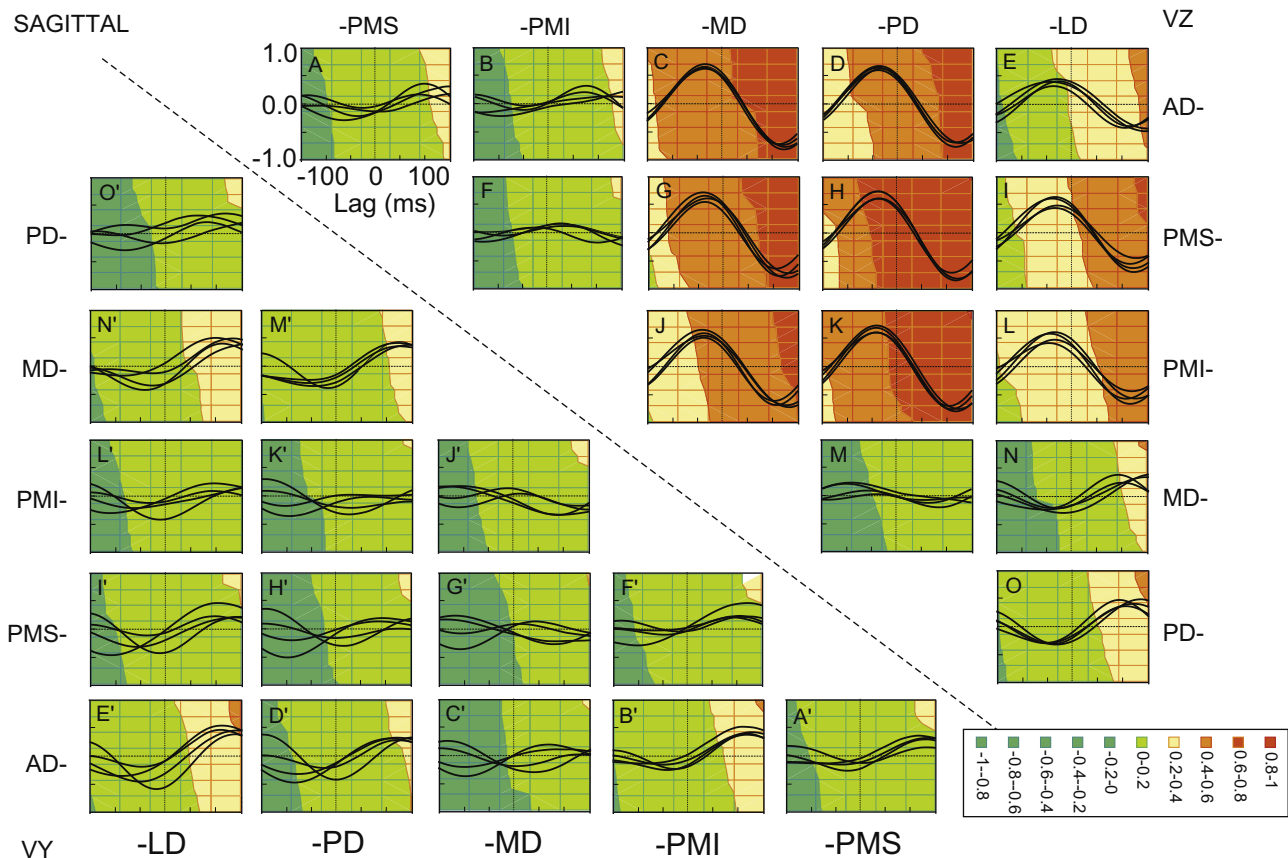


Fig. 7. Mean CCF and similarity index for composite EMG signals and the vertical and horizontal component of the velocity for the sagittal workspace. Each panel indicates the CCF function for a single composite EMG signal (row muscle–column muscle) versus the corresponding velocity component. Graphs above the diagonal (top-right corner of the figure) correspond to the CCF between the EMG compound signals and the horizontal component of the velocity. Graphs below the diagonal (lower-left corner) correspond to the CCF between the EMG compound signals and the vertical component of the velocity. The 4 CCF curves in each graph correspond to the CCF mean (4 subjects * 2 movements) for each initial movement direction. Colors in the background correspond to the similarity index between composite EMG signals for pairs of movements with different initial directions (6 direction combinations (up-left versus up-right, up-left versus down-right, etc.) * 4 subjects * 2 movements = 48 samples organized in a 8 × 6 grid, sorted for increasing similarity value from left to right and from bottom to top.

depended on the rotational sense of the global figure. (2) Two sets of synergistic muscles acting in a reciprocal mode was at the basis of this complex movement. (3) These reciprocal commands were highly correlated with the spatial component of the velocity presenting the highest frequency and these correlations remained invariant whatever the initial direction of the movement. These findings show the existence of at least two simplifying processes

Table 3

Similarity indices for the compound EMG and the horizontal component of the velocity.

	Frontal IS (mean ± SD)	Sagittal IS (mean ± SD)
AD–PMS	0.09 ± 0.12	0.08 ± 0.12
AD–PMI	0.04 ± 0.08	0.07 ± 0.10
PMS–PMI	0.05 ± 0.06	0.03 ± 0.06
MD–PD	0.06 ± 0.18	0.02 ± 0.04
MD–LD	0.07 ± 0.09	0.09 ± 0.12
PD–LD	0.19 ± 0.15	0.16 ± 0.14
AD–MD	0.41 ± 0.19	0.54 ± 0.11
AD–PD	0.41 ± 0.15	0.49 ± 0.14
AD–LD	0.18 ± 0.17	0.20 ± 0.15
PMS–MD	0.47 ± 0.19	0.51 ± 0.15
PMS–PD	0.59 ± 0.17	0.61 ± 0.15
PMS–LD	0.33 ± 0.17	0.36 ± 0.17
PMI–MD	0.36 ± 0.19	0.45 ± 0.14
PMI–PD	0.54 ± 0.16	0.59 ± 0.11
PMI–LD	0.28 ± 0.17	0.35 ± 0.12

in the CNS for rapid drawing movements of complex shapes. One simplification is that the central command is not made muscle by muscle, but rather through a neural network organized into agonistic and antagonistic muscles groups. The other simplification arises at a higher level of the trajectory planning where the behavioral synergies and the temporal commands seem to be programmed depending on the global aspects of the figure-eight. In the following we develop further the reasoning behind each of these assertions and the resulting conclusions.

4.1. Global versus local tuning of muscle activations

In humans, the temporal aspects of muscle activations depend on both muscle mechanical action (intrinsic constraints) and movement direction in space (extrinsic parameters) (Buneo et al., 1997; Hogan, 1985; Flanders et al., 1994, 1996). In this context, one would expect to find a complex modulation of the muscular activation sequences depending on the shoulder position and/or the initial direction of the figure-eight movement. Yet, despite the changes in the movement direction induced by our protocol the CCF analyses revealed only two types of activation patterns for the full set of 6 muscles and these two types of activation sequences were in anti-phase. The CCF revealed that movements initiated with the same horizontal component, despite having opposing vertical components, presented the same sequence of activation for each muscle. By contrast, movements that were ini-

tiated with opposing horizontal components but having the same vertical components were activated in anti-phase. Furthermore, this limited set of temporal sequences was the same for each muscle in both shoulder positions despite the modification in their mechanical actions.

It could be criticized that our results emerges from the global nature of the CCF analysis itself; i.e., that we have prioritized the global modulation of the EMG signal rather than the detailed modulation of each burst. In fact, the CCF method is relatively insensitive to the modulation in the amplitude of each burst, but amplitude modulation is, of course, critical as well. For instance, Hoffman and Strick (1999) demonstrated that the direction of wrist movements in a step-tracking task was mainly determined by modulating the amplitude, rather than the phase, of fixed muscle bursts. Even in our experiment, it is inherently obvious that only two activation patterns could not produce a total of 8 different movements. Something must have changed to create these different movements, and if it was not the temporal pattern then it must be the amplitude. Indeed, identification of the EMG patterns measured here using a dynamic recurrent neural network (DRNN), which can take into account both timing and amplitude, was able to differentiate between different movement directions and different areas of the workspace (Bengoetxea et al., 2005). Nevertheless, given the variety of preferred directions for the muscles used in this task (Cheron et al., 1996; Herrmann and Flanders, 1998; Flanders et al., 1994) one would expect to see a more nuanced set of CCF outcomes when drawing a figure-eight, considering the fact that the figure-eight requires movement in all possible directions within the plane. For example, muscles like MD that have a vertical preferred direction, or even AD and PMI, that have oblique preferred directions, showed a modulation of the temporal sequence of activation according to the horizontal component of the hand velocity. Why were the vertically-acting muscles not more correlated with the vertical velocity component? Why were phase relationships other than in-phase (0°) or out-of-phase (180°) not detected? The temporal pattern of activations does not seem to be strictly determined by the extrinsic parameters (3D direction) of the movement.

The CCF analysis also failed to capture differences in intrinsic constraints such as the changes in the mechanical action of muscles in the two different workspaces. This lack of dependence on workspace could be explained by the fact that the chosen shoulder positions, flexed at 90° or abducted at 90° , did not modify the moment arms of muscles in a substantial way. Indeed, Buneo et al. (1997) showed that it is the vertical position of the humerus that primarily influences the biomechanical action of the muscle AD. In our paradigm, the change of the shoulder position was made in the horizontal plane, which would explain why we did not see a change in temporal activation according to the change of the shoulder position. Nevertheless, the same dynamic recurrent neuronal network mentioned above, when trained with figure-eight movements from one workspace, was able to reproduce the kinematics of movements from the EMG patterns only for movements performed in the same workspace; it was unable to correctly reproduce movement trajectories in the other workspace (Bengoetxea et al., 2005). Even if the shoulder positions of our protocol did not change the mechanical action of muscles in a significant way, the DRNN identified a difference between the multi-muscular commands corresponding to each workspace. It is interesting to note that when applied to EMG patterns from the 'other' workspace, the DRNN reproduced the horizontal, but not the vertical, component of the finger velocity.

The fact that the muscular activation sequence was not modulated specifically according to the preferred direction of activation of each muscle suggests that the modulation is instead in relation with a feature inherent to the figure-eight as a whole, rather than

to local components such as the instantaneous velocity or acceleration. This global feature may be revealed by considering how the figure-eight is composed. Even if the figure-eight is made with 4 different initial directions and with 8 different joint initial directions, it has only 2 directions of global rotation: Whenever the horizontal component of the initial direction is conserved, the sense of rotation of the figure-eight is the same. For instance, if the figure-eight is initiated towards the right, whether it be upward and to the right or downward and to the right, will have an upper loop that turns counter-clockwise and a lower loop that turns clockwise. The only difference between these two cases is whether the upper or lower loop is drawn first. On the other hand, when the vertical component of the initial direction is conserved between two drawings (i.e., upward to the right versus upward to the left) or when the figure-eights are initiated in diametrically opposed directions (upward to the right versus downward to the left), then the sense of rotation of the two figures is opposed. The temporal patterns appear to reflect the global characteristics of the figure-eight itself, rather than being tied to either intrinsic (muscle actions) or extrinsic (movement direction) parameters. The CNS may exploit this characteristic of the figure-eight (and other Lissajous-type figures) to simplify motor planning.

4.2. Muscle grouping acting in rhythmic and reciprocal mode

Our CCF analysis also revealed that muscle temporal coordination for drawing a figure-eight is organized into ensembles of muscles acting in a synergistic (in-phase) or a reciprocal (anti-phase) mode. This result is yet another demonstration that despite the large degree of redundancy and the numerous muscle combinations that are available for performing a given spatial, only a few possibilities are actually performed (Bernstein, 1967; Morasso, 1981; Kelso et al., 1979; Atkenson and Hollerbach, 1985; d'Avella et al., 2006). This question of synergies and reduced degrees-of-freedom has been extensively studied for fast-reaching movements of the arm with different end-points (d'Avella et al., 2006). The figure-eight that we have studied here differs fundamentally from simple reaching. In fact, if reaching can be considered as a discrete movement, a figure-eight can be considered as a combination of both rhythmic and discrete movements (Hogan and Sternad, 2007; see below). Further analysis of how the degrees-of-freedom are reduced when drawing a figure-eight is therefore warranted, given the neurophysiological evidence and theoretical basis supporting the idea that rhythmic and discrete arm movements rely on different control processes (Schaal et al., 2004; Miall and Ivry, 2004; Zelaznik et al., 2005).

To illustrate the contrast between performing a discrete reaching movement and drawing a figure-eight, consider the following observations: A figure-eight movement, like reaching, can be considered to be discrete in the sense that the movement lasts a finite duration with the hand starting and ending at zero velocity. The figure-eight differed, however, from discrete point-to-point movements by the presence of multiple peaks in the endpoint velocity profile (Richardson and Flash, 2002). Nevertheless, one could consider a figure-eight to be composed of a series of superimposed discrete segments, thus allowing for a common control structure for these two classes of movement. But kinematic segmentation doesn't imply a segmented control of the movement (Sternad and Schaal, 1999). Indeed, the figure-eight can be just as easily described as the result of two coupled oscillators acting in perpendicular directions over a finite number of cycles (two horizontal cycles and one vertical cycle, to be exact). That fact, plus the observation that the act of drawing figures is associated with emergent timing properties involving different parts of the SNC (Ivry et al., 2002), argue for different control schemes for discrete movements versus figure-eights. In this context our temporal EMG analysis showing a

rhythmic EMG activation pattern suggests that pattern-generator circuits may be involved in the control of figure-eight drawing movements. This concept of a central pattern generator (CPG) proposed for human locomotion (Dimitrijevic et al., 1998; Dietz, 2002) has been enlarged to the upper limb (Zehr et al., 2004).

Why did the muscle grouping for this complex movement correspond to the directional grouping of a cyclic right–left movement and not that of an up–down movement? In a previous work (Cheron et al., 1999), we showed that the temporal aspect of the horizontal velocity component presents the same features as the tangential velocity and is invariant whatever the initial direction of the vertical figure-eight movement. If we consider that each phase of the tangential velocity corresponds to a change in the direction of the hand, one can see that the temporal sequences of the horizontal velocity component correspond to directional changes in the up–right figure-eight. We therefore propose a more general hypothesis that the groupings of muscles for figure drawing are determined by the component of the movement with the highest frequency of directional changes (Buchanan et al., 1996).¹

If this grouping we found for a vertical figure-eight corresponds to a right–left cyclic movement, the question remains as to what level is this grouping and its timing of activation defined? Neurophysiologic evidence exists for the grouping of muscles into functional working groups at both cortical (Jackson et al., 2003; Fetz et al., 1989, 2002) and subcortical levels (Bizzi et al., 2000; Mussa-Ivaldi et al., 1994; Engberg and Lundberg, 1969; Jankowska et al., 1965). In the performance of the figure-eight movement, the grouping of muscles into agonists and antagonists could occur at any one of these levels. But the selection of agonist and antagonist groupings appears to be a supraspinal process, because each muscle has more than one preferred direction (Desmedt and Godaux, 1977; Herrmann and Flanders, 1998) and the action of the two muscular groups that emerged depended on one of the two components of oscillations of the figure-eight movement.

The role of higher neural structures is supported by the studies of Schwartz and Moran (1999) in which monkeys drew lemniscates and spirals. They clearly demonstrated that the timing of cortical activity was well related to hand velocity profiles, EMG patterns and movement segmentation. Neural population and movement vectors displayed the same number of action sequences (5 components) as in the present EMG study (3 agonistic bursts interspersed with 2 antagonistic bursts). These experimental results support the hypothesis that the timing of muscle activation is generated by the central neural structures (Averbeck et al., 2003; Carpenter et al., 1999; Schwartz, 2007). Concerning reciprocal activation, the activity of a subset of neurons are correlated in cortical maps, with activation of one group of muscles linked to a simultaneous decrease in the activity of the opposing set of muscles (Cheney et al., 1985; Jackson et al., 2003, 2007; Capaday, 2004). This functional grouping could be viewed as resulting from a motor binding process (Sanes and Truccolo, 2003) such as that inferred from the neural synchrony of M1 cells (Jackson et al., 2003; Hatsopoulos et al., 2003, 2007; Rubino et al., 2006) forming functional assemblies more often when a pre-programmed (bound) movement is realized (Hatsopoulos et al., 2003, 2007). These neurophysiological data suggest that primary motor cortex and the adjacent premotor cortex may be the level where the grouping is made, depending on the movement trajectory.

¹ The principle of grouping based on the highest frequency of directional changes would explain why for an up–right figure-eight PMS and PD act as they did for a right–left cyclic movement and not to an up–down movement. Since the directional changes in a figure-eight drawn on its side follow the temporal sequence of the vertical velocity component, the PMS–PD grouping corresponding to an up–down movement is to be expected. Currently our experiments focus on verifying this hypothesis.

In conclusion, our study shows that the drawing of regular figures such as a figure-eight present muscular temporal synergies specifically organized according to the rhythm of the end-effector trajectory. This result supports the idea that arm gestures that combine features of both rhythmic and discrete movements differ in the control processes as compared to more simple discrete motions such as reaching to a target. The CNS takes advantage of the rhythmicity by partitioning the muscles into sets of synergistic muscles acting in a reciprocal mode, assigning muscles to one group of another depending on the anticipated number of direction changes in the overall movement.

Acknowledgements

This work was funded by the Belgian Federal Science Policy Office, the European Space Agency (AO-2004, 118), the Belgian National Fund for Scientific Research (F.N.R.S.), the Research Fund of the University of Brussels (U.L.B.) and the FEDER Fund (BioFact project). The authors thank T. Pozzo and specially J. McIntyre for fruitful comments about the manuscript and his help with the redaction. We thank M. Dufief, E. Hortmanns and T. d'Angelo for expert technical assistance and C. de Scoville for secretarial assistance.

References

- Accornero N, Berardelli A, Argenta M, Manfredi M. Two joints ballistic arm movements. *Neurosci Lett* 1984;46(1):91–5.
- Atkenson CG, Hollerbach JM. Kinematic features of unrestrained vertical arm movements. *J Neurosci* 1985;5:2318–30.
- Averbeck BB, Chafee MV, Crowe DA, Georgopoulos AP. Parallel processing of serial movements in prefrontal cortex. *Proc Natl Acad Sci USA* 2002;99:13172–7.
- Averbeck BB, Crowe DA, Chafee MV, Georgopoulos AP. Neural activity in prefrontal cortex during copying geometrical shapes. II. Decoding shape segments from neural ensembles. *Exp Brain Res* 2003;150:142–53.
- Bengoetxea A, Leurs F, Cebolla AM, Wellens S, Draye JP, Cheron G. A dynamic recurrent neural network for drawing multi-directional trajectories. *Comput Methods Biomech Biomed Eng* 2005;8:29–30.
- Bernstein N. *The coordination and regulation of movements*. London: Pergamon; 1967.
- Bizzi E, Tresch MC, Saltiel P, d'Avella A. New perspectives on spinal motor systems. *Nat Rev Neurosci* 2000;1:101–8.
- Buchanan JJ, Kelso JA, Fuchs A. Coordination dynamics of trajectory formation. *Biol Cybern* 1996;74:41–54.
- Buneo CA, Soechting JF, Flanders M. Postural dependence of muscle actions: implications for neural control. *J Neurosci* 1997;17:2128–42.
- Capaday C. The integrated nature of motor cortical function. *Neuroscientist* 2004;10(3):207–20.
- Carpenter AF, Georgopoulos AP, Pellizzer G. Motor cortical encoding of serial order in a context-recall task. *Science* 1999;283:1752–7.
- Cheney PD, Fetz EE, Palmer SS. Patterns of facilitation and suppression of antagonist forelimb muscles from motor cortex sites in the awake monkey. *J Neurophysiol* 1985;53:805–20.
- Cheron G, Draye JP, Bourgeois M, Libert G. A dynamic neural network identification of electromyography and arm trajectory relationship during complex movements. *IEEE Trans Biomed Eng* 1996;43:552–8.
- Cheron G, Draye JP, Bengoetxea A, Dan B. Kinematics invariance in multi-directional complex movements in free space: effect of changing initial direction. *Clin Neurophysiol* 1999;110:757–64.
- d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci* 2003;6:300–8.
- d'Avella A, Portone A, Fernandez L, Lacquaniti F. Control of fast-reaching movements by muscle synergy combinations. *J Neurosci* 2006;26(30):7791–810.
- Desmedt JE, Godaux E. Fast motor units are not preferentially activated in rapid voluntary contractions in man. *Nature* 1977;267:717–9.
- Dietz V. Do human bipeds use quadrupedal coordination? *Trends Neurosci* 2002;25(9):462–7.
- Dimitrijevic MR, Gerasimenko Y, Pinter MM. Evidence for a spinal central pattern generator in humans. *Ann N Y Acad Sci* 1998;860:360–76.
- Engberg I, Lundberg A. An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiol Scand* 1969;75:614–30.
- Evarts EV. Relation of pyramidal tract activity to force exerted during voluntary movement. *J Neurophysiol* 1968;31:14–27.
- Ferrigno G, Pedotti A. ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing. *IEEE Trans Biomed Eng* 1985;32:943–50.

- Fetz EE, Cheney PD, Mewes K, Palmer S. Control of forelimb muscle activity by populations of corticomotoneuronal and rubromotoneuronal cells. *Prog Brain Res* 1989;80:437–49 [discussion 427–430].
- Fetz EE, Perlmutter SI, Prut Y, Seki K, Votaw S. Roles of primate spinal interneurons in preparation and execution of voluntary hand movement. *Brain Res Brain Res Rev* 2002;40:53–65.
- Flanders M, Soechting JF. Kinematics of typing: parallel control of the two hands. *J Neurophysiol* 1992;67:1264–74.
- Flanders M. Temporal patterns of muscle activation for arm movements in three-dimensional space. *J Neurosci* 1991;11:2680–93.
- Flanders M, Pellegrini JJ, Soechting JF. Spatial/temporal characteristics of a motor pattern for reaching. *J Neurophysiol* 1994;71:811–3.
- Flanders M, Pellegrini JJ, Geisler SD. Basic features of phasic activation for reaching in vertical planes. *Exp Brain Res* 1996;110:67–79.
- Fu QG, Suarez JJ, Ebner TJ. Neuronal specification of direction and distance during reaching movements in the superior precentral premotor area and primary motor cortex of monkeys. *J Neurophysiol* 1993;70:2097–116.
- Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J Neurosci* 1982;2:1527–37.
- Georgopoulos AP, Schwartz AB, Kettner RE. Neuronal population coding of movement direction. *Science* 1986;233:1416–9.
- Georgopoulos AP. News in motor cortical physiology. *News Physiol Sci* 1999;14:64–8.
- Hatsopoulos NG, Paninski L, Donoghue JP. Sequential movement representations based on correlated neuronal activity. *Exp Brain Res* 2003;149(4):478–86.
- Hatsopoulos NG, Xu Q, Amit Y. Encoding of movement fragments in the motor cortex. *J Neurosci* 2007;27(19):2114–5105.
- Herrmann U, Flanders M. Directional tuning of single motor units. *J Neurosci* 1998;18:8402–16.
- Hof AL, Van den Berg J. EMG to force processing I: an electrical analogue of the Hill muscle model. *J Biomech* 1981;14:747–58.
- Hoffman DS, Strick PL. Step-tracking movements of the wrist. IV. Muscle activity associated with movements in different directions. *J Neurophysiol* 1999;81:319–33.
- Hogan N. The mechanics of multi-joint posture and movement control. *Biol Cybern* 1985;52:315–31.
- Hogan N, Sternad D. On rhythmic and discrete movements: reflections, definitions and implications for motor control. *Exp Brain Res* 2007;181(1):13–30.
- Ivry RB, Spencer RM, Zelaznik HN, Diedrichsen J. The cerebellum and event timing. *Ann N Y Acad Sci* 2002;978:302–17.
- Jackson A, Gee VJ, Baker SN, Lemon RG. Synchrony between neurons with similar muscle fields in monkey motor cortex. *Neuron* 2003;38:115–25.
- Jackson A, Mavoori J, Fetz EE. Correlations between the same motor cortex cells and arm muscles during a trained task, free behavior, and natural sleep in the macaque monkey. *J Neurophysiol* 2007;97(1):360–74.
- Jankowska E, Jukes MG, Lund S, Lundberg A. Reciprocal innervation through interneuronal inhibition. *Nature* 1965;206:198–9.
- Kakei S, Hoffman DS, Strick PL. Muscle and movement representations in the primary motor cortex. *Science* 1999;285:2136–9.
- Kalaska JF, Crammond DJ. Cerebral cortical mechanisms of reaching movements. *Science* 1992;20:1517–23.
- Kalaska JF, Scott SH, Cisek P, Sergio LE. Cortical control of reaching movements. *Curr Opin Neurobiol* 1997;7:849–59.
- Kelso JA, Southard DL, Goodman D. On the nature of human interlimb coordination. *Science* 1979;203:1029–31.
- Lacquaniti F. Central representations of human limb movement as revealed by studies of drawing and handwriting. *Trends Neurosci* 1989;12(8):287–91.
- Lacquaniti F, Terzuolo C, Viviani P. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychol (Amst)* 1983;54(1–3):115–30.
- Lashley KS. In: Jeffress LA, editor. *Cerebral mechanisms in behavior*. New York: Wiley; 1951.
- McIntyre J, Stratta F, Droulez J, Lacquaniti F. Analysis of pointing errors reveals properties of data representations and coordinate transformations within the central nervous system. *Neural Comput* 2000;12:2823–55.
- McKiernan BJ, Marcario JK, Karrer JH, Cheney PD. Correlations between corticomotoneuronal (CM) cell postspike effects and cell-target muscle covariation. *J Neurophysiol* 2000;83:99–115.
- Miall RC, Ivry R. Moving to a different beat. *Nat Neurosci* 2004;7(10):1025–6.
- Moran DW, Schwartz AB. Motor cortical activity during drawing movements: population representation during spiral tracing. *J Neurophysiol* 1999;82:2693–704.
- Morasso P. Spatial control of arm movements. *Exp Brain Res* 1981;42:223–7.
- Mussa-Ivaldi FA, Gister SF, Bizzi E. Linear combinations of primitives in vertebrate motor control. *Proc Natl Acad Sci USA* 1994;91:7534–8.
- Plamondon R. A kinematic theory of rapid human movements. Part I. Movement representation and generation. *Biol Cybern* 1995a;72(4):295–307.
- Plamondon R. A kinematic theory of rapid human movements. Part II. Movement time and control. *Biol Cybern* 1995b;72(4):309–20.
- Poppele R, Bosco G. Sophisticated spinal contributions to motor control. *Trends Neurosci* 2003;26:269–76.
- Richardson MJ, Flash T. Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis. *J Neurosci* 2002;22(18):8201–11.
- Rubino D, Robbins KA, Hatsopoulos NG. Propagating waves mediate information transfer in the motor cortex. *Nat Neurosci* 2006;9(12):1549–57.
- Saltiel P, Tresch MC, Bizzi E. Spinal cord modular organization and rhythm generation: an NMDA iontophoretic study in the frog. *J Neurophysiol* 1998;80:2323–39.
- Sanes JN, Truccolo W. Motor “binding:” do functional assemblies in primary motor cortex have a role? *Neuron* 2003;38(1):3–5.
- Schaal S, Sternad D, Osu R, Kawato M. Rhythmic arm movement is not discrete. *Nat Neurosci* 2004; 7(10): 1136–43. Erratum in: *Nat Neurosci* 2004; 7(11):1279.
- Schwartz AB, Moran DW. Motor cortical activity during drawing movements: population representation during lemniscate tracing. *J Neurophysiol* 1999;82:2705–18.
- Schwartz AB. Motor cortical activity during drawing movements: single-unit activity during sinusoid tracing. *J Neurophysiol* 1992;68:528–41.
- Schwartz AB. Useful signals from motor cortex. *J Physiol* 2007;579(Pt. 3):581–601.
- Soechting JF, Lacquaniti F, Terzuolo CA. Coordination of arm movements in three-dimensional space. Sensorimotor mapping during drawing movement. *Neuroscience* 1986;17:295–311.
- Sternad D, Schaal S. Segmentation of endpoint trajectories does not imply segmented control. *Exp Brain Res* 1999;124(1):118–36.
- Tresch MC, Saltiel P, Bizzi E. The construction of movement by the spinal cord. *Nat Neurosci* 1999;2:162–7.
- Tresch MC, Saltiel P, d’Avella A, Bizzi E. Coordination and localization in spinal motor systems. *Brain Res Brain Res Rev* 2002;40:66–79.
- Viviani P, Flash T. Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *J Exp Psychol Hum Percept Perform* 1995;21:32–53.
- Viviani P, McCollum G. The relation between linear extent and velocity in drawing movements. *Neuroscience* 1983;10:211–8.
- Viviani P, Cenzato M. Segmentation and coupling in complex movements. *J Exp Psychol Hum Percept Perform* 1985;11(6):828–45.
- Viviani P, Terzuolo C. Trajectory determines movement dynamics. *Neuroscience* 1982;7(2):431–7.
- Weiss EJ, Flanders M. Muscular and postural synergies of the human hand. *J Neurophysiol* 2004;92(1):523–35.
- Wu W, Hatsopoulos N. Evidence against a single coordinate system representation in the motor cortex. *Exp Brain Res* 2006;175(2):197–210.
- Zehr EP, Carroll TJ, Chua R, Collins DF, Frigon A, Haridas C, Hundza SR, Thompson AK. Possible contributions of CPG activity to the control of rhythmic human arm movement. *Can J Physiol Pharmacol* 2004;82(8–9):556–68.
- Zelaznik HN, Spencer RM, Ivry RB, Baria A, Bloom M, Dolansky L, Justice S, Patterson K, Whetter E. Timing variability in circle drawing and tapping: probing the relationship between event and emergent timing. *J Mot Behav* 2005;37(5):395–403.