

Theoretical Analysis of the Force and Position Synergies in Two-Joint Movements

A. I. Kostyukov^{1,2}

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A theoretical approach is proposed to define the *force* and *position singular points* (FSPs and PSPs) in the circular, ellipsoidal, and linear planar two-joint movements produced under steady loadings directed along the movement traces. The FSPs coincide with changes in the direction of the force moments acting around the joints; the PSPs show the locations of the extrema at the joint angle trajectories. The *force synergy* (defined by the location of FSPs) provides a strong influence on the *activation synergy*; the latter is largely described by correlations between the activities recorded from the muscles participating in the movement. The *position synergy* (defined by the location of PSPs) is responsible for a hysteresis-related modulation of the *activation synergy*. Geometrical procedures are proposed to define positions of the FSPs and PSPs along various movement traces; this can provide a general description of the *force* and *position synergies* for the movements. The *force synergies* in the circular movements cover four sectors with diverse loading combinations of the flexor and extensor muscles belonging to different joints. The variability of the synergy effects for changes in the size and position of the circular trajectories is analyzed; the synergy patterns are also considered for ellipsoidal and linear movement traces. A *Force Feedback Control Hypothesis* is proposed; it allows one to explain the decrease in the number of controlled variables during real multi-joint movements.

Keywords: motor control, two-joint movements, muscle synergy, central commands, electromyogram.

INTRODUCTION

Three interdependent types of muscle synergies are usually considered when describing human movements. Both anatomical and neural factors are combined in coordinated joint movements, thus participating in various forms of the *kinematic synergy* that is displayed in simultaneous covariations during independent changes in the joint angles [1] and in various tasks of manual exploration [2]. The *kinetic synergy*, described usually by covariation of the forces (torques), has also been observed during grasping movements [1], in forced interaction of various fingers [3, 4], or during handwriting [5]. The *muscle synergy*, based on spatial and temporal coordination of multiple muscle activities, has been observed during static hand efforts [6] or in active force interactions of muscles of the digits [7, 8].

The anatomy of the human limbs usually does not allow experimenters to control all essential parameters defining the synergy effects; at least partly, this is related to practical impossibility of EMG recording from deeply located muscles. As a result, not all fundamental synergies can be identified experimentally in multi-joint movements of the limbs. In previous experimental studies carried out by of our group [9-11], we proposed an approach allowing one to analyze quantitatively the simplest form of the synergy effects in circular movements of the subject's right arm. The obtained results were used to find the functional relationships between basic mechanical parameters of two-joint movements and the related central commands. In order to determine inter-joint muscle interactions for these movements, we proposed a simplified classification of the synergy effects [11]; the same classification is used in the present study. In accordance with definitions accepted in the above study, we will further use the terms of *position*, *force*, and *activation synergies*, which are based on temporal changes in the following parameters, correspondingly: (i) joint angles, (ii) force moments at the joints, and (iii) activities of the muscles

¹ University of Physical Education and Sport, Gdansk, Poland.

² Department of Movement Physiology, Bogomolets Institute of Physiology, National Academy of Sciences, Kyiv, Ukraine.
Correspondence should be addressed to A. I. Kostyukov (e-mail: kostyuko@biph.kiev.ua).

participating in a given movement. The terms *force and position singular points*, FSPs and PSPs, respectively, have also been introduced.

As was shown in [11], waveforms of the averaged EMG activities of the elbow and shoulder muscles are closely related to the correspondent sectors of the movement trajectories between neighboring FSPs, in which the force moments acting around the correspondent joints change their directions. Waves of the activity of flexors and extensors in these sectors are alternated the activation patterns are reversed with changes in the loading direction. On the other hand, the EMG intensities are also dependent on the movement direction; such hysteresis-related effects are defined by sets of the PSPs (i.e., positions of the extrema at the joint angle traces).

The locations of the FSPs and PSPs were defined in [11] by computation of the time courses of the force moments and joint angles. At present, graphical methods begin to be widely used for the analysis of the synergy effects (see, e.g., [12]). In this study, we propose a graphical method for a theoretical definition of the *force and position synergies* for planar two-joint arm movements. In accordance with the methods described in [11], the axis of the proximal joint in our model is assumed to be in a fixed position, while the distal end of the other limb segment moves with a small constant velocity along the circular trajectory; the movements are produced under the action of constant loadings directed tangentially with respect to the trajectory. Afterwards, we extrapolated this consideration on the

ellipsoidal and linear movement traces.

Hypothesis. Central commands to the muscles in two-joint movements and the related synergy effects are largely dependent on the relative positions of the FSPs belonging to different joints; muscle hysteresis participates in modulation of the commands in accordance with the location of the PSPs. An assumption has been put forward that, in order to decrease the number of the controlled variables in multi-joint movements, the CNS may use the force feedback channels from the antagonist muscles of different joints (a *Force Feedback Control Hypothesis*).

RESULTS

Curvilinear System of Coordinates. The present model is based on the two-joint planar upper limb movements produced under conditions of the fixed positions of the trunk and shoulder joint (see Methods in [11]). Naturally, the proposed consideration may be applied to the movements of the lower limbs, which are realized, in particular, during a bicycle ride. The test movements, according to natural positioning patterns of the limb segments, can be analyzed within the framework of the curvilinear coordinate system shown schematically in Fig. 1. Four parameters, R_s , R_e , α , and β , completely define the “hand” position (point H) within the operational space Ω . The first two of them, the shoulder and forearm lengths, R_s and R_e , are characterized by fixed values for a given

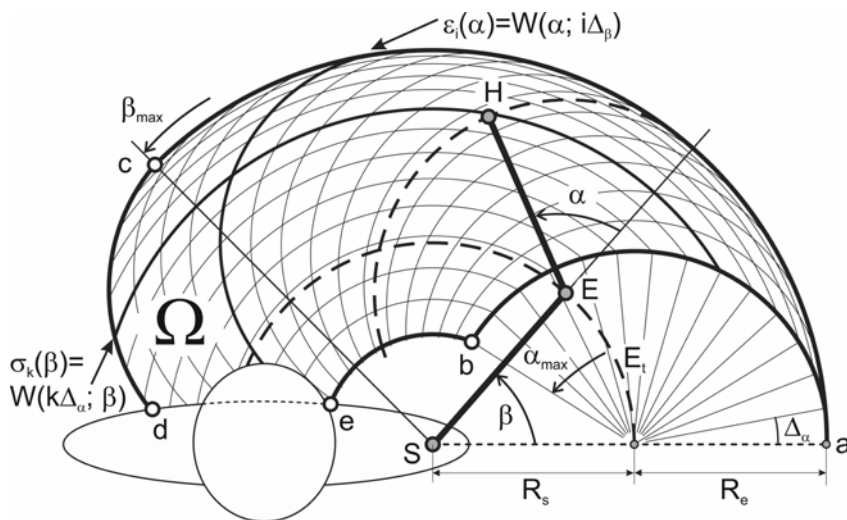


Fig. 1. Operational space of two-joint planar movements and definition of the curvilinear coordinate system. Parameters: α and β) elbow and shoulder joint angles changing within the following ranges: $\alpha_{max} \leq \alpha \leq 0$; $\beta_{max} \leq \beta \leq 0$; R_s and R_e) lengths of the arm segments; S and E) positions of the axes of the shoulder and elbow joints; H) “hand” position, i.e., position of the distal end of the second (distal) arm segment that can be called provisionally the “forearm”; $\epsilon_i(\alpha)$ and $\sigma_k(\beta)$) basic elements of the curvilinear coordinate system (isolated movement traces in one of the joints when another joint is fixed). The curve a-b-c-d-c-a indicates the boundary of the operational space Ω .

subject, whereas the two other parameters, namely angles α and β (in the elbow and shoulder joints), change as independent coordinates within the ranges $0 \leq \alpha < \alpha_{\max}$ and $0 \leq \beta < \beta_{\max}$. Any target point within the operational space Ω can be presented as a function of the two variables, $W(\alpha, \beta)$, which is based on simple trigonometric relationships (for details see [11]). Boundaries of the operational space Ω are as follows: $W(0, \beta)$ (arc ac in Fig. 1); $W(\alpha, \beta_{\max})$ (arc cd); $W(\alpha, 0)$ (arc ab); $W(\alpha_{\max}, \beta)$ (arc be). Additionally, the curve de is defined by a natural trunk border of the subject.

Finally, the curvilinear coordinate system may be presented graphically by two sets of the intersected arc lines, $\varepsilon_i(\alpha) = W(\alpha; i\Delta_\beta)$ and $\sigma_k(\beta) = W(k\Delta_\alpha; \beta)$, where Δ_β and Δ_α define the extent of discretization

of the coordinates (Fig. 1). In the former case, arcs of radius R_e are distributed with a constant density; in the latter one, arcs of the concentric circles with center S show an increased density with a shift toward the outer boundary of the operational space.

Force Singular Points Related to the Elbow Joint. A scheme of the hypothetical test movements is presented in Fig. 2A. During the test, the subject was asked to produce a slow circular-form steady movement; the movement trajectory is shown in Fig. 2A by the circle with center O and radius r . It is assumed that test movements are produced under the action of a constant external loading applied tangentially with respect to the movement trace in clockwise or counterclockwise directions.

The force moment acting around the elbow joint

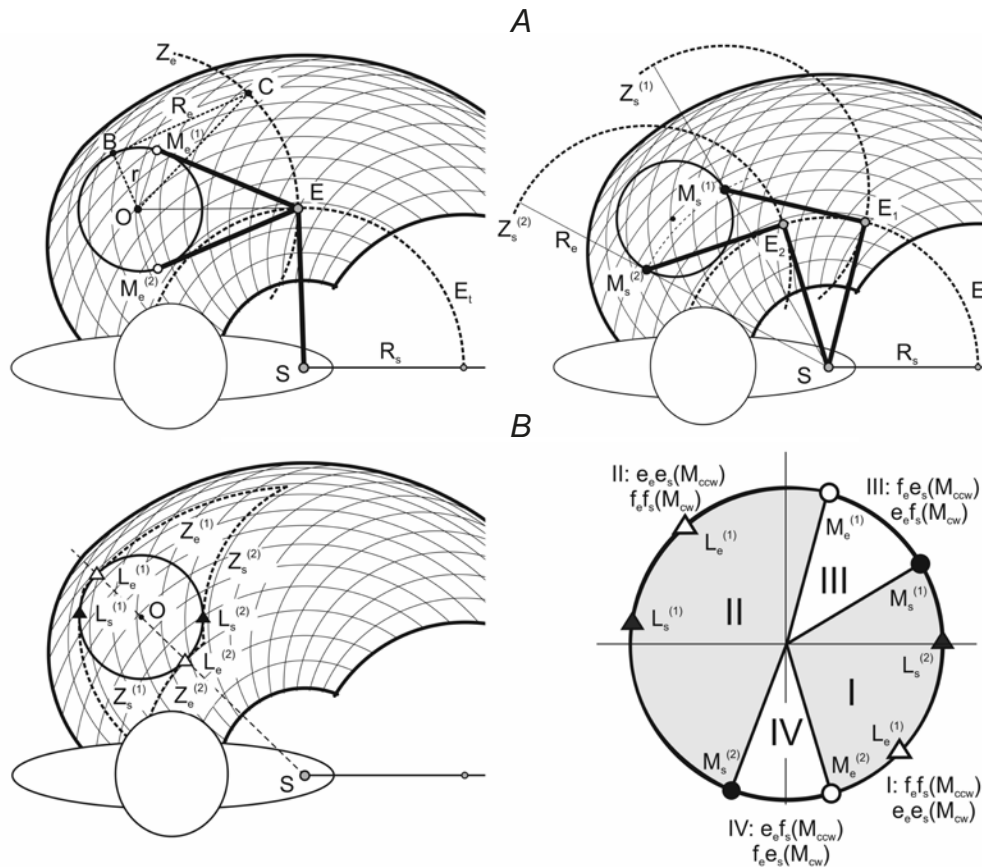


Fig. 2. Definition of the force and position singular points (FSPs and PSPs) and synergy sectors during circular movements of the hand. A) Definition of the FSPs at the elbow joint; $M_e^{(1,2)}$; Z_e) virtual trajectory of the elbow joint positions at a zero moment; E_1) trajectory of possible spatial shifts of the elbow joint; E_2) elbow location defined by crossing of the Z_e and E_1 curves. B) Definition of the FSPs at the shoulder joint; $M_s^{(1,2)}$; auxiliary circles $Z_s^{(1,2)}$ have the centers in $M_s^{(1,2)}$ and radii R_s ; E_1 and E_2) elbow locations defined by crossing the $Z_s^{(1,2)}$ and E_1 curves. C) Elbow PSP, $L_e^{(1,2)}$ (open triangles), and shoulder PSP, $L_s^{(1,2)}$ (closed triangles), coinciding with the extremal positions of the circle in the curvilinear coordinate system; the auxiliary curves are $Z_e^{(1,2)}$ and $Z_s^{(1,2)}$ (dashed lines). D) Location of the FSPs and PSPs, and of the force synergy sectors I–IV, in which the correspondent combinations of the elbow and shoulder muscles obtain the external loading; symbols f and e designate flexor and extensor muscles; subscripts e and s show muscles belonging to the elbow and shoulder joints; M_{cw} and M_{ccw} are clockwise and counterclockwise directions of the external loading.

attains a zero value when the external force vector is going via the joint axis; therefore, the “forearm” should be directed in this case tangentially with respect to the movement trace. The term “forearm” is used here in quotation marks to designate the distance from the elbow joint axis to the point of the external force application; it is assumed that the subject’s wrist is rigidly fixed along the line connecting centers of the wrist and elbow joints. The scheme in Fig. 2A demonstrates the geometrical procedure used to determine the FSPs at the circular movement trajectories. The equilibrium elbow joint position E is defined as the point of intersection of the auxiliary curve Z_e and elbow trace E_t . The arc Z_e is the part of the circle passing via ends of the “forearm” length segments placed tangentially with respect to the movement trajectory. The point E is connected with two different “forearm” positions corresponding to two FSPs ($M_e^{(1,2)}$) in the movement trajectory. These FSPs divide the circle into two unequal segments differing from each other by the sign of the force moments applied to the elbow joint muscles. For the clockwise directions of both external loading and movement, the force action at the elbow joint is changed from extension to flexion during transition via point $M_e^{(1)}$; a further passing via point $M_e^{(2)}$ evokes a reverse action. Therefore, for the clockwise-directed loadings, the elbow joint will undergo the action of extending/flexing forces during the movement along the longer/shorter segments of the circle divided by points $M_e^{(1,2)}$; for the counterclockwise loadings, the force moments will change in the opposite direction.

Force Singular Points Related to the Shoulder Joint. The force moment acting at the shoulder joint attains a zero value when the vector of the external force is going via the joint axis; therefore, the FSPs are shown by points of touching of the movement circle by two tangent lines $Z_s^{(1,2)}$ passing via the joint axis (Fig. 2B). The shoulder FSPs are placed symmetrically with respect to the line connecting the center of the movement circle and the joint axis. The definition of the elbow joint positions E_1 and E_2 for the given FSPs can be derived as points of intersection of the elbow trace E_t with the circles of the radius R_e that are centered in $M_s^{(1,2)}$. Similarly with the elbow joint, the shoulder FSPs define changes in the force moments during the movement. When both external force and movement have the clockwise direction, the force moment changes its action from extension to flexion at point $M_s^{(1)}$; further movement via point $M_s^{(2)}$ will produce an

opposite effect. Therefore, the shoulder joint will undergo the action of extending/ flexing forces during the movement along longer/shorter segments of the circle.

Position Singular Points. The PSPs at the elbow and shoulder joints coincide with the points of the movement trace where directions of the length changes of the proper muscles are inverted (Fig. 2C). Pairs of the PSPs, $L_e^{(1,2)}$ (open triangles) and $L_s^{(1,2)}$ (closed triangles), correspond to extremal positions at the circle for the respective joint angles α and β ; the extrema are defined by points where the corresponding coordinate traces $Z_e^{(1,2)}$ and $Z_s^{(1,2)}$ are touching the movement circle. Note that the elbow PSPs $L_e^{(1,2)}$ are on the line passing via the axis of the shoulder joint S and center of the movement trace O .

Singular Points and Force Synergy Sectors. Figure 2D describes the summarized location of FSPs and PSPs defined above (Figs. 2A-C) and illustrates the definition of the force synergy sectors (I-IV). The force correlations between different functional muscle groups belonging to different joints are most important for interpretation of the processes of central activation; therefore, it may be useful to define sectors at the movement trajectory with different combinations of the loadings on various muscle groups acting at different joints. During the movement in sectors I and II, muscles of the same modality, flexors (f) or extensors (e), are loaded at both joints; the choice between the combinations $f_e f_s$ and $e_e e_s$ (subscripts e and s denote elbow and shoulder) within the sectors I and II depends on the direction of the external force moment (M_{ccw} and M_{cw}). Combinations of the opposite modalities of the muscle loadings are observed in sectors III ($f_e e_s$ and $e_f f_s$) and IV ($e_f f_s$ and $f_e e_s$); these sectors are noticeably smaller, as compared with sectors I and II.

Force Synergy Sectors for the Movement Circles of Different Radiuses. The nonlinear nature of the system under study creates obvious prerequisites for complex reordering in relative positions of singular points at the circular movement traces with changes in their radiuses. During such changes (Fig. 3A, B), steady angle positions are typical only of elbow joint PSPs (open triangles), whereas other singular points at both joints shift along specific smooth curves. Changes in the positions of the FSPs are accompanied by reordering of the synergy sectors as well. When the radii are decreased, a certain smoothing of the differences between dimensions of the synergy sectors I and II

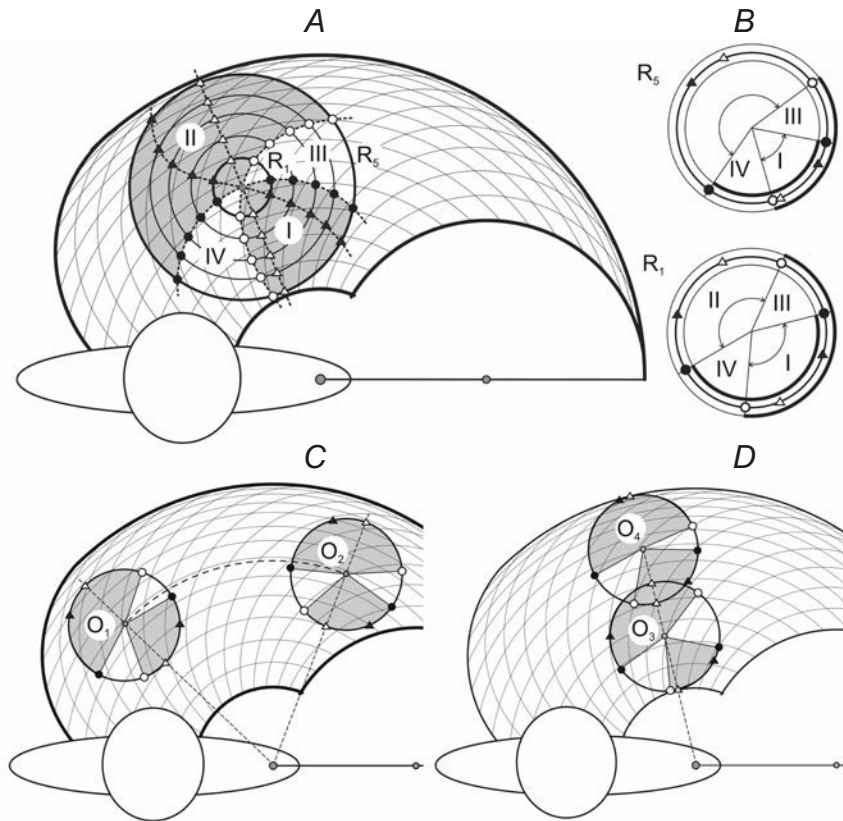


Fig. 3. Analysis of the differences between the patterns of singular points and force synergy sectors depending on the magnitude of the movements and on their location within the operational space. A) Singular points and force synergy sectors for the movement traces corresponding to concentric circles of different radii. B) Comparison of the force synergy sectors for circles of the maximal and minimal radii shown in A. C and D) Transitions of the movement circle center along a fixed “shoulder” coordinate line O_1-O_2 (C) and perpendicularly with respect to “shoulder” coordinate lines O_3-O_4 (D).

is observed, while weights of the sectors III and IV remain almost invariable (Fig. 3B). It seems that these effects may be related to the varying degree of curvature of movement traces.

Change in the Placement of Movement Traces.

Patterns of singular points in the identical circular movement traces remain unchanged for all traces placed at the same distance from the shoulder joint axis (Fig. 3C). In Cartesian coordinates, the set of singular points turns in the clockwise/counterclockwise direction in accordance with rightward/leftward turning of the line connecting the axis of the shoulder joint and the center of the movement circle. The relative weights of the force synergy sectors are also not changed in this case. On the contrary, shifts of the movement traces in the distal direction along the line passing via the axis of the shoulder joint (Fig. 3D) lead to increases in sectors I and II and corresponding decreases in sectors III and IV. It has been noted above that the distribution of the synergy sectors and their weights may depend on the degree of curvature of movement traces. In this case, the latter parameter is invariable; thus, it can be assumed that the observed changes depend on the curvature of the “shoulder” coordinate traces (concentric circles of different

radii). On the other hand, these effects may also be related to turning of the “elbow” coordinate traces for more distal movement trajectories.

Ellipsoidal Movement Traces. Ellipsoids may be used for the description of more complex movement trajectories. Experimental setups in this case should be significantly more complicated, as compared with those used for studying circular movements [11]. These movements, however, may also be interpreted theoretically using the methods proposed above (Fig. 4). Determination of the “shoulder” FSPs would not differ from that described above for the circular traces. For the “elbow” FSPs, however, it is necessary to introduce two different curves, $Z_e^{(ccw)}$ and $Z_e^{(cw)}$, describing opposite movement directions separately (Fig. 4A). These curves are constructed using (i) several defined points at the ends of the tangential segments R_e (five points for each loading direction are shown in Fig. 4A), and (ii) any kind of the nonlinear smooth approximation procedure. Further positioning of the ellipsoidal trace within the operational space should be further considered with $Z_e^{(ccw)}$ and $Z_e^{(cw)}$ curves fixed to the movement trace (Fig. 4B-D). Transections of these auxiliary curves with the elbow trace E_t define the elbow joint positions (E_1, E_2), which correspond to the required

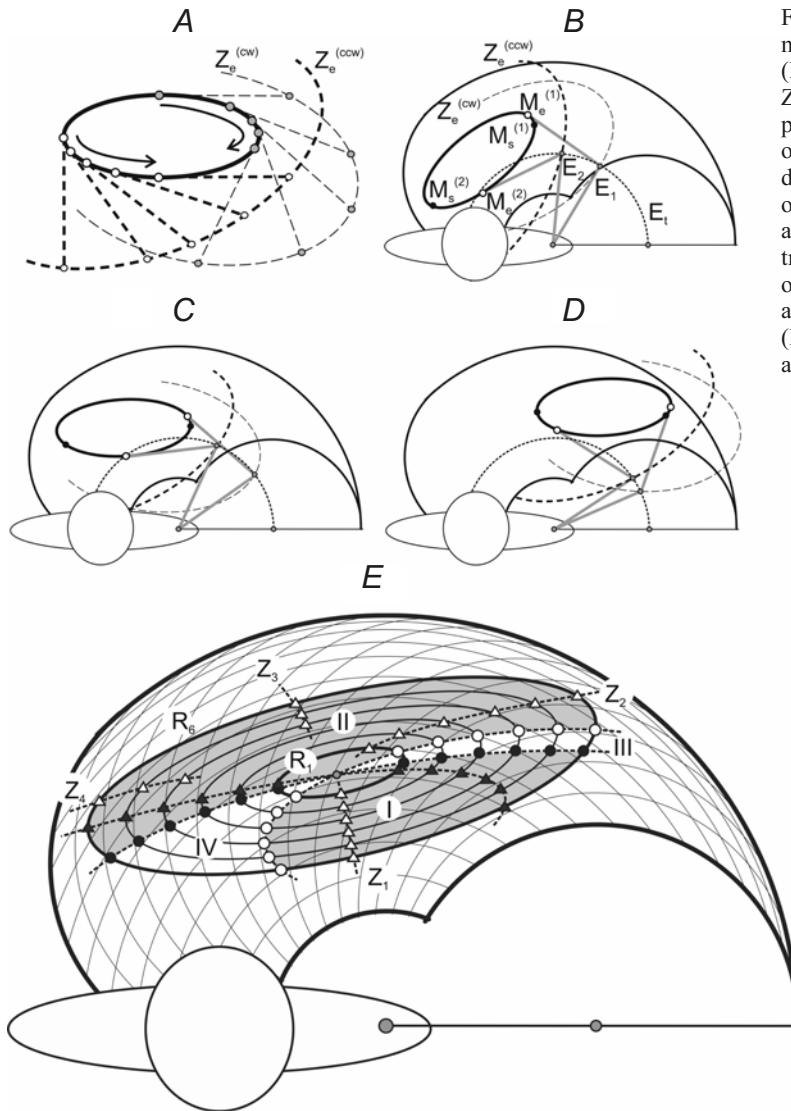


Fig. 4. Analysis of ellipsoidal trajectories of the movement. A) Definition of the force singular points (FSPs) for the elbow joint; auxiliary curves Z_{e}^{ccw} and Z_{e}^{cw} coincide with virtual trajectories of the elbow joint positions with a zero moment. B, C, and D) Definition of the FSPs and proper elbow joint positions for different placements of the ellipsoids within the operational space. E) Location of the singular points and force synergy sectors at the ellipsoidal movement traces of various dimensions; note the complex pattern of the “elbow” PSPs; in addition to the PSPs located along the lines Z_1 and Z_2 , in a part of the larger ellipses (R_4-R_6), pairs of additional PSPs (Z_3 and Z_4 branches) appear.

FSPs $M_e^{(1,2)}$.

Ellipsoidal Movement Traces of Different Sizes. Using the methods described above, we can define singular points for a system of ellipsoidal movement traces of different sizes (Fig. 4E). The distributions of the FSPs and of the force synergy sectors is largely similar to those of the concentric circular traces presented in Fig. 6, although some elongation of the traces leads to the respective shifts of the FSPs along larger axes of the ellipses, thus changing the force synergy sectors. It may be emphasized that sectors III and IV decrease in this case, as compared with those in the circular traces (Fig. 3A). Elongation of the movement traces also evokes an interesting phenomenon, namely the appearance of two additional elbow PSPs (lines Z_3 and Z_4) at larger-size traces

($R_4 - R_6$) in Fig. 4E. Most likely, this can be related to differences in the curvature degree of different traces and/or to the dependence on positioning of the ellipses within the operational space.

Singular Points in the Linear Movement Traces. Linear (or quasi-linear) traces may be considered important elements of many real movements. A method allowing one to define the “elbow” FSPs for the linear movements is considered below. Similarly to the circular and ellipsoidal movements, the loadings are in this case also directed along the movement trajectory (Fig. 5). The main problem for linear movements is related to the definition of the “elbow” FSPs. For this purpose, we shall analyze two traces, the circular R_1 and the linear R_2 , going through two points, A_1 and A_2 . In accordance with the method described earlier, for circle R_1 we can

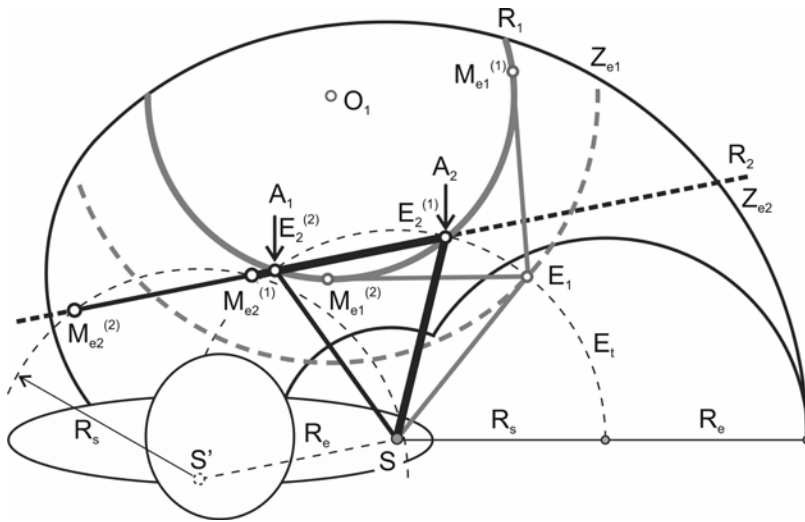


Fig. 5. Elbow force singular points (FSPs) at the linear movement traces. The linear trace R_2 , passing via points A_1 and A_2 , corresponds to a limit passage of the circle R_1 passing via the same points during an endless radius increase. The virtual trajectory of the elbow joint positions with a zero moment for the R_1 circle is presented by arc Z_{e1} , whereas such a trajectory for the line R_2 (Z_{e2}) coincides with the movement trace itself. In this case, it is possible to define two joint positions, $E_2^{(1,2)}$, and corresponding FSPs, $M_{e2}^{(1,2)}$, for the movement line R_2 . An important condition for the existence of the “elbow” FSPs is the necessity for the linear movement trace to intersect (or, at least, to touch) the trajectory of possible movements of the elbow joint E_i ; the FSPs defined in this way cannot exit out of the limits of the operational space.

define both the position of the elbow joint E_1 (as the point of crossing of the auxiliary curve Z_{e1} with the elbow trace E_i) and the related FSPs $M_{e1}^{(1,2)}$. On the other hand, the linear trace R_2 may be presented as a result of the endless increase in the radius of circle R_1 under conditions of its going through points A_1 and A_2 . In this case, the auxiliary curve Z_{e2} will coincide with the movement trace itself, i.e., with the R_2 line. Therefore, since A_1 and A_2 are points of crossing of the curves Z_{e2} and E_i , they also coincide with the elbow positions $E_2^{(1,2)}$ where the forces are going through the joint axis, and the “forearm” is oriented along line R_2 . The additional condition for the appearance of the FSPs in the linear movement trace is its crossing of (or, at least, touching to) the *elbow trace* E_i . On the other hand, there are positions where possible FSPs could exit out of the operational space.

Synergy Areas for Sets of Parallel Linear Movement Traces. The above-described approach for finding the “elbow” FSPs in the linear movement traces may be used to define the synergy areas for sets of parallel linear movement traces having various slopes (Fig. 6). In the movement traces going orthogonally with respect to the frontal plane (Fig. 6A), the “elbow” FSPs are defined using the auxiliary curve Z_e . This curve coincides with the elbow trace E_i shifted vertically for the distance R_e along the movement trace of a zero loading (line z in Fig. 6A). The FSPs can be defined as points of crossing of curve Z_e with the movement traces located rightward from line z . The “forearm” locations at these FSPs coincide with the movement traces; the proper positions of the shoulder segment

are shown by dotted lines going toward small circles at curve E_i . Note that the FSPs are absent on the left with respect to line z , because points of crossing of the auxiliary curve Z_e with the movement traces do not obey to a natural condition of positivity for the elbow joint angles (the forearm cannot be placed along these traces without destruction of the joint).

The arc Z_e and line z constitute natural boundaries confining the synergy area III (marked in gray in Fig. 6A), where muscles of different modality acting on the elbow and shoulder joints are loaded. In two other areas of synergy (I and II), muscle groups of the same modality are loaded. Similarly to the situation with circular movements, the antagonistic muscles are loaded with a change in the direction of the external loading. The synergy areas may also be defined in a similar way for other directions of the movement traces (Fig. 6B - D). In these cases, the corresponding rotation of the same synergy areas (I - III) is observed in accordance with turning of line z . For positions of the movement traces shown in panels B and D of Fig. 6, it is possible to observe the disappearance of both line z and area II due to natural limitations of the operational space. In accordance with the general definition, the z lines in all sets of the parallel movement traces divide the entire operational space in accordance with the sign of the force moment at the shoulder joint. The absence of the line z at a given movement direction signifies that the force moment at the shoulder joint does not change its sign within the entire operational space.

In addition to the FSPs and the respective synergy areas, all panels in Fig. 6 include lines of

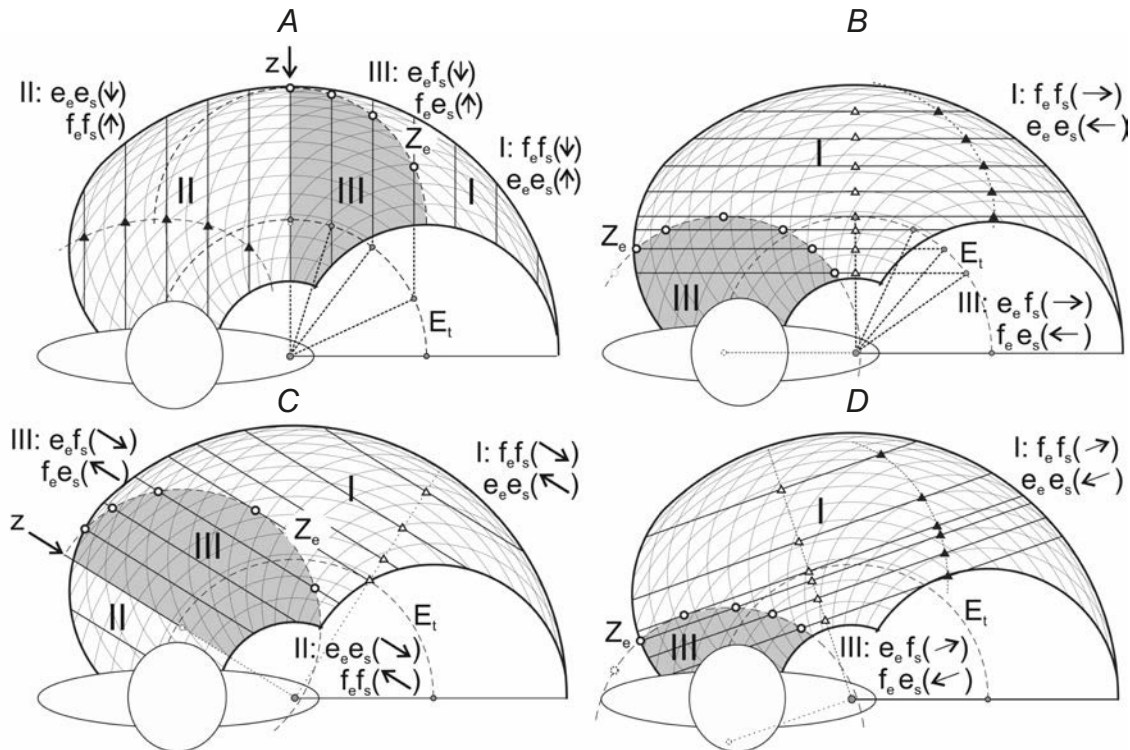


Fig. 6. Force and position singular points (FSPs and PSPs) and force synergy areas defined for sets of the parallel linear movement traces of different directions. A–D) Areas III (marked in grey) correspond to the opposing patterns of loading, when the elbow flexors are loaded together with the shoulder extensors, and *vice versa*; areas I and II correspond to the coinciding patterns of loading for the muscles belonging to different joints. Designations are the same as in Fig. 5; the load directions are shown by arrows in brackets. The lines marked by arrow z in panels A and D designate traces of the zero moment at the shoulder joint.

distribution of the PSPs, where the directions of the muscle length change in the corresponding joints are reversed.

DISCUSSION

Force and Position Synergies. Our study is devoted to a theoretical analysis of various types of planar movements produced under different combinations of directions of both the external force moment and the movement itself. It has been shown earlier that central commands to the muscles in two-joint movements depend predominantly on the relative positions of the FSPs where the force moments change their directions [11]. At the same time, the commands are also dependent on the PSPs connected with the extremal points at the joint angle traces. In this study, the positions of singular points in the movement traces were defined graphically. This approach allows the researcher to analyze not only circular traces, but separate elements of more

complex trajectories as well.

Formally, the *force synergies* may be classified in accordance with the functional modality of the muscles belonging to different joints, which are loaded simultaneously. The *coinciding synergy* corresponds to simultaneous loading of muscles of the same modality (flexors-flexors; extensors-extensors); while the *opposing synergy* belongs to combinations of muscles of different modality (flexors-extensors; extensors-flexors). Muscle combinations within both types of the synergy effects depend on the loading direction. It is interesting that, in all the considered types of movement trajectories, both closed (circular and ellipsoidal) and open (linear) ones, the prevalence of the *coinciding synergies* is manifested. In the circular traces, the weight of the *coinciding synergy* sectors (I, II) is greater, as compared with that of the *opposing synergy* ones (III, IV). In ellipsoidal traces, these differences seem to be expressed even more clearly (compare Figs. 3A and 4E). In the general case of the parallel movement traces going

under different angles to the subject's frontal plane (Fig. 6), the operational space is usually divided into three areas, two of which are connected with the *coinciding synergy* (I, II), while the third one is related to the *opposing synergy* (III). Similarly, the weight of the *coinciding synergy* areas seems to be relatively greater as compared to that of the *opposing synergy*.

The *force synergy* patterns are changed for identical circular movement traces going at different distances from the shoulder axis (Fig. 3D). At the same time, both relative distribution of singular points and weights of the synergy sectors remain unchanged for the same distances from the shoulder axis, and the pattern of all synergy points is simply rotated in the course of such a transition (Fig. 3C). At present, preliminary analysis of the FSPs (Figs. 3 and 4) allows us to conclude that the observed variabilities of the *force synergy* patterns at various parts of the operational space are likely related to the differences in the curvature indices of both movement trajectories and traces of the curvilinear coordinate system.

The *position synergy* is defined by the distribution of PSPs along the movement trajectories, and its influence is directly related to muscle hysteresis (for review, see [13]). The effects of the *position synergy* are often smoothed when PSPs are placed close to the nearest FSPs, although the movement-dependent differences in the EMG intensities may be also rather significant, especially for distal muscles [11].

Activation Synergy. Despite strong experimental support for the assumption of existence of connections between *force* and *activation synergies* in real circular movements [11], it has been demonstrated in the cited study that EMG activities of the elbow and shoulder muscles may be rather noticeable out of the zones of their direct loading. This phenomenon may be related to a more complicated arrangement of the joints, as compared with that in a simple pivotal model. An exhausting analysis of the complex geometry of the rotation movements in the shoulder joint can be found in [14]. The elbow joint biomechanics is highly intricate as well; recently, it has been considered as an assemblage of three interactive joints [15]. It seems that such complex mechanical systems as the elbow and shoulder joints can provoke indeterminacy in the force moments acting around these joints.

It is quite clear that, with change in the movement pattern, muscle activities are rearranged in

correspondence to new movement tasks. At the same time, it should be noted that a routine classification of the muscles as belonging exclusively to the elbow or shoulder joints is noticeably oversimplified; sites of the force applications can be fixed only for the monoarticular muscles, while the procedure of their identification for the biarticular muscles is significantly more complex [16].

The set of efferent activities controlling two-joint movements is often localized within separate time or space zones where which programs of co-contraction can predominate. The movement phases are primarily accompanied by co-contractions of the antagonistic muscles within the areas adjacent to the zones of their direct loading. The co-contraction patterns can distinctly reduce both the after-effects of the ongoing residual movements at the apexes of movement and the uncertainty effects related to muscle hysteresis [13, 17]. Behavioral studies of postural tasks have demonstrated that subjects use muscle co-contraction as a strategy of stabilization of the limb joints in the presence of external loadings [18]. Humans are also able to modulate independently the relative balance of co-contraction and limb stiffness in different spatial directions [19] and at different joints [20]. At the same time, co-contraction of the antagonistic muscles should increase the energy costs of the real movements.

Force Feedback Control Hypothesis. The close resemblance of the *force* and *activation synergies* allows us to propose the *Force Feedback Control Hypothesis*, which introduces a hypothetical mechanism via which the CNS can regulate descending motor commands in multi-joint movements. This mechanism can be based on using feedback signals with information on the presence or absence of loading of the antagonistic muscles acting on joints participating in a given movement. During the movement, any crossings of the FSPs belonging to a given joint would evoke "inversion" of the corresponding feedback signals, thus informing the motor control system on the necessity to redirect descending activity between the groups of antagonistic muscles of a given joint. As a result, muscles that were active earlier become silent, while their antagonists are activated. At any moment, predominant activation is directed toward the muscles loaded by the force moment acting at the proper joint. The Golgi tendon organs seem to be the best candidates for providing this force afferent signals, although the involvement of other proprioceptor types in this process cannot be ruled

out as well. Voluntary control can also participate in this case for both co-contraction of the antagonistic muscles and the desired shaping of the movement trajectories. Co-contraction of the antagonistic muscles is better seen within the trace areas located near the correspondent FSPs [11]. The *force feedback control hypothesis* can probably explain the decrease in the number of controlled variables during multi-joint movements due to the possibility for the CNS to use simultaneously the complex of proprioceptive information coming from all joints involved in a given movement program. Moreover, such “force information matrix” might be created without any additional expense for the CNS on the assessment of the real position and forces at the joints involved in the movement. In this case, it is likely that this automatically obtained information concerning the *force synergy* is simply “transformed” into a preliminary pattern of the *activation synergy*, which is naturally needed in some voluntary modifications, in order to obtain the desired parameters of the movements.

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This study is devoted to theoretical analysis of the processes of motor control; it was not directly related to experiments on animals or tests on humans. Therefore, it does not require the confirmation of compliance with the existing international ethical standards for experimental studies.

The author, A. I. Kostyukov, confirms the absence of any conflict related to the commercial or financial problems and to the relations with organizations or persons, which could in any way be associated with the investigation.

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