A mechanical analysis of force distribution between redundant, multiple degree-of-freedom actuators in the human: Implications for the central nervous system

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Abstract

This paper is a mechanical analysis of the apparent redundancy of muscles in the human body. Because differentiation of motor commands appears to occur at the motor unit level, the analysis examines possible distributions of motor unit activation levels for a given motor task. The transformation from these motor commands to movement is defined mathematically. Each motor unit, regardless of how many joints it crosses, produces a single *action*, a vector describing multi-joint motor tasks including control of position and/or force. These individual actions, even for apparently antagonistic muscles, are summed to produce overall movement. Because there are many possible combinations of motor unit actions which produce a desired net action, it is hypothesized that the central nervous system uses some consistent criteria for selecting favored combinations. Modeling these criteria with optimization cost functions, it is shown that the potential cost for producing movement decreases with increasing numbers of actuators, distributed in a variety of configurations. This approach is compatible with self-organizing topographic feature maps, which demonstrate how the central nervous system may perform the described transformations.

1. Introduction

Study of human control of movement is complicated by the large number of degrees of freedom in the body (~ 244), as well as the even larger

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number of muscles (~ 600). The central nervous system (CNS) appears to be confronted with many possible ways of coordinating these muscles to produce a given movement. Unfortunately, understanding of motor control is presently insufficient to determine the mechanism by which this coordination is achieved. For this reason, a number of modeling, analytical, experimental, and other approaches have been used to study the distribution of forces between muscles. Of particular interest in these studies are the implications of a large number of muscles and degrees of freedom, and whether this apparent redundancy is an aid or an obstacle to the CNS.

Many modeling studies have proposed that the CNS can solve the force distribution problem by a means analogous to computational optimization. The individual muscle forces may thus be calculated by selecting a suitable cost function to be minimized, usually while matching kinematic data. Common cost functions include functions of summed muscle stress or force, as well as powers of these functions (e.g., Pedersen et al., 1987; Dul et al., 1984; Crowninshield and Brand, 1981; Patriarco et al., 1981). The results have shown that low powers of muscle stress prove adequate for reproducing movement profiles. However, in the absence of experimental measurements of individual muscle forces, it is difficult to make definitive conclusions.

Much analytical work has been devoted to the study of muscles classified as uni-articular or bi-articular, based on the number of joints they cross. Hogan (1985) proposed that the redundancy afforded by bi-articular muscles could be exploited by the CNS to control the orientation of the stiffness ellipse for a given arm posture. Experimental data, however, have indicated that central control of the stiffness ellipse appears limited to varying its magnitude through co-contraction rather than fine control of bi-articular muscles (Flash and Mussa-Ivaldi, 1990).

Other analytical studies have concentrated on unique properties of bi-articular muscles for specific tasks such as cycling and jumping, which could help dictate solutions to the force distribution problem (see review by Van Ingen Schenau, 1990). These studies have shown that, as compared to uni-articular muscles, bi-articular muscles can in specific instances produce forces at more advantageous lengths and velocities, or perform work more efficiently (e.g., Van Ingen Schenau, 1989a,b). However, these task-specific analyses have not been placed in a mathematical framework for generalizing the conclusions into fundamental concepts. It has not been proven that uni-articular muscles cannot perform similar functions in different motor tasks.

Experimental work has suggested that the force distribution problem lies at a lower level than that of the muscle. Data show that motor units within muscles do not always share common motor commands (Ter Haar Romeny et al., 1984; Zuylen et al., 1988). This differential activation depends on the particular configuration of the degrees of freedom the muscle crosses. For example, different motor units within biceps tend to be activated depending on the degree of supination. There exists insufficient evidence for shared commands within higher-level groups, such as neuromuscular compartments, as demonstrated by Chanaud and Macpherson (1991). It therefore appears that control is subject to greater redundancy than is obvious when the number of muscles is compared to the number of degrees of freedom (considering that muscles can only pull, 600 muscles are not far in excess of what is needed to control 244 degrees of freedom). Rather, the CNS seems to produce commands at the level of the motor unit rather than the muscle (even though humans appear to have little independent volitional control of individual muscles, let alone motor units). A study of CNS coordination must therefore be relevant to force distribution between not only muscles, but motor units as well.

This summary, however incomplete, reveals the need to unify many analytically- and experimentally-derived concepts. To this end, a general description of multi-DOF motor tasks is needed. This description can serve as a basis for general principles of how the CNS distributes motor commands or desired forces to the motor units – the *force distribution problem*. Descriptions in terms of movement according to the number of joints crossed by a muscle are inadequate, because many joints have more than one DOF (e.g., 3 at hip, at least 4 at shoulder), and even simple planar movements involve control of muscles or motor units exerting moments about DOFs outside the plane of movement. Moreover, some motor tasks are isometric, for which kinematic description of movement is inappropriate. A general description of motor tasks must be applicable to control of both position and force.

An analysis of CNS-controlled movement must also consider evidence that the CNS performs more like a parallel distributed processor (PDP; Rumelhart et al., 1988) than a serial computer. The traditional robotics difficulties of inverse dynamics, inverse kinematics, and inverse actuation (i.e., resolving actuator redundancy) have been based on the problems of computing numerical solutions in real time (see, e.g., Craig, 1986). A PDP is subject to different complications, such as the problem of setting synaptic weights between neurons so that the system converges on a correct solu-

tion. In addition, these weights must be compatible with physiological evidence of somatotopic mappings within the CNS, in which nearby neighborhoods of neurons correspond to related movements.

A PDP approach to the force distribution problem is made difficult by the relative inaccessibility of the CNS and its methods for encoding information such as movement commands. Recognizing that researchers' familiar terms such as joint angles, moments, and forces are unlikely to correspond directly to weightings and neuronal firing rates, it may not prove advantageous to study force distribution using these terms. Rather, a more abstract approach, in which the results are invariant with respect to CNS coding, appears more suitable. In other words, the choice of coordinate systems for this analysis must be arbitrary and cannot affect the conclusions.

This paper presents an abstract approach to the force distribution problem, based on an analysis of the mechanics of multi-DOF movement. The conclusions are general in the sense that they are applicable to any motor task involving control of force and/or position, about any number of DOFs. The findings apply to either individually activated motor units or "ideal" muscles composed of motor units sharing the same activation. This approach must necessarily make use of considerable abstraction to maintain generality (though examples are given). Nevertheless, the approach brings insight to the problem of translating movement commands into the vast number of motor unit commands, and demonstrates how the large number of actuators lowers the potential cost of movement, for a large class of possible cost functions. In addition, the interpretation of movements in terms of action is shown to be compatible with PDP networks.

The analysis begins with a definition of the force distribution problem and the term *action* which is used to describe motor tasks. Following are analyses of multi-DOF mechanics, the cost of actions using multi-DOF actuators, the feasible actions using multi-DOF actuators, and implications for self-organizing maps which translate voluntary movement commands into motor unit commands.

2. Problem definition

This paper dissociates the question of how forces are distributed between redundant actuators from the question of how stability is controlled, based on the model shown in Fig. 1. Decoupling the two problems makes it
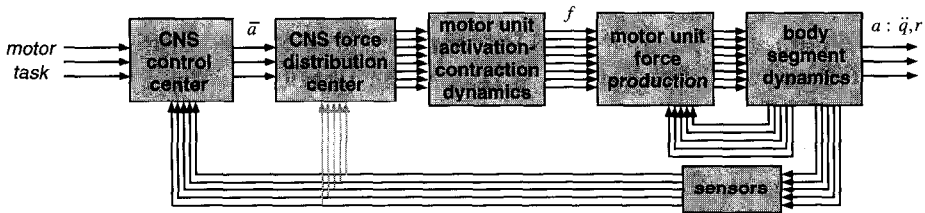
Motor Control System

Fig. 1. Model for the motor control system. Motor task commands are encoded and sent to the CNS control centre, which uses sensory feedback to control timing and stability and deliver a desired action $\bar{a}$, in unknown coordinates, to the force distribution centre. This centre transforms the action command into motor commands for a large number of motor units. Activation-contraction dynamics determine the normalized motor unit forces f, and motor unit characteristics determine actual forces. Body segment dynamics translate force into movement, which determines feasible motor unit forces, and is also fed back to the CNS control centre (and possibly the force distribution centre). Resulting movement is the actual action a, which is sensed in unknown coordinates. Humans observers measure a as joint accelerations $\ddot{q}$ and reaction forces r.

possible to study force distribution without regard to problems of stability, timing, or the structure of feedback or feedforward control. This decoupling is based on two assumptions: first, that it is mathematically valid to separate control functions from force distribution functions, and second, that the activation-contraction dynamics for muscle fibres are the same (homogeneous) from one fibre to the next.

While it is unknown whether control and force distribution are physically separable within the CNS, the assumption of mathematical separability facilitates the study of a general movement command, the output of the control centre (see Fig. 1), which is then mapped by the force distribution centre into individual commands to the motor units. The basis for this assumption is that the CNS appears to effectively distribute forces among the motor units for all motor tasks, whether ballistic (feedforward) or controlled, as well as uncontrolled tasks, where the feedback fails. Humans have the conscious, voluntary ability to specify gross movements, but not to individually activate single motor units or muscles. It is therefore possible that learning and implementation of control is separated from the translation of desired movement into motor unit commands. This study is confined to the distribution of commands (or forces) to motor units, given a desired movement produced by other parts of the CNS.

If muscle activation-contraction dynamics, which act as a low-pass filter

on excitation levels, are relatively homogeneous, they can be regarded as part of the control problem, and hence disregarded in the force distribution problem. Homogeneity implies that the same low-pass filter is applied to all inputs, and therefore only affects the temporal rather than spatial aspects of force development. These temporal aspects are therefore relevant to stability rather than force distribution, and can effectively be "moved" into the domain of the CNS control centre of Fig. 1.

The force distribution problem is defined as one portion of the overall movement control loop. In this model, the CNS control centre performs a motor task by mediating the time course of a command, $\bar{a}$, termed the *desired action*, with sensory feedback. Examples of typical actions include reaching tasks, flexion of single joints, and application of contact forces. The CNS force distribution centre maps the desired action into motor unit activation levels, which are effectively regarded as *normalized* forces, f (that is, each component of vector f varies between 0 and a maximum of 1). *Actual* force production depends on muscle parameters, as well as fibre length and velocity, which depend on the body segment dynamics. The resulting movement is the actual action a, which, given perfect conditions, equals $\bar{a}$. However, no existing instrumentation is capable of measuring a in the units used by the CNS; units convenient for observation often take the form of angular accelerations, $\ddot{q}$, or contact forces, r, with the external environment.

Multiple lines of communication between the blocks in Fig. 1 imply that the quantities $\bar{a}$, f, and $\ddot{q}$ are vectors whose dimensions reflect the number of degrees of freedom in a signal. The kinematics q has a dimension equal to the number of mechanical degrees of freedom, n_d, while f has a dimension equal to the number of motor units, n_M. The number of motor units far exceeds the number of DOFs. The dimension of $\bar{a}$, n_a, is more difficult to specify. Consider that humans have voluntary control over most, but not all, mechanical degrees of freedom. For example, the finger musculature is insufficient to independently control the joints of the phalanges, nor can humans independently move the individual articulations of the spine. It is therefore reasonable to hypothesize that $n_a < n_d \ll n_M$.

The force distribution problem may be considered a problem of mapping from a space of dimension n_a to one of dimension n_M. A vectorial approach to this problem offers graphical insight to the mechanics of movement, which have considerable bearing on the possible solutions without regard to a particular configuration or task.

3. Analysis of movement mechanics

A mathematical analysis shows that mechanics may be interpreted and visualized as a mapping of motor unit forces into movement defined by actions. After muscle fibres are grouped into motor units, successive transformations of force to moment about a DOF, and moment to acceleration or contact force, can be described as *affine mappings*, meaning that a linear transformation (i.e., matrix multiplication) is followed by the addition of a constant vector (Rockafellar, 1970). Because affine mappings are transitive, the succession of these transformations is itself affine. Visualization demonstrates the characteristics of these mappings, beginning with the muscle fibres. This section describes how mathematics may be used to interpret the coordination of multi-actuator, multi-DOF movement.

3.1. Muscle fibres produce moments dependent on musculoskeletal geometry

Consider a simplified model of n_f muscle fibres, producing forces described by the n_f-vector

$$f^{\mathrm{Mf}}(q, \dot{q}, f^f) = F_{\max}^{\mathrm{Mf}}(q, \dot{q}) \cdot f^f, \tag{1}$$

where $0 \leq f^f \leq 1$ is the column vector of normalized fibre forces, q and $\dot{q}$ are column vectors of joint angles and velocities, respectively, and $F_{\max}^{\mathrm{Mf}}(q, \dot{q})$ is the diagonal matrix of maximum possible fibre forces. Implicit in $F_{\max}^{\mathrm{Mf}}(q, \dot{q})$ are force-length and force-velocity properties, as well as peak isometric active muscle fibre forces. In a typical musculoskeletal system, each muscle fibre will simultaneously produce moments about several degrees of freedom, described by the n_d-vector of moments

$$t^{\mathrm{Mf}}(q, \dot{q}, f^f) = R^{\mathrm{Mf}}(q) \cdot f^{\mathrm{Mf}}(q, \dot{q}, f^f) = R^{\mathrm{Mf}}(q) \cdot F_{\max}^{\mathrm{Mf}}(q, \dot{q}) \cdot f^f, \tag{2}$$

where n_d is the number of degrees of freedom, and $R^{\mathrm{Mf}}(q)$ is an $n_d \times n_f$ matrix describing the muscle fibre moment arms about each DOF. Each muscle fibre will generally have a unique moment arm, depending on the aponeurosis and origin and insertion points. One possible interpretation of Eq. (2) is that t^{Mf} is a weighted sum of the columns of R^{Mf}, with weightings provided by the elements of f^f. Each fibre therefore produces moments which contribute to t^{Mf} in an additive manner. The number of non-zero elements in each muscle fibre's contribution is given by the corresponding column of R^{Mf}, and depends on the number of degrees of freedom a given fibre spans.
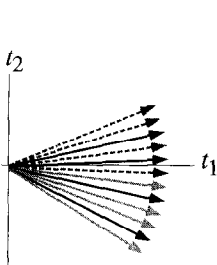
3.2. Motor units form the smallest indivisible units of force and moment production

Each fibre within a muscle receives excitation common to certain other fibres comprising a motor unit (Ghez, 1991). Thus, while individual fibres cannot be excited independently, individual motor units are likely to receive some degree of independent excitation. The moment arising from a motor unit is the sum of the moments arising from its constituent fibres. Because these fibres receive common excitation, they can be lumped together, even if they are distributed throughout a muscle, with the moment vector given by

$$t^M(q, \dot{q}, f) = RF^M(q, \dot{q}) \cdot f, \tag{3}$$

where the deletion of the superscript ^{f} in t^M and f denotes *motor unit*, rather than muscle fibre, moment and normalized force vectors. For n_M motor units, f is an n_M-vector, and RF^M is an $n_d \times n_M$ matrix with a column for each motor unit corresponding to the summed maximal moments of its constituent muscle fibres. Note that RF^M could be decomposed into lumped moment arm matrix and maximum motor unit force vector if needed. Fig. 2 demonstrates how muscle fibre moments can be lumped into motor unit moments.
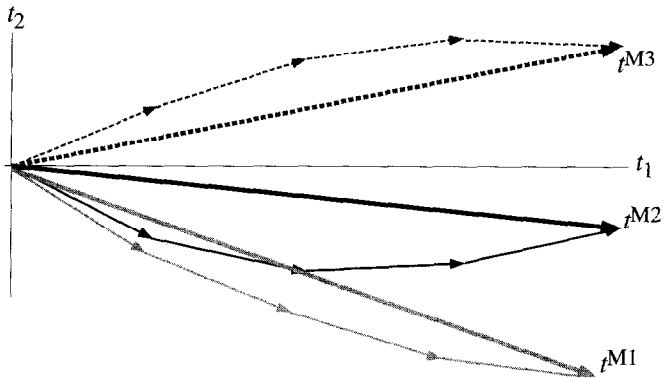

Fig. 2. Muscle fibre actions are grouped into motor unit actions. Example: a two degree-of-freedom (DOF) system. (a) Each muscle fibre produces a moment about the two DOFs, described by a vector. Each vector in the figure represents the moment produced by one of the fibres within a muscle. (b) For each motor unit, the constituent fibres receive equal activation, so that the total moment resulting from excitation of one unit is the sum of the constituent fibre moment vectors. The vectors t^M describe motor unit moments.

3.3. The mass matrix maps joint moments into joint accelerations

Equations of motion describing body segment dynamics can be written as

$$\ddot{q} = M^{-1}(q)\left[t^{M}(q, \dot{q}, f) + g(q) + \nu(q, \dot{q}) + RF^{M}(q, \dot{q}) \cdot f_{p}(q, \dot{q}) \right.$$
$$\left. + d(q, \dot{q}) \right], \tag{4}$$

where the elements are defined as follows:

$\ddot{q}$ n_{d}-vector of joint angular accelerations,
$M(q)$ $n_{d} \times n_{d}$ positive-definite mass matrix (Kane and Levinson, 1985),
$g(q)$ n_{d}-vector of terms due to gravity,
$\nu(q, \dot{q})$ n_{d}-vector of Coriolis and centripetal terms,
$f_{p}(q, \dot{q})$ n_{M}-vector of normalized passive motor unit forces,
$d(q, \dot{q})$ n_{d}-vector of friction and other dissipative terms.

Terms $g(q)$, $\nu(q)$, $f_{p}(q)$, and $d(q, \dot{q})$ depend purely on the state comprising q and $\dot{q}$. After substituting Eq. (3), Eq. (4) can be written as two terms – one that is (state-dependent but) linear in the motor unit forces, and one that is independent of motor unit forces – in an *affine* mapping from f to $\ddot{q}$ (Kuo and Zajac, 1993b):

$$\ddot{q} = L_{q}(q, \dot{q}) \cdot f + s_{q}(q, \dot{q}). \tag{5}$$

The equations of motion therefore can be interpreted as an affine mapping between motor unit forces and joint angular accelerations.

Dynamic coupling between body segments is described by the off-diagonal terms of the mass matrix, which is in general not diagonal. The effect of this coupling is that actuation of a moment about a given joint (DOF) results in acceleration about many joints (DOFs). Conversely, the acceleration of a single joint generally requires the production of moment about several DOFs. Moments about other DOFs are necessary to cancel the dynamic coupling from the joint to be moved.

3.4. Joint moments also map into reaction forces

A similar relation also holds for reaction forces, which may include contact forces with the environment or reaction forces internal to a joint. Newton's Law states that the sum of forces acting on a body is proportional to that body's translational acceleration. Euler's equation generalizes this relationship to moments and angular accelerations (Craig, 1986). Separa-

tion of forces or moments acting on a body into input and output general-
ized forces reveals that output forces are affine in input forces. By grouping
together joint moments into input forces, and reaction forces into output
forces, and substituting Eq. (3) for joint moments, it is evident that reaction
forces are affine in muscle fibre and motor unit forces, The relationship
may be written in the form:

$$r = L_r(q, \dot{q}) \cdot f + s_r(q, \dot{q}), \tag{6}$$

where r is the vector of reaction forces of interest, $L_r(q, \dot{q})$ is a (generally
non-diagonal) matrix, and $s_r(q, \dot{q})$ is a vector (see Kuo and Zajac, 1993a,
for a detailed derivation).

3.5. Actions are affine in motor unit forces

The development above leads to a generalized description of motor tasks
based on the term *action*. The popular use of kinematics to describe
movement proves inadequate when considering the ability of humans to
control force alone (as in an isometric contraction against an immovable
object) or even control force and position simultaneously (as in turning a
screwdriver). A fully generalized description of movement must be flexible
enough to describe any combination of force or position control.

Because both accelerations and forces are affine in motor unit (input)
forces, both can be combined into a single affine equation defining *action*:

$$a = \begin{bmatrix} \ddot{q} \\ r \end{bmatrix} = \begin{bmatrix} L_q(q, \dot{q}) \\ L_r(q, \dot{q}) \end{bmatrix} f + \begin{bmatrix} s_q(q, \dot{q}) \\ s_r(q, \dot{q}) \end{bmatrix} = L_a(q, \dot{q}) \cdot f + s_a(q, \dot{q}). \tag{7}$$

Thus, the time-varying action vector is a full description of motor tasks,
whether of movement or isometric contraction. It can describe all the joint
angles and contact forces in the body. Though Eq. (7) defines a explicitly,
the action is abstract, in the sense that the coordinates that the CNS uses
for it are unknown, so that a cannot be assigned an actual value. It is
useful to describe actions in terms such as pushing against a wall or flexing
the elbow as mentioned in the previous section, although these terms do
not describe how the CNS encodes these commands. (Note that matrix L_a
is not in general square or full rank, i.e., accelerations and reaction forces
are not linearly independent.)

It is important to note that the experimentalist has access to only a subset of the information describing an action. Moreover, this subset is biased by the choice of coordinate systems and units in which it is measured. The possible operations of scaling, change of coordinates, re-ordering of elements, and extraction of a subset of the action vector can be described by

$$\hat{a} = L_T(q, \dot{q}) \cdot \begin{bmatrix} \ddot{q} \\ r \end{bmatrix} + s_T(q, \dot{q})$$

$$= \left[L_T(q, \dot{q}) \cdot L_a(q, \dot{q}) \right] \cdot f + \left[L_T(q, \dot{q}) \cdot s_a(q, \dot{q}) + s_T(q, \dot{q}) \right]. \quad (8)$$

The result is an *instance* of the action a, that is in coordinates which are convenient for the observer and the task. The symbol $\hat{a}$ denotes a task-oriented instance of a. Note that while the dimension n_a of a may be large, $\hat{a}$ may be any dimension that is useful for studying a particular motor task. The various types of actions are summarized as follows:

$\bar{a}$ the desired action, encoding a motor command (e.g., a joint flexion, a push, etc.),

a the actual action, the result of a motor command, which is fed back after being sensed,

$\hat{a}$ the action measurement made by experimentalists, in coordinates convenient for analysis; each set of measurements is an instance of a.

It is important to recall that a and $\bar{a}$ are abstract vectors, encoded by the CNS in an unknown coordinate system, while $\hat{a}$ is a vector which can be measured in some particular coordinate system and which contains a useful subset of the information contained in a.

3.6. Effects of musculoskeletal mechanics may be visualized

Affine mappings of actions may be visualized to offer interpretations of the effects of dynamic coupling. Consider the simple example of a two-segment planar linkage, actuated by six homogeneous ideal muscles (in which all motor units have identical activation) with equal moment arms (see Fig. 3a). Actuation of forces within these muscles, comprising vector f (Fig. 3b), produces a moment vector which can be visualized in moment space (Fig.
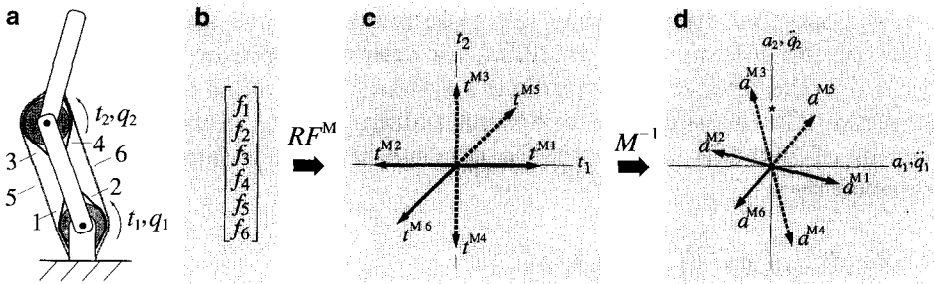
Fig. 3. Dynamic coupling and coordinated use of actuators. (a) A sample two degree-of-freedom system, with six actuators. (b) Normalized forces are described in a vector. (c) Matrix RF^M maps normalized forces into moments. Each actuator produces a moment vector as shown. (d) Inverse mass matrix maps moments into actions. In this example, the actions correspond to angular accelerations of the two joints. Each actuator produces an action vector. To produce a desired action, the individual actuator actions are summed in a weighted combination, with the weights determined by normalized forces f. In this example, a pure joint extension, denoted by the asterisk, requires the coordinated activation of more than one muscle. One likely combination involves actuators 2, 3, and 5. Although actuators 2 and 5 are traditionally considered antagonists, they can work together to produce action.

3c). Each muscle's moment, weighted by the fraction of muscle force exerted, contributes to the total moment vector.

Multiplying the inverse mass matrix by the moment vectors results in acceleration vectors for each muscle (Fig. 3d). One possible interpretation of this matrix multiplication, based on singular value decomposition (Strang, 1988), is that the moment axes are rotated, followed by an additional compression or elongation of the axes, the result of which is subjected to an additional rotation, leaving the system in its output coordinate frame. The overall projection from f to $\ddot{q}$ depends upon body configuration, as does the state-dependent vector of Eq. (5) which is added to this result (and assumed to be zero in this example) to form the net action. This paper considers the general form of the f to $\ddot{q}$ projection, so that the actual matrix values forming the projection are unimportant.

The result of a muscle or motor unit contraction is not generally confined to acceleration of the DOF(s) it actuates. Rather, to accelerate only a single DOF, as with most actions, generally requires the proportioned activation of more than one muscle (see Fig. 3d). The action due to muscles is the vector sum of the appropriately weighted individual muscle action vectors. There are often many weighting combinations that will produce a given action. For example, the desired action of extending joint 2 in Fig. 3d can be achieved by activating muscles 3 and 5, or muscles 1 and

3, muscles 1, 3, and 5, etc. Of special note is the combination of muscles 2 and 5, traditionally regarded as antagonists, but which work together in this example to produce the joint extension.

The visualization of actions demonstrates that the execution of actions requires coordinated activity of muscles, whether or not they are regarded as antagonists. Herzog and Binding (1992) used optimization techniques to show how antagonists may be co-activated in some motor tasks. The example of Fig. 3d is a graphical interpretation of the same phenomenon. The desired action acts as an additional constraint on the muscle forces, which nevertheless outnumber all constraints. Optimization is used to resolve the system, so that muscle forces are distributed to minimize a cost function. Whatever the particular cost function chosen, the co-activation of muscles 2 and 5 remains a viable solution, despite the inconvenient label of antagonistic activity. In fact, the only instance when two muscles are truly antagonistic is when their actions entirely oppose each other. In systems consisting of hinge joints, this situation occurs with uniarticular muscles on opposite sides of each joint or when bi-articular muscles have moment arms which are perfectly configured to achieve opposite actions. In other cases, the sum of two non-opposing muscle actions together will generally result in a non-zero action. In more realistic systems, in which joints have multiple DOFs (e.g., ball-and-socket joints), there are in fact few cases in which two muscles perfectly oppose each other. Thus, in multi-DOF systems, muscles can rarely act as pure antagonists.

4. Cost of coordinated movement

The vectorial approach to describing multi-DOF movement shows that when muscles are coordinated, they produce actions with components opposing each other and components acting together. Presuming that some combinations of actuators may be more effective than others at producing a given action, it is possible to assess a cost to activating muscles which in some way reflects the cost (metabolic and otherwise) to the human body. The CNS could use this cost as a criterion for distributing forces between motor units.

The hypothesized requirements for a useful measure of movement cost are that the cost must increase both with effort or force exerted, and with increasingly antagonistic behavior (ignoring possible benefits of coactiva-

tion, such as increased joint stability). These requirements are met by the mathematical measure of the magnitude of a vector, the p-norm of an n-vector x (denoted $\| x \|_p$; see Chvatal, 1983):

$$\| x \|_p = \left(\sum_{i=1}^{n} | x_i |^p \right)^{1/p}. \tag{9}$$

The norm is a scalar whose description of the size of a vector depends on the value of p. For example, $\| x \|_1$ gives the summed absolute values of x, $\| x \|_2$ gives the familiar Euclidean length of x, and $\| x \|_\infty$ gives the largest magnitude of the individual elements of x.

The p-norm may be used to assess the cost of coordinating motor units by substituting the normalized force vector f for x in Eq. (9). Because peak isometric force is proportional to physiological cross-sectional area (Zajac, 1989), muscle stress (defined as force divided by cross-sectional area) is proportional to normalized motor unit force. Thus, $\| f \|_p$ is a norm of muscle stress, similar to the objective functions used in other studies, with values of p between 2 and 4 (Dul et al., 1984; Pedersen et al., 1987). Minimization of $\| f \|_1$ may be regarded as minimizing the summed total stress exerted, at the expense of activating some muscles much more than others. Higher values of p will tend to encourage greater distribution of stresses, with minimization of $\| f \|_\infty$ producing maximum sharing of stresses, at the possible expense of larger summed total stress.

Using a simple 2-DOF system as an example, the p-norm may be used to demonstrate the effect of the number of actuators on the cost of producing an action, regardless of what value of p best mimics the CNS criterion for distributing forces. As shown in Fig. 4, the hypothetical system consists of m homogeneous actuators, distributed evenly about the 2-dimensional action space. (This system could, for example, correspond to the two degrees of freedom of a ball-and-socket joint, or the two joint rotations of Fig. 3, in which the actuators have a variety of origins and insertions.) To produce any given action a of Euclidean length 1, there exists a force distribution, specified in vector f, minimizing $\| f \|_p$. Because the minimum $\| f \|_p$ varies with a, the costs will lie in a range between best and worst possible cases for the generic a of length 1.

Fig. 5 shows the range of possible costs for varying numbers of actuators and varying values for p. The results show that whatever the value for p used in the force distribution objective, the potential cost for executing an
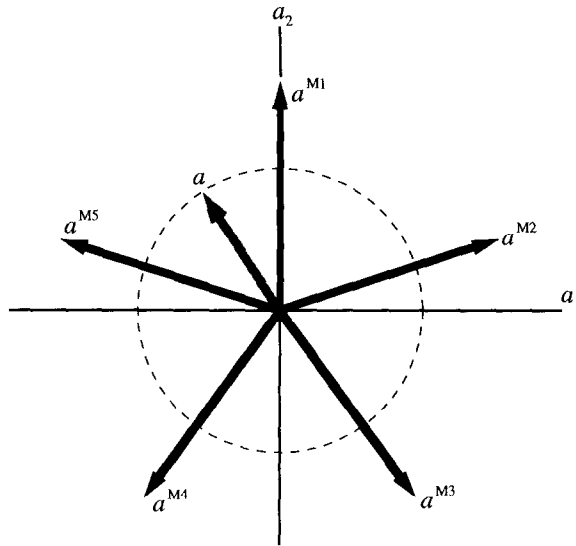
Fig. 4. Sample two degree-of-freedom system with m homogeneous actuators, distributed evenly through action space. The figure shows the configuration for $m = 5$. The cost of producing an action a with length 1 (arbitrary coordinates) is to be determined. An example of a corresponding physical system is the hip joint, with five muscles distributed around the ball-and-socket joint.

action decreases with increasing numbers of actuators. The cost saving is most dramatic between small values for m, such as between 3 and 4.

In the general case, actuators are neither homogeneous nor evenly distributed through the action space (which is also of higher dimension). It is also possible that the objective of minimizing the p-norm poorly models the criteria by which the CNS distributes forces. Nevertheless, cost of performing an action can potentially be reduced even for different conditions, as a simple induction argument demonstrates. Beginning with a minimal, non-redundant set of heterogeneous actuators, consider the addition of another muscle which does not duplicate the action of any other actuator. This additional actuator cannot increase the cost for any desired action, because the CNS always has the option of leaving that muscle unactivated. In general, there exists a desired action collinear with the additional actuator's action, which can then be achieved at lower cost than possible before the additional muscle was included. Each additional actuator will similarly lower the potential cost of performing an action.

5. Feasible actions and muscle strength

Aside from lowering the cost of producing many actions, actuator "redundancy" has the effect of increasing the range of actions possible. The set of all feasible actions can easily be computed using methods described by Kuo and Zajac (1993b). This feasible action set (FAS) depends on the characteristics of individual actuator actions, and represents the entire range of possible actions, given all possible combinations of muscle activations.

Visualization demonstrates how redundant actuators affect the size of the feasible action set. Consider a two DOF system which must, at the
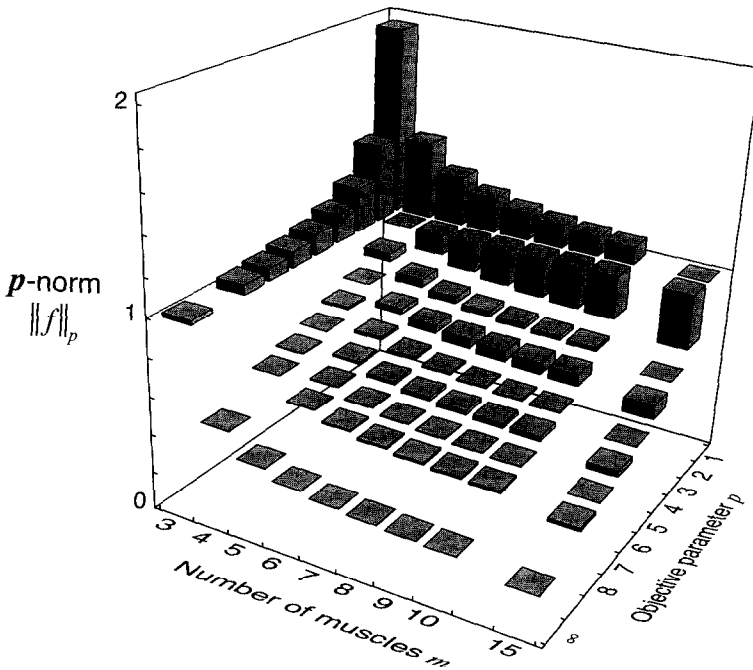

Fig. 5. Possible range of costs for producing actions of length 1 for a two degree-of-freedom system. The number of actuators m is varied, but actuators are always evenly spaced and have equal lengths as in Fig. 4. Costs are shown for minimum p-norm solutions to the force distribution problem for varying values of p. The p-norm describes the optimization objective, and is equivalent to the summed muscle stresses, raised to the power p. Higher values of p encourage greater degree of shared stress. Actual cost always lies within the range shown, and depends on what particular action a is desired. The figure shows that regardless of the value of p, increasing the number of muscles lowers the potential cost of executing a motor task.
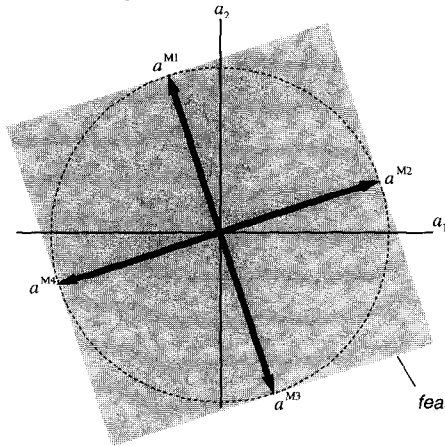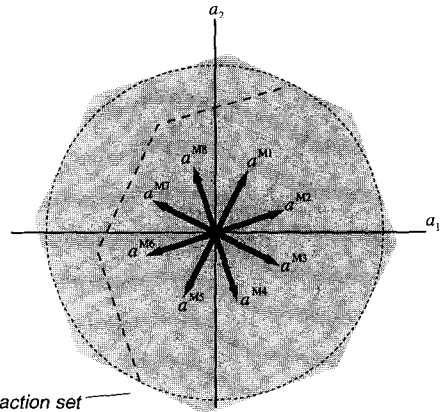
a. 4-Muscle System   **b. 8-Muscle System**

Fig. 6. Feasible actions for four- and eight-actuator, two degree-of-freedom systems. Actuators are homogeneous and evenly distributed. The circle signifies the minimum requirement of achievable actions. (a) For a four-actuator system, feasible actions lie within a square (shaded region). (b) For an eight-actuator system, feasible actions lie within an octagon, and actuators capable of producing 41% of the force of actuators in the four-actuator system are able to achieve minimum required actions. When actuator 7 is removed, the feasible action set is significantly reduced in size, as shown by dashed line, so that minimum requirements can no longer be achieved. When many actuator are available, less force is required of each of them to produce necessary actions. But loss of any one actuator significantly reduces the feasible action set.

minimum, be able to produce actions of Euclidean length 1. (For example, nominal function may require a minimal moment about the hip in both flexion/extension and abduction/adduction.) A comparison of systems with four and eight actuators shows that with a larger number of actuators, each actuator needs to produce an action of smaller magnitude to fulfill the minimum specifications (see Fig. 6).

The removal of an actuator will analogously reduce the size of the feasible action set. In the example, the effect of removing a single actuator is a severe reduction in the range of actions possible (Fig. 6b). This trade-off makes it difficult to study redundancy in terms of muscles in excess of a theoretical minimal set. Given bounds on achievable forces, muscles cannot be considered redundant in the sense of being superfluous. Rather, the large number of muscles, while indeterminate, are placed and sized to fulfill the requirements of a biomechanical system confronted by the need to perform a variety of motor tasks.
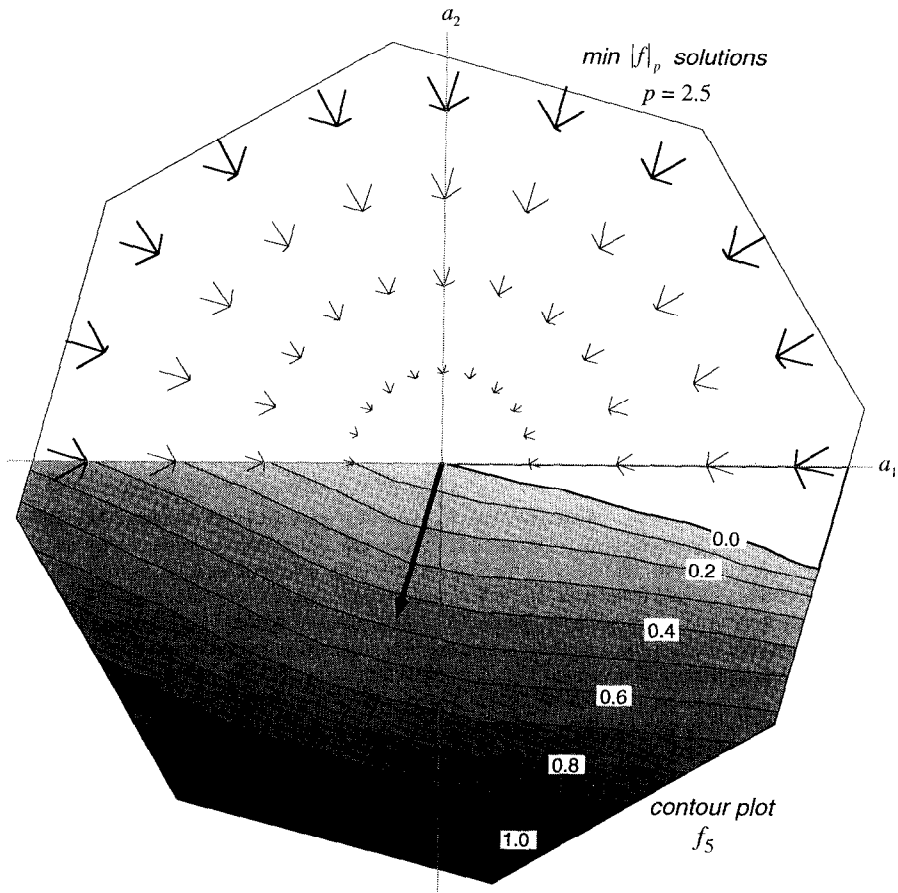
Fig. 7. Diagram showing force distribution solutions for the 8-actuator system of Fig. 6b. The figure shows the feasible action set delineated by an octagon. In the top part of the figure, line segments show relative weights (normalized forces) for each of the eight actuators. Solutions are shown for minimum $\| f \|_p$, with $p = 2.5$. The bottom part of the figure shows the normalized force for actuator 5 (action denoted by arrow) varying with action in a contour plot. For nearly half of the feasible actions, a non-zero force in actuator 5 contributes to the overall action. A topographic feature map stores the relative weights for each action direction, shown in the outer ring of the top part of the figure.

The force distributions necessary to produce a range of actions within the feasible action set are shown in Fig. 7. For a given action, the minimum-$\| f \|_p$ solution specifies the relative excitation of each actuator. These solutions vary as the action direction varies, and scale with the action magnitude (Fig. 7, top). From the viewpoint of a single actuator, the amount of excitation also varies with the action. In this example, each

actuator produces a non-zero force for nearly half the feasible actions (Fig. 7, bottom). As discussed below, these characteristics of minimum-$\| f \|_p$ solutions to the force distribution problem are amenable to implementation in the CNS.

6. CNS solution of the force distribution problem

The CNS appears to solve the force distribution problem using parallel distributed processing circuitry to perform the transformation from action commands into a large number of motor unit commands. In addition, this solution appears to be found without expending the considerable computational and often iterative effort usually assorted with resolution of indeterminacies by computer. It is perhaps more appropriate to examine how a PDP solves such problems than to study the computational steps that would be performed by more traditional serial computers.

It is also suggested that the mapping must be at least partially plastic and have an ordered structure. The difficulty of encoding a vast number of interneuronal connections in a genetic program, as well as the fact that the body and its dynamics change over time, imply that the force distribution centre must have some ability to adapt. An ordered structure is hypothesized to be simpler to specify in a genetic code.

Kohonen (1982b, 1982a) has shown that self-organizing networks fulfill many of these specifications. These maps have a topographical structure, meaning that input signals excite specific regions of the network, with the locations varying regularly and continuously with the input signal. Moreover, neurons within the network tend to connect primarily to their closest neighbors, in fast, short paths. As discussed below, many similar characteristics are embodied in the spinal cord and primary motor cortex.

The self-organizing network consists of a layer of neurons which constitute a topographic feature map (Kohonen, 1982b). Each neuron produces a graded response according to the weighted sum of its inputs. Nerves carrying incoming signals synapse on neurons within the layer. These neurons interact laterally in a simple fashion: nearby neurons tend to have excitatory synapses, while spatially-distant neurons tend to have inhibitory synapses. This internal feedback results in spatially bounded "excitation zones" for particular input signals. If related input signals result in spatially-related excitation zones, the layer functions as a "topographical feature map". A simple variation of the Hebbian learning rule, in which a

correlation between pre- and post-synaptic activity results in strengthening of a given synapse, causes a network to converge on such a feature map (Ritter et al., 1992).

A simple model based on a previous example (Figs. 6b and 7) shows that topographic feature maps are ideally suited for solving the force distribution problem. Initially assuming that action *magnitude* is encoded in neural firing frequency, the action *direction* can be stored as relative weights to associated motor neurons. For example, consider the actions lying on the outer edge of the feasible action set (Fig 7). Each action (of twenty circumscribing the feasible action set in Fig. 7), when delivered to the map as input, excites a local excitation zone. Consider the case in which the local excitation zone consists of a single neuron (hereafter referred to as an *action neuron*) in the map. Each action neuron excites up to four of the eight motor neurons in the example, with the magnitude of the action regulated by firing frequency, and direction regulated by synaptic weights, which govern relative weights of the outputs. A topographic arrangement implies that neurons encoding actions of similar direction are located close to one another. (In fact, one possible arrangement is a ring, as in Figs. 7). Fig. 8 depicts the mapping from action command to motor unit command pictorially.

The synaptic weights for this network are determined through learning. The information necessary to adjust each weight includes pre- and post-synaptic activity (a Hebbian learning rule), augmented by feedback on the resulting action, which is necessary to achieve a minimum-norm solution.

Two characteristics are immediately recognized from this model. First, nearby action neurons in the feature map have similar, but not identical, outputs which vary spatially. Second, each motor neuron has a "receptive field" on the feature map which corresponds to a physical region within the map. The upper half of Fig. 7 illustrates the spatial variations in output weightings, while the bottom half shows how each motor neuron's receptive field varies.

The topographic feature map also makes it possible to spatially encode action magnitude. Starting with a local excitation zone of one target action neuron, local feedback (excitatory interconnections between nearby neurons) will cause nearby neurons to fire, as input magnitude increases. The output from these nearby action neurons will augment the output from the target action neuron, increasing not only the input to the target motor neurons, but also triggering additional, nearby motor neurons. In other words, the network provides for modulation of action magnitude through
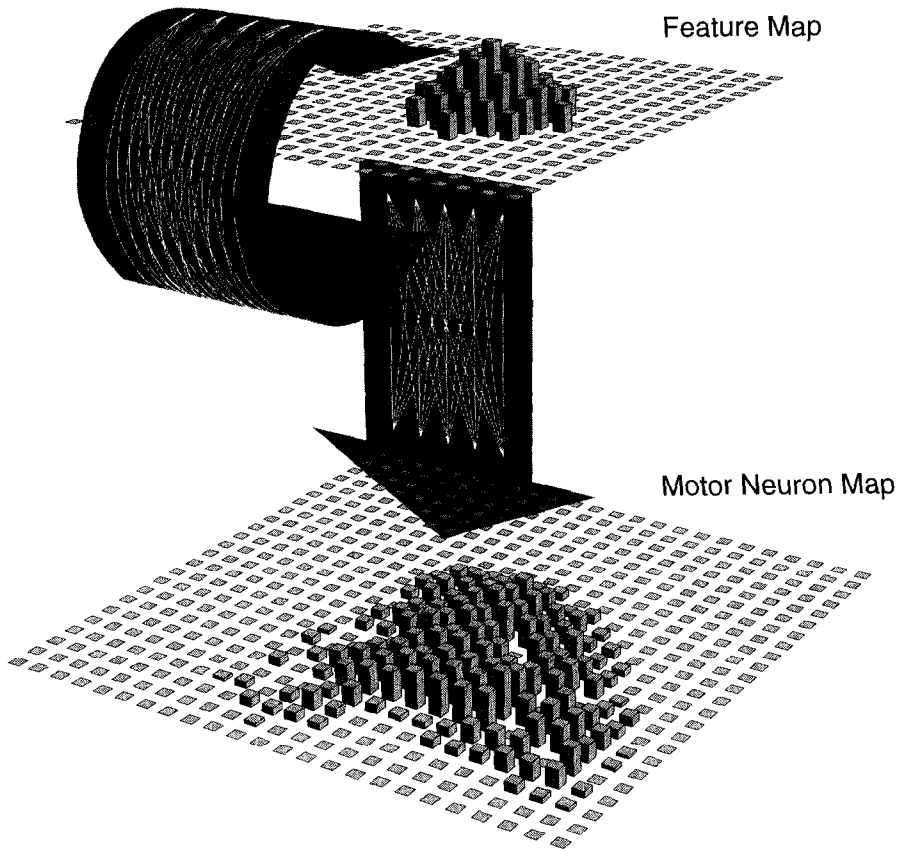
Fig. 8. Schematic diagram of hypothesized force distribution neural network. Neurons are arranged in two 2-dimensional layers (height of bars indicates level of activation in a neuron). Input to the feature map encodes a desired action. Internal feedback guarantees that the resulting excitation is confined to a region within the feature map, a *local excitation zone*. The local excitation zone varies regularly and continuously with the input, so that the feature map has a topographic organization. Output from this map is associated with a layer comprising the motor neurons. A particular local excitation zone therefore activates a group of motor units, resulting in an action. This association implies that the feature map is somatotopic, and maps action commands into motor unit commands. Given sufficient sensory feedback in conjunction with a simple learning rule, this network can produce minimum-norm solutions to the force distribution problem.

both firing frequency and motor unit recruitment. Excitation zones larger than one neuron also make it possible to vary action continuously, rather than as discrete jumps between successive action neurons.

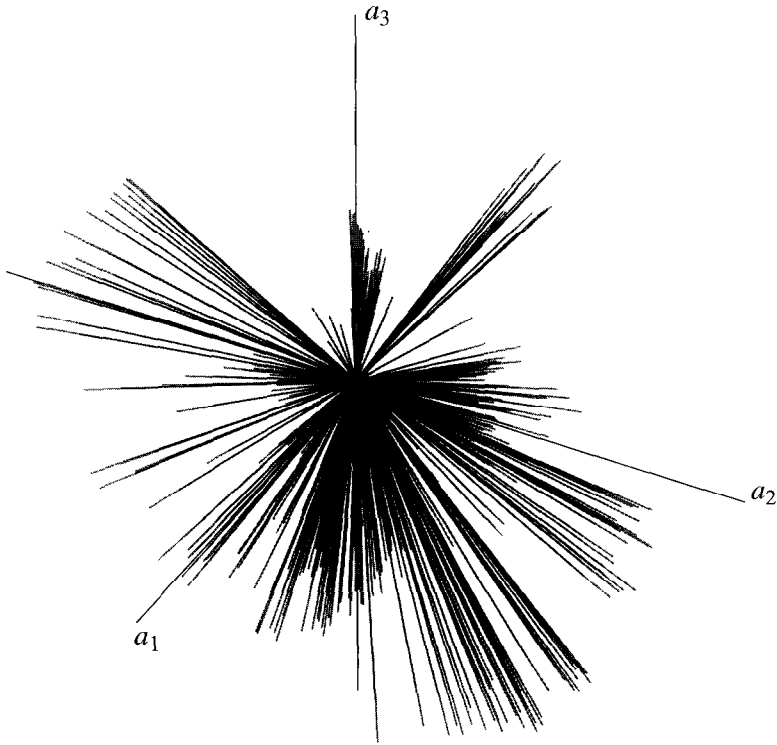One interpretation of the map is that excitation location encodes the

Fig. 9. Imaginary three degree-of-freedom system populated by heterogeneous, varied muscles. Each muscle comprises a bundle of motor units, shown by line segments. To produce a desired action, the CNS must excite an appropriate combination of motor units, possibly across several muscles. The CNS must have some adaptive ability to adjust for changes in the biomechanical or nervous systems. The number of joints crossed by a muscle does not impinge on how it is controlled, but a wide distribution of muscles facilitates the production of a wide variety of actions by "covering" regions of action space.

action direction (i.e., the type of movement) while excitation size and firing frequency encode the action magnitude (i.e., the magnitude of movement). The action magnitude corresponds directly to muscle forces and to contact forces and joint accelerations. Taking into account muscle activation-contraction dynamics, the network neurons could alternatively be interpreted as encoding rate of change of force.

When the model is extended to a more realistic system, it becomes evident that the input signal need not correspond to a single target action neuron. A system consisting of many muscles, many motor units within these muscles, and many DOFs (Fig. 9) will require a complex motor unit

activation pattern. For example, the act of throwing a baseball is an action requiring activation of many muscles in the lower extremity and torso in addition to the upper extremity. The multi-dimensional action space must somehow be mapped into a physically realizable two- or three-dimensional layer of neurons. However cleverly nature "unwraps" this multi-dimensional space, it is likely that many actions are associated with multiple excitation zones.

If input signals can correspond to multiple locations in the topographic feature map, it is possible to envision the production of multi-dimensional actions. In the case of the baseball throw, the upper and lower extremities need not be spatially related. Instead, the input signal could trigger a target location within each of the upper and lower extremity feature maps. The multi-dimensional nature of the upper extremity alone suggests that the arm itself may be broken into several feature maps. It would therefore not be surprising if a given motor unit's "receptive field" were non-contiguous, so that multiple representations could occur within the overall map.

The telephone directory offers an analogy to the problem of unwrapping multi-dimensional spaces. A phone book may be regarded as a one-dimensional map, with information listed in rows. The information given is typically three-dimensional, consisting of names, addresses, and phone numbers. While it is possible to form a topographic feature map using an alphabetical listing of names, it is impossible to simultaneously organize the other two dimensions topographically. This impossibility implies that two persons sharing the same phone number cannot be grouped spatially within the one-dimensional alphabetical listing. Thus, the shared number may have multiple representations in the book.

A neural network simplifies the problem of multi-dimensionality somewhat because it acts as a look-up table only on learned portions of the action space. More neurons are dedicated to actions involving fine control, in which more information is required, while few neurons are dedicated to grossly controlled or rarely used actions. Still, the mathematical model of projections between multi-dimensional spaces is inadequate for predicting the actual form of a topographic feature map. A more advanced model must take into account the amount of information stored in these maps as well as possible topologies for such a neural network.

The theoretical development above, when combined with experimental observations, suggests that the spinal cord, possibly in conjunction with the primary motor cortex, may be responsible for mapping between action commands and motor commands. The spinal cord contains motor neurons

and interneurons arranged in a topographical manner, while in the motor cortex, neurons organized in micro-columns form a two-dimensional layer of functional units, which act as a somatotopical map of movements (Kelly and Dodd, 1991). Experiments have shown that contiguous joints occupy contiguous (and overlapping) areas within the cortex. Voluntary movements involve the excitation of populations of neurons, which vary in an orderly manner with the direction of movement and activate groups of motor neurons in the spinal cord (Georgopoulos et al., 1992; Georgopoulos et al., 1982). Moreover, individual motor units have been shown to have non-contiguous, multiple representations (Kwan et al., 1978; Lemon, 1988). A rich set of sensory information is also fed back to both the motor cortex (Murphy et al., 1978) and spinal cord, facilitating adjustments of the map and minimization of an appropriate motor unit weighting function (such as the p-norm) through learning.

7. Discussion

The vectorial analysis of mechanics above shows that the large number of muscles distributed throughout the body, rather than posing a problem to the CNS, could be interpreted as offering efficient and flexible solutions to the CNS. More complicated models may reproduce biomechanical characteristics more faithfully, but the principles remain the same. These principles may be relevant to both biomechanists and motor control physiologists, and may suggest different interpretations of multi-joint movement.

One important principle to be extracted from this work is that the paradigm of single-joint movement does not generalize easily to multi-joint movement. In particular, the concepts of agonist/antagonists become confusing when two supposed antagonists (such as a uni-articular muscle opposite a bi-articular muscle in a two-joint planar linkage) can actually work together to perform an action. Also considering that many joints have multiple DOFs and thus require multiple actuators, it becomes especially difficult to even define which muscles act as antagonists.

A simpler interpretation regards motor units as producers of actions more general than rotations about one or more joints. Each motor unit produces one action, which may consist of multiple joint rotations and/or reaction forces. A muscle can produce only those actions conferred by its motor units, and the number of joints crossed by a muscle does not confer additional actions.

This interpretation reveals that the very notions of redundancy and indeterminacy are inconvenient for studying human movement. Because different actuators work together to perform movement, and because each muscle is physically limited in its force production, a mathematical redundancy poorly describes the true situation. The actual system must be able to coordinate these limited muscles (or motor units) in such a way as to produce a wide repertoire of movements. The significant reduction of the feasible action set caused by the removal of almost any muscle makes it difficult to consider any muscle superfluous. It is therefore perhaps inappropriate to consider the system redundant.

It must also be stressed that indeterminacy is a "problem" only to scientists, who presently lack the means to measure or deduce individual motor unit or muscle forces. But unlike the analytical or computational solutions to the force distribution problem, the CNS stores the necessary information in such a way that "solutions" may be found in real-time, without lengthy calculations. Consider the analogy of a lattice of a large number of springs, to which are applied a small number of static perturbation forces. Such a system could be considered indeterminate, because the individual displacements of the springs is not immediately evident. A lengthy series of nontrivial calculations can yield the solution. But the lattice of springs "solves" the problem simply by resting at a point of lowest potential energy. Similarly, a network of neurons solves problems by seeking states of lowest "energy" (Ritter et al., 1992; Hopfield, 1982). Just as the large number of springs in the lattice allows for flexible solutions for a wide variety of inputs, the large number of muscles in the body similarly provide the flexibility to produce many actions.

The fact that the CNS easily maps action commands into motor unit commands nevertheless does not solve the problem of predicting or choosing a value for p in an optimization. However, the findings above explain why several possible values for p are reported in the literature (Dul et al., 1984). In Fig. 6b, the octagon defining the external boundary of the feasible action set may be regarded as the contour of constant $\| f \|_\infty$, while the dashed circle may be regarded as the contour of constant $\| f \|_2$. As the number of actuators increases, the constant-$\| f \|_2$ through constant-$\| f \|_\infty$ contours become increasingly similar. The minimum-norm costs therefore also become similar, regardless of the value for p. This makes it difficult, in "over-actuated" systems, to use optimization to predict p from kinematics. But it also makes the choice of p in an optimization-based simulation non-critical.

While this paper focuses on the mapping from action to motor unit commands, it does not address how the desired time-varying action trajectory is influenced. Other work (Kuo and Zajac, 1993b,c; Kuo, 1993) has shown that body dynamics and musculoskeletal geometry dictate features of the feasible action set, so that not all actions are equal. The CNS appears to have a dynamic awareness, which is used to harness more favorable actions when possible to minimize the overall cost of movement over time. But whatever the choice of desired action, it is formed by the coordination of (many) motor unit actions.

Another obstacle to understanding CNS coordination is the choice of coordinate systems used for analysis. Familiar kinematic measurements such as joint angles or Cartesian coordinates necessarily bias any study, because they have limited relation to neural coding of movement. Using joint moment coordinates, it is tempting to define uni-articular muscles as the canonical muscles for movement, and therefore to consider bi-articular muscles to be special additions to this canonical set. But the fact that roboticists consider uni-articular muscles to be a minimal, a canonical set does not imply that the CNS does so as well. This analysis has shown that a large variety of muscles facilitates efficient production of a wide repertoire of actions. This variety is constrained by biomechanical considerations, such as the difficulty of routing muscles with exceedingly disparate origins and insertions or excessive length during development. In addition, the efficiency advantages of "over-actuated" systems are greatest for small numbers of additional muscles. Whatever the number of muscles, uni-articular and bi-articular designations are biased by the joint coordinate system, and do not take into account the DOFs involved.

It is in fact entirely possible that the CNS knows nothing of joints, but only of multi-DOF movements. While local excitation zones in the primary motor cortex could correspond to individual joint rotations, it is also possible that they correspond to combinations of DOF rotations. Movements subject to dynamic coupling, such as shoulder and elbow movements, would likely have overlapping representations in the motor cortex. But movements which are not strongly coupled dynamically, such as finger and toe movements, would likely have separate, possibly non-contiguous, excitation zones. Of course, the apparent two-dimensional structure of the motor cortex could hide an underlying multi-dimensional network, which would remove some of the topological considerations of which excitation zones are contiguous.

Nor need the CNS know of uni-articular or bi-articular muscles. All

types of muscles make unique contributions to actions, and their representation in the motor cortex is not likely to be differentiated on the basis of number of joints, or even DOFs, crossed. Rather, the CNS needs only to associate each actuator with its unique action.

This work leads naturally to future studies of force distribution. Neural network simulations may lead to new insights to the encoding of the action command, and to specifics of the force distribution mapping. Information theory may yield data on what portions of action space are learned with high resolution, and the number of bits encoded in the action command. Topological studies may offer likely structures for the self-organizing force distribution map, as well as shapes and arrangement of excitation zones.

While the analysis above ignores issues of control, stability, and timing, the force distribution for dynamic movement must have some dependence on these issues. Since muscle time constants are in reality heterogeneous, the CNS must coordinate motor units based not only on the actions they produce but also on their ability to produce force within a time frame. Optimal control is a useful technique for simulating this activity. But as always, it is important to understand the problem being studied.

Acknowledgments

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