



## Action and perception at the level of synergies

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### Abstract

Meeting the challenge of assembling coherent organizations of very many muscles characterizes a functional level of biological movement systems referred to as the level of muscular–articular links or synergies. The present article examines the issues confronting the forming, regulating, and ordering of synergies and the hypothesized principles, both classical and contemporary, which resolve them. A primary goal of the article is to highlight the abstractness of the concepts and tools required to understand the level's action-perception competence. Coverage is given to symmetry groups, task space, order parameters, metastability, biotensegrity, allometric scaling, and impredicative definitions.

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### 1. Introduction

A traditional intuition is that the human movement system is hierarchical, with each level solving a particular class of motor problems in the assembling of an act (Bernstein, 1996; Jackson, 1898; Weiss, 1941). The term hierarchy is used broadly, referring to an organization analyzable into successive sets of subsystems without implying, necessarily, a relation of subordination among them (Jordan & Rosenbaum, 1990; Simon, 1962;

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Turvey, 1977). In Bernstein's functional hierarchy, the level responsible for forming synergies of large muscle groups and different patterns of locomotion is referred to as *the level of muscular-articular links* or *synergies*. The shape of this level is defined by the central problem of movement control and coordination: The problem of degrees of freedom – the problem of how to compress the movement system's state space of very many dimensions into a control space of very few dimensions. This compression is the expertise of the level of muscular-articular links or synergies. The coherence, harmony and precision timing of rhythmic limb movements and speech movements typify the level's special expertise.

### 1.1. Speech and concinnity

When one considers speech, there is a tendency to view the expertise somewhat narrowly as resolving issues of sequence. A little consideration suggests that more pertinent issues may be of the adaptive fit of parts of the speech system to each other and to the speech system as a whole – that is, issues of *concinnity*. Table 1 identifies the muscles of speech. They are approximately 70 in number and the simplest utterance, e.g., a consonant vowel syllable such as /pa/, seems to involve all of them (Abbs & Connor, 1989). Respiratory movements of the diaphragm, rib cage, and abdomen, laryngeal movements of the

Table 1  
The muscles of speech (adapted from Abbs and Connor, 1989)

<i>Respiratory</i>	<i>Velar</i>	<i>Laryngeal</i>
Diaphragm	Levator palatini	Sternohyoid
Pectoralis major	Tensor palatini	Omothyoid
Pectoralis minor	Musculus uvulae	Thyrohyoid
Subclavius	Palatoglossus	Thyrohyocallis
Serratus anterior	Palatopharyngeus	Posterior cricoarytenoid
External intercostals		Lateral cricoarytenoid
Levator costalis		Cricothyroid
Serratus posterior superior	<i>Facial</i>	
Sternocleidomastoid	Buccinator	<i>Lingual</i>
Scalenus medius	Risorius	Superior longitudinal
Scalenus posterior	Quadratus labii superior	Transverse
Latissimus dorsi	Quadratus labii inferior	Vertical
Sacropinalis	Zygomaticus	Genioglossus
Triangularis sterni	Mentalis	Styloglossus
Subcostals	Traingularis	Palatoglossus
Serratus posterior inferior	Caninus	Hyoglossus
Iliocostalis dorsi	Incisvis labii superior	
Iliocostalis lumborum	Incisvis labii inferior	
Quadratus lumborum	Platysma	<i>Masticatory</i>
External oblique		Digastricus
Internal oblique		Mylohyoid
Transversus abdominus	<i>Pharyngeal</i>	Geniohyoid
	Inferior constrictor	External pterygoid
	Middle constrictor	Masseter
	Superior constrictor	Temporalis
	Stylopharyngeus	Internal pterygoid
	Salpinopharyngeus	
	Pharyngoplatinus	

trachea, thyroid, cricoid, and arytenoid cartilages, and articulatory (upper airway) movements of the pharynx, tongue, soft palate, lips, and jaw, must be coordinated. The required concinnity of event timing in the respiratory, laryngeal and articulatory systems for the simplest of utterances is demanding. This demand is much greater than that suggested by the division into three systems, however. The required concinnity is manifest simultaneously over multiple linkages among respiratory, laryngeal and articulatory events. For example, the synergy that produces the single gestural feature of bilabial closure – a feature that is concurrent with many other features in the production of a consonant such as *p* – involves coordinate activity in muscles of all three systems. In sum, an account of speech that addressed issues of sequencing but not issues of concinnity would be far from complete.

### *1.2. Defining synergy: First approximations*

How should the concinnity of muscles and muscle systems be characterized? How should the coordination of synergies and the transitions among synergies be addressed? How should synergy be defined? The latter question is taken as the starting point.

The literature tends to retain an anatomical perspective on synergy, in the sense of a fixed arrangement of agonists and antagonists. Traditionally, “synergists” are muscles having similar actions at a joint. There is much that argues against this tradition, as emphasized by *Boylls (1975)* and *Gelfand et al. (1971)*. For them, synergy is a functional concept, not an anatomical concept. It should connote a usage of linkages among muscles *in a behavioral situation*.

The arguments in question have provided good reason for dallying with alternative designations for the synergic phenomena of biological movement. Given inadequacies in traditional applications of the term synergy, other terms have been nominated such as coordinative structure (e.g., *Fitch, Tuller, & Turvey, 1982*), uncontrolled manifold (*Latash, Scholz, & Schönner, 2002*), and coordination mode (*Balasubramaniam & Turvey, 2004*). To anticipate, at issue is a label that conveys the notion of a collection of relatively independent degrees of freedom that behave as a single functional unit – meaning that the internal degrees of freedom take care of themselves, adjusting to their mutual fluctuations and to the fluctuations of the external force field, and do so in a way that preserves the functional integrity of the collection.

#### *1.2.1. Agonist–antagonist–stabilizer distinction*

When muscles act on multiple limb segments or about multiple axes of rotation, the division into agonist, antagonist and stabilizer is not an anatomical given but a (complicated) function of joint angles, lengths of the links, moment arms, and force directions. The classical diatribe against anatomically oriented accounts of coordination and the conventional overemphasis on the hinge joint is that of *Weiss (1941)*. While a sharp separation of the muscles of a hinge joint into agonists and antagonists is easy, Weiss highlighted that it is neither a separation nor a classification with warrant in the case of a ball joint. Any one of the muscles at the shoulder, for example, can be engaged in-phase or antiphase with any other muscle. For each arm movement, the grouping of muscles is different. With the proper muscle groupings, the proper phasing, and the proper contractile states, the humerus can be made to move in a complete circle and along all of the circle’s diameters (e.g., *Levin, Ouamer, Steyvens, & Swinnen, 2001*). Weiss (1941) argued that, whereas the

adoption of a single degree-of-freedom joint as the model system gives license to anatomical accounts of coordination (e.g., excitatory and inhibitory paths between neural centers for flexion and extension), adoption of a multiple degrees-of-freedom joint does not. At the shoulder and hip, the organizational problems of coordination are illuminated: What principle(s) select the muscles in specific roles for a given limb trajectory? What principles realize the requisite phasing and gradations of muscle contractions for the selected grouping?

### 1.2.2. *Rapid, remote adjustments*

Arguably, a movement synergy (alias coordinative structure, uncontrolled manifold, coordination mode) is an analogue of a physical cooperativity (Kugler & Turvey, 1987). The latter is stable by virtue of irreversible processes at the atomistic or components level. The stability is evident in the resistance of the cooperativity to perturbation. When perturbed, a physical cooperativity preserves its macroscopic steady state (a potential distribution) through systematic adjustments of its atomistic level. Speech production research (Kelso, Tuller, Vatikiotis-Bateson, & Fowler, 1984) has provided elegant examples for such cooperative resistance.

A speaker repeating a single-syllable utterance can be perturbed while doing so, for example by a brief load applied to the jaw. If the utterance (the macroscopic steady state) is “bab” and the perturbation is delivered as the jaw moves upward to perform its role of enabling vocal tract closure for the final phoneme /b/, adjustments of other involved articulators, specifically the upper and lower lips, occur within delays of 15–30 ms. The adjustments in question preserve the acoustic integrity of the utterance. Importantly, in respect to grasping the essentials of *synergy as cooperativity*, the rapid and adaptive adjustments are not at the site of the perturbation but at some remove from it.

Producing “bab” is one synergy of the muscles of tongue, lips, and jaw. But the same muscles and articulators, the same subsystems or degrees of freedom, can most obviously be called upon to produce other syllables. The latter is simply a way of saying that the muscular organization for “bab” cannot be one of hard assembly. It can only be one of soft assembly (Kugler & Turvey, 1987). The softness is clarified by the following fact: perturbation of the jaw temporally proximate to the completion of the production of “baz” is not responded to by the lips but by the tongue. Amplification of activity in the genioglossus, expediting movement of the tongue to the roof of the mouth, ensures production of the fricative /z/. The adaptive readjustment of the tongue occurs rapidly, within 20–30 ms of the perturbation.

Given the facts highlighted in Section 1.1 and Table 1, the remote and rapid readjustments ensuring the integrity of syllable production (of “baz” and “bab”) must necessarily involve more than the vocal tract degrees of freedom measured in the experiments. In the following remarks, Bernstein (1967, p. 69) foreshadows the larger story:

“Movements react to changes in one single detail with changes in a whole series of others which are sometimes very far removed from the former both in space and in time, and leave untouched such elements as are closely adjacent to the first detail, almost merged with it. In this way *movements are not chains of details but structures that are differentiated into details*; they are structurally whole, simultaneously exhibiting a high degree of differentiation of elements and differing in the particular forms of the relationships between these elements”.

Inter-digital coordination parallels the coordination observed among speech articulators. Investigations of the normal and tangential forces exhibited by the hand in the execution of a prismatic precision grip (thumb and fingers in opposition) present a rich picture of a global pattern of change among 15 elemental variables in response to a local change in one of them (Zatsiorsky & Latash, 2004; Zatsiorsky, Latash, Gao, & Shim, 2004).

### 1.2.3. Context-sensitive roles

The inadequacy of the agonist–antagonist–stabilizer classification of muscles is more severe than Weiss (1941) anticipated. *In vivo* work-loops reveal that depending upon the action context, a muscle can function as a brake, a strut, a tuner, a meter, and a spring, as well as functioning as a motor (Dickinson, Farley, & Full, 2000). A muscle can also function in ways that await appropriate labels (e.g., redistributing moments or finely tuning the ground reaction force, Jacobs & Van Ingen Schenau, 1992; Kargo & Rome, 2002). An important implication is that muscles in a single anatomical group (e.g., the muscles that swing a leg) do not necessarily share a common mechanical function (Ahn & Full, 2002). The implication, stated more generally, is that redundancy in a multiple-muscle group may represent diversity in muscle function (Dickinson et al., 2000). If such is the case, then the coordination that characterizes a synergy may not be so much a cooperativity of individuals (i.e., muscles) as it is a *cooperativity of roles* (i.e., context-dependent functions) (Turvey & Fonseca, in press).

### 1.2.4. Synergies as a “basis”

It has been hypothesized that particular patterns of muscular activities could form a base set analogous to the concept of *basis* in the theory of vector spaces: a minimal number of (linearly independent) elements that under specific operations generate all members of a given set, in this case, the set of all movements (Easton, 1972; Turvey, 1977). If synergies could compose such a basis, and if each synergy was self-monitoring, then the duties of other functional levels of the movement system would reduce to orchestrating the specific operations (Turvey, 1977). Patently, the synergies-as-basis hypothesis implies that all movement patterns share the same synergies.

The hypothesis is currently receiving considerable attention (e.g., d’Avella & Bizzi, 2005; d’Avella, Saltiel, & Bizzi, 2003). Multidimensional factorization can help identify muscles whose activations cohere in the course of a functionally well-defined movement (such as hindlimb kicking in frogs) and are observed to do so in similar fashion over multiple variants of the well-defined movement. The identified coherent organizations can then be tested for their ability to accommodate the variance in the multi-muscle activity of a new instance of the same movement or of instances of different movements. Ideally, relatively few of all coherent muscle groupings suffice to accommodate the variances of the same and different movement types (d’Avella et al., 2003). Data and simulations suggest that any basis synergy defined in the preceding manner can be scaled in amplitude by a non-negative coefficient (leaving the relation among the individual muscle amplitudes invariant) and shifted in time by an onset delay (leaving invariant the phase relations among the individual muscle onsets). In theory, the basis set of synergies, the two operations performable upon them (tuning the amplitude and delay coefficients), and a principle of aggregation, could yield each and every member of an animal’s repertoire of movement patterns. The factorization method, however, does not reveal only task-independent

coherent muscle organizations. It also finds task-dependent coherences (d'Avella & Bizzi, 2005). That is, some of the “synergies” revealed by factorization procedures are softly assembled for specific purposes.

In respect to potential operations for a base set, Boylls (1975) identified two adjustable prescriptions, the structural and the metrical. For Boylls, the prescriptions are for a *muscle linkage*, a notion that he saw fit to keep distinct from that of a synergy. The structural prescription refers to the relative amounts of activity present in a muscle linkage's constituent muscles. The metrical prescription refers to a scalar quantity multiplying the activities in all of a muscle linkage's constituent muscles (Turvey, Shaw, & Mace, 1978). For Boylls (1975), however, the temporal relation among the activities of muscles within a muscle linkage is not a property of like kind with relative muscle activity and overall level of muscle activity. That is, relative timing is not an operator.

#### 1.2.5. Co-organization of efference and afference

Somewhat hidden in the preceding is the all-important fact that a synergy as a controllable organization of many skeletal-muscular degrees of freedom is simultaneously and necessarily an organization of afference. If the degrees of freedom are cast in terms of efference, then the degrees of constraint that render them controllable and adaptive must be cast in terms of afference. But afference is no less many-dimensional than efference and no less in need of a principled means of dimensionality reduction (Turvey, 1990; Turvey et al., 1978). The problems of degrees of freedom and degrees of constraint are dual (Fig. 1a).

At issue is how efference and afference, motor and sensory, freedoms and constraints, relate within a synergy. The historical model is that of the reflex arc in which afferent signals trigger efferent reactions in a linear causal link. The model has long been questioned (e.g., Dewey, 1896, p. 139):

“The reflex arc is defective, in that it assumes sensory stimulus and motor response as distinct. . . in reality they are always inside a coordination and have their significance purely from the part played in maintaining or reconstituting the coordination. . . The arc. . . is virtually a circuit, a continual reconstitution. . .”.

Dewey's critique suggests that afference and efference, constraints and freedoms, relate as a cycle, or better, as a Möbius band, rather than as an arc (Turvey, 2004).

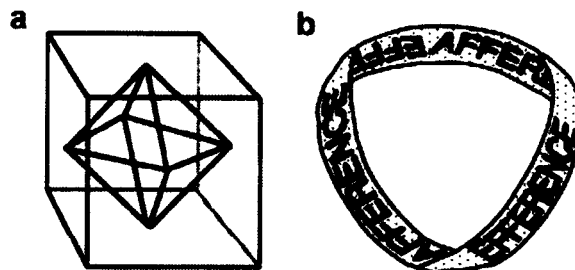


Fig. 1. (a) Duality of problems of degrees of freedom and degrees of constraint. Every symmetry (see Section 3.1) of the cube (here, degrees of constraint) is also a symmetry of the dual octahedron (degrees of freedom) and vice versa. (b) Möbius-band image of afference and efference as continuously related and – in terms of (a) – dual aspects of the same event.

The word *continual* referring to a process that goes on repeatedly seems to be an appropriate adjective for a cyclic interpretation of the relation between afference and efference. Applied to an ongoing synergy, *continual* implies intermittent afferent and intermittent efferent processes, with periods of non-afference and non-efference. In contrast, the qualifier *continuous* means that afferent and efferent activity within a synergic process are unending and without interruption. It is a qualifier that befits the Möbius band construal of the afferent–efferent relation (Fig. 1b).

Defining and understanding the notion of synergy may require, therefore, a theoretical advance beyond the reflex arc and cycle models: an ability to express afference and efference as concurrently continuous. Presumably this means that variables assigned to afference and variables assigned to efference, either by convention or for convenience, will need to be enfolded in, ideally, single variables that are neither strictly afferent nor efferent.<sup>1</sup> The central idea is that the afferent and efferent flows comprising a synergy enfold in a collective variable (alias order parameter) – a measurable quantity that expresses a coherent relation among the synergy’s parts and processes (see Section 3.5 below). The time-evolution of a synergy subject to continuous afferent and efferent influences can then be captured, in principle, by a single first-order equation in the collective variable (Section 3.5).

### 1.3. Bernstein’s perspective on synergies

For **Bernstein (1996)** the achievements of the level of synergies are both remarkable and insular. They are remarkable because they pertain to the formation and selection of a relatively small number (considering the possibilities) of highly reliable movement patterns involving very many degrees of freedom (subsystems) at multiple length and time scales. The achievements are insular because the patterns the level produces are largely independent from intentions and the meanings of environmental objects and events. Synergies owe their allegiance primarily to the dynamical criteria of concinnity, pattern stability and reproducibility. Their deployment in accord with intentions, and their adaptation to environmental circumstances are, for **Bernstein (1996)**, the duties of other functional levels.

Taking **Bernstein’s (1996)** perspective, studying the level of synergies is significant for the general comprehension of biological movement in three ways. First, the level’s achievements in the face of complexity are so fluent, reliable, and widely manifest in animals, that they must be underwritten by principles of the most basic and general kind. Second, and key to the first, is the level’s repertoire of *sensory corrections* as Bernstein chooses to call the *haptic perceptual capabilities* that underwrite the level’s fluency. The term haptic perception refers to the perception based in the mechano-receptive machinery embedded in the body’s deformable tissues – in the skin, in the muscles, and in the fascia that connects muscles to bone and possibly in the fascia that connects muscles to muscles. Haptic perception is perception by means of the body and in concert with the general definition of

<sup>1</sup> A well-known example, although rarely recognized as such, is Feldman’s  $\lambda$  variable (**Feldman, 1998; Feldman & Levin, 1995; Latash, 1993**). Lambda comprises aspects of the central and peripheral nervous systems, multiple motor and sensory units, and properties of muscle tissue. It is an abstract variable that, in principle, can readily be scaled up (as the notion of a spatial reference frame) from muscle, to joint, to body, to body-environment control (**Feldman, 1998**). The abstractness and the apparent emergence of lambda from a multiplicity of components at different levels do not warrant its typical attribution to a “central command”.

perceptual systems (Gibson, 1966, 1979) it functions in two distinct ways often concurrently. It functions proprioceptively – perception of the body and perception of the body's segments relative to the body as a unit and relative to each other – and it functions exteroceptively – perception of attachments to the body (e.g., handheld objects) and of surfaces adjacent to the body.

The third way in which studying the level of synergies is of theoretical significance is that the systematic exploitation and modulation of the level by other functional levels must engage further abstract principles. These, roughly speaking, must be smart recipes for indirectly organizing autonomous systems to perform in the manner that one wishes them to perform (Greene, 1972, 1982; Turvey et al., 1978).

## 2. Bernstein's functional hierarchy

In terms of his suggested labels, Bernstein's (1996) levels order successively as *tone*, *synergies*, *space*, and *action*. In the construction of movements a level may take either a leading role or a background role. It is the case, however, that the opportunities to lead are rare for tonus and synergies and commonplace for space and action.

The base of Bernstein's hierarchy is the level of tonus. Despite frequent references to tonus in past and contemporary literature, its description, definition and measures are far from settled. As Walsh (1992, p. 6) remarks, an assessment of seven decades ago still rings true:

“[t]here is no such single property... as tonus. Rather tonus is a convenient term which includes many different properties such as elasticity, viscosity, and muscle reflexes. The continued employment of the term, convenient as it is, serves to avoid the necessity of analyzing 'tonus' into its various components”.

Bernstein (1996) respected the elusiveness of tonus. It is for him “the background of all backgrounds (p. 115)”. deeply concealed but necessary to movement's achievements in the manner that the hidden foundations of a large building are necessary to its integrity and uses. Granit (1979) opined that tone was not a reflex phenomenon, as conventionally interpreted, but a state of motor preparedness. Fig. 2 supplies a useful image. It communicates the different consequences of being in a state of readiness or not for an upcoming synergic activity (Wiesendanger, 1997).

### 2.1. Body dexterity and handobject dexterity

The levels of space and actions are readily articulated, and most easily understood, in terms of the dexterous activities in which they assume a leading role. Roughly, dexterity is the ability to find an action solution for any environmental situation – to solve adequately any emerging action problem (Bernstein, 1996). Dexterity is an *ecological* concept. It refers to the control of a changing, task-specific relation between self and environment. Bernstein's (1996, p. 23) comments on this matter deserve more than a moment's reflection: “Demand for dexterity is not in the movements themselves but in the surrounding conditions. There is no movement that would not place high demands on dexterity, given appropriate conditions”. He asks that we compare walking when the base of support is narrow and walking when the base of support is broad, for example, a tight rope versus the floor of a conventional room.



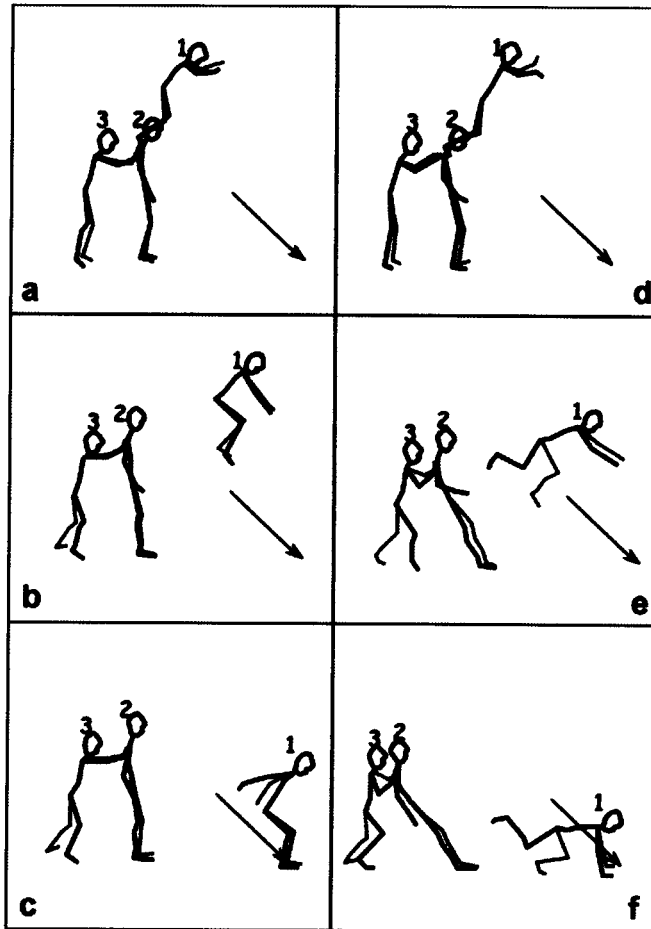


Fig. 2. Person 1 represents a goal-directed movement, Person 2 represents postural support, and Person 3 represents tone. In a–c, Person 3 is prepared (tone is proactive) and Person 1 is successful. In d–f, Person 3 is unprepared (tone is reactive) and Person 1 is unsuccessful. (Figure is based on Fig. 2 of Wiesendanger, 1997.)

Body dexterity is schematized in Fig. 3, via the circumstance of an outfielder in a game of baseball moving to catch a ball. The central panel defines the form of body dexterity: leading level/background level(s) = (level of space)/(levels of tonus and synergies). The space level comprises the optical information about (a) the surrounding layout of surfaces, objects, and players, and (b) the outfielder relative to the ball (primarily) and the surface layout (secondarily). Information of type (a) is the basis of exteroception and information of type (b) is the basis of ex-proprioception (Lee, 1976; Turvey, Carello, & Kim, 1990). The outfielder's body dexterity entails sensitivity to the exproprioceptive information. The right panel of Fig. 3 depicts a candidate level-of-space control rule that, if followed, would bring the outfielder to the right place at the right time without requiring that he predicts either (McBeath, Shaffer, & Kaiser, 1995; see Michaels & Zaal, 2002, for an overview). The left panel provides a schematic of the background levels that must

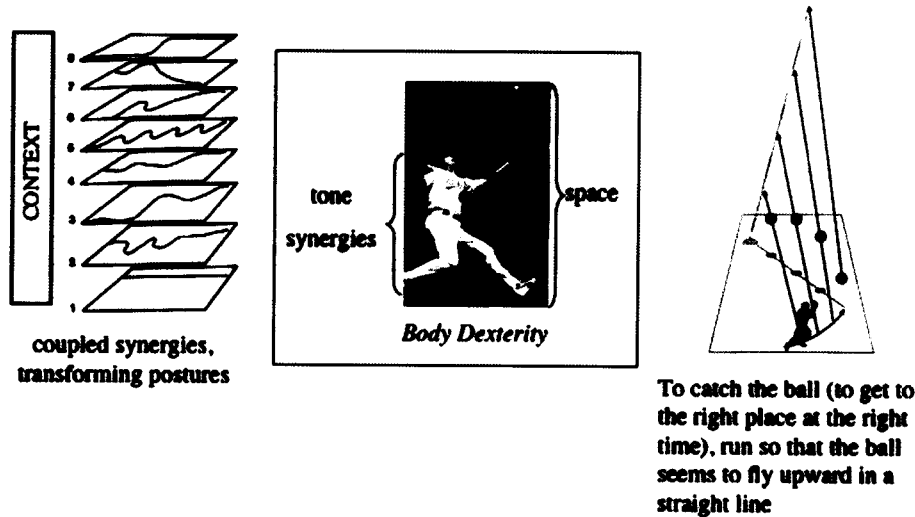


Fig. 3. The central panel is an act of body dexterity with level of space as the leading level (depicted by the right panel) and levels of tone and synergies as the background levels (depicted by the left panel). See text for details. Left panel is adapted from Thelen, E., and Smith, L. *A dynamic systems approach to the development of cognition and action*, Fig. 4.3. © 1994 Massachusetts Institute of Technology, published by the MIT Press. Right panel is from Cipra, B. (1995). Catching fly balls: A new model steps up to the plate. *Science*, 268, 502. Reprinted with permission from AAAS.

so adapt as to satisfy the control rule. The synergies are depicted as context-dependent time-evolving dynamical systems (Thelen & Smith, 1994). Assembling and disassembling the requisite organizations of hundreds of muscles in an appropriate and timely fashion is the responsibility of the level of synergies.

For the dexterity that is focused on the hands and objects, the conceptual challenge is how to express the leading level. Hand/object dexterity involves a sequencing of movements. The movements differ in meaning and purpose with each related to its neighbors by the overall meaning of the problem. Activities of everyday living that are frequently the concern of physical and occupational therapists have as constituent parts the movement, rearrangement, and use of objects in order to achieve specific outcomes. Think of getting dressed, eating a meal, brushing one's teeth. Borrowing from Reed (1982; Reed et al., 1992), such relations among behavior, object and environmental outcome can be regarded as the basic units of the level of actions. The relation among these meaningful/purposeful units is an inclusion relation. They are nested in the sense that within any two units one can expect to find identical movements alongside non-identical movements.

A dexterity in which actions constitute the leading level will have the levels of space and synergies as background. Candidate hand synergies as background for hand/object dexterity, comparable to the limb and body synergies that are the background for body dexterity, have been suggested by factorization procedures (Masson, Theverapperuma, Hendrix, & Ebner, 2004; Santello, Flanders, & Soechting, 1998) and by analyses and modeling of conjoint changes in finger forces and moments during multifinger gripping tasks (e.g., Shim, Latash, & Zatsiorsky, 2005).

### 3. Organizational principles

Understanding the level of synergies is far more than identifying and understanding the functional structure of individual synergies. It is, in addition, understanding how synergies can transform smoothly and continuously, how different synergic functions can interleave smoothly and continuously, how one synergy can give way spontaneously to another at the right moment and/or right spatial orientation, how distinct synergies can co-exist in the same components, and how components constituting a synergy can be added or deleted specific to changing circumstances. The competence of the level of synergies in respect to the foregoing implies general principles that organize and constrain its functioning. In the present section, a number of these principles, as currently understood, are identified and discussed.

#### 3.1. Symmetry and bifurcation

Strong hints as to the potentially deep (abstract) principles that underwrite the fluency of the level of synergies are made manifest in the rhythms that characterize the level. These hints point to *symmetry* as a primary constraint on the patterns of movements incorporating many body segments and multiple muscles. In approximate terms, a symmetry is a transformation (a change) that you can apply to something, call it  $X$ , that leaves  $X$  invariant (unchanged). If two symmetries are applied successively and  $X$  remains unchanged then the combination is also a symmetry of  $X$ . A special condition, referred to as a *symmetry group*, arises when the combination of any two symmetries of  $X$  is another symmetry of  $X$ , that is, when  $X$ 's symmetries are closed. In this latter condition the set of  $X$ 's symmetries has an internal structure. Breaking that structure, breaking  $X$ 's symmetry, is understandable as removing some of the symmetries, rendering the original symmetry group a subgroup of itself.

The dihedral symmetry group  $D_3$ , that of the equilateral triangle and consisting of three rotations and three reflections (see Fig. 4 lower panel), arises in the theory of coupled oscillators. It seems to fix the patterns of rhythmic movements exhibited by the three arm segments (Fig. 4 upper panel). Preliminary to appreciating how this is so is recognition of the significance of the *Hopf bifurcation* to the symmetries of rhythms.

A bifurcation is a change in the type and or number of qualitatively distinct system states. Bifurcations are associated with symmetry breaking. A Hopf bifurcation is a change from a steady state to a periodic state, a natural process akin to the “switching on” of an oscillator. The customary image is of a marble at the bottom of a bowl that is sitting on a turntable. At slow turns the marble is stationary, its center aligned with the center of the bowl. The marble is said to be invariant under time translation and reflection (its state will be the same later as it is now, its state sequence in the time interval  $t_0$  to  $t_1$  would be indistinguishable from the reverse, namely, the state sequence in the time interval  $t_1$  to  $t_0$ ). At quicker turns the marble begins to adopt a small circular motion about the bowl's center (a wobble) that becomes, with increasing turning rate, movement up the side of the bowl and a pronounced periodic motion around the bowl's interior. Temporal symmetry is broken. The full translational symmetry is reduced to whole number multiples of the marble's period of excursion.

Consider the oscillations about the shoulder, elbow, and wrist schematized in Fig. 4 (upper panel) as based in a symmetric coupling among three identical oscillators.

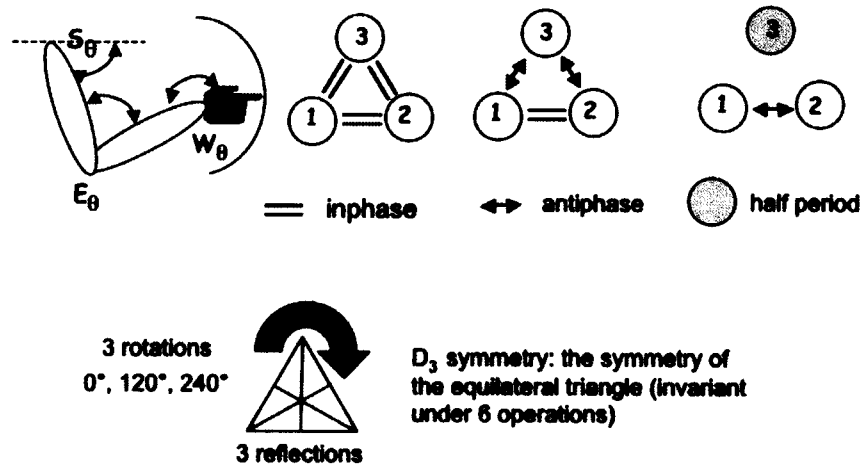


Fig. 4. Upper panels depict a rhythmic curve reproduction task satisfied by oscillations about shoulder (S), elbow (E), and wrist (W) and the patterns of coordination among the three oscillating joints that are realized for different curvatures. The depicted patterns are expected from an organization – a synergy of oscillators – that possesses  $D_3$  symmetry shown in the lower panel (see text for details).

(Geometrically, the image is the oscillators as the vertices, and the symmetric couplings as the sides, of an equilateral triangle, Fig. 4, lower panel.) Then, the theory of Hopf bifurcations for  $D_3$  symmetry identifies several patterns of phase relationships among the oscillators as a function of a symmetry breaking parameter (Collins & Stewart, 1994). In the experiment summarized in Fig. 4 (upper panel), the parameter in question is the curvature traced out by the finger for a fixed shoulder–finger distance and fixed speed (Buchanan, Kelso, & De Guzman, 1997; De Guzman, Kelso, & Buchanan, 1997).

Fig. 4 (upper panel) identifies three shoulder–elbow–wrist patterns observed experimentally. The first pattern is equivalent to three clocks all going “tick” together and all going “tock” together. The second pattern is equivalent to two clocks going “tick” together and “tock” together with the third doing something different, say, “thud-bonk” (Stewart & Golubitsky, 1992). The third pattern is equivalent to two clocks in antiphase, one going “tick-tock”, the other going “tock-tick”, with the third clock going “thud-thud”, repeating “thud” twice every period of the whole system (Stewart & Golubitsky, 1992). Each of the three patterns is a subgroup of the symmetry group  $D_3$ . That is, each has its own characteristic symmetry; each is invariant under a specific set of transformations (Collins & Stewart, 1994). For example, for the third pattern the symmetries are (a) interchanging two oscillators and (b) translating time by  $1/2$  period. It is the symmetry (b) that dictates that the oscillator that is not one of the two interchanged oscillators must be  $1/2$  period out of phase with itself or, synonymously, twice the frequency of the other two oscillators (Stewart & Golubitsky, 1992). The third pattern has been observed in another case of coupled biological oscillators (Takamatsu et al., 2001). It is important to highlight that the existence of the third pattern with its  $1/2$  period follows naturally from symmetry breaking of  $D_3$  but it could not have been guessed at in the absence of the symmetry-group perspective.

Analogous issues may arise in respect to role diversity of muscles identified in Section 1.2.3. A major challenge is identifying the number of roles and their types, and the contexts in which they arise. From a symmetry-group perspective the roles would be the defining symmetry and its subgroups and the contexts would be the conditions of symmetry breaking. A little insight comes in the form of the simple spring pendulum – a spring fixed at one end with a mass at the other and with compression restricted to the direction of the spring. For our purposes we might want to think of the spring pendulum as somewhat like a muscle with proximate and distal attachments to skeletal segments. The symmetry of the spring pendulum has five subgroups associated with the periodic oscillations of a spring, a pendulum, a brake, a symmetric ellipse and an antisymmetric ellipse (Golubitsky & Stewart, 2000). It is reasonable to expect that the symmetry of a collection of spring pendulums analogous to a collection of muscles would be considerably richer, sufficiently so, perhaps, to accommodate the diversity of muscular roles. That the symmetry-group perspective can be brought to bear on such a problem is suggested by the work of McCollum and Boyle (2004).

### 3.2. Bifurcations of locomotion

A prominent bifurcation parameter is movement speed. (In the broader physical, chemical literature it is equivalent to stressing the system.) For quadrupeds, faster speeds of locomotion entail in-phase coordination of limbs of the same girdle in contrast to the anti-phase coordination that characterizes the dominant walking gait. If an animal were to locomote at ever increasing speed then the organization of its locomotion would be seen to switch spontaneously from antiphase to in-phase. There is evidence to suggest that this bifurcation may occur at the same speed – regardless of the kind of quadruped – when speed is scaled to body mass (Heglund, Taylor, & McMahon, 1974). Fig. 5 plots log stride frequency at the moment of bifurcation against log body mass, over the range extending from the lighter mouse to the heavier horse. The power law relation points to the invariance of the bifurcation over differences in scale.

The bifurcations in quadruped locomotion are most aptly described as bifurcations of gait. In Fig. 5, the gait transition is from trot to gallop. Analogous speed-related gait changes occur in hexapedal locomotion (Full & Tu, 1991). When locomoting freely on a horizontal plane surface, the American cockroach (*Periplaneta americana*) can be seen to use the six-legged alternating tripod gait in the range 0.4–1.0 m/s but switch to either

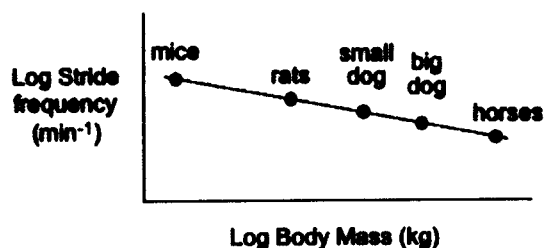


Fig. 5. The stride frequency at which different-sized quadrupeds transition to running follows a power law (see text for details).

a quadrupedal (middle and hind legs) or a bipedal (hind legs) gait in the range 1.0–1.5 m/s. By the symmetry-group argument, the different synergies of locomotion, the different coherent organizations of the cockroach's muscular–articular links, co-exist in a (dihedral) symmetry that fixes invariant gait patterns for different degrees of symmetry breaking.

The potential universality of gait bifurcations is brought into sharp relief by evidence that they similarly occur in animals not typically thought of as presenting gaits such as birds (Hedrick, Tobalske, & Biewener, 2002; Fig. 6) and fish (Drucker & Lauder, 1999; Fig. 7). In both Figs. 6 and 7, gait differences are manifest as differences in vortex flow. The shedding of vorticity is the hallmark of force production in fluids, reflecting the transfer of momentum to the wake. The bifurcations in vortex patterns are accompaniments of reorganizations of wings and fins that are often subtle and hard to describe in detail. An important lesson to be learned from Figs. 6 and 7 is that gait patterns are not strictly a property of muscular–articular links. Rather, they are a property of those links as embedded in an environment (Dickinson et al., 2000). The environment – that is, the animal's surroundings when defined in the way that matters to the level of synergies – is one of forces. A valuable, albeit crude, image of the level of synergies is that it “bends” the force structure that is given to produce the force structure that is required (Fowler & Turvey, 1978).

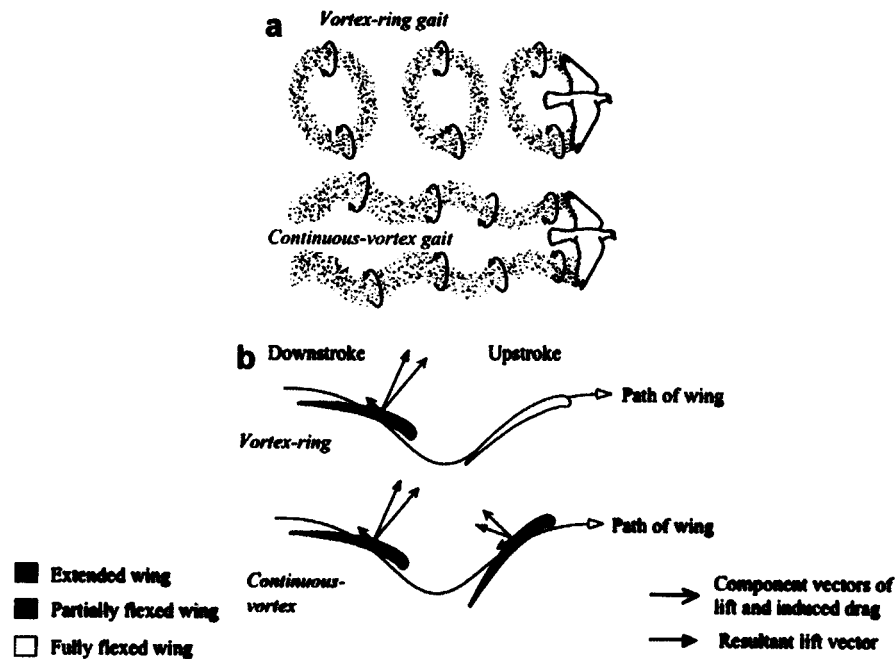


Fig. 6. (a) Birds have gaits and switch spontaneously from one (vortex ring) to the other (continuous vortex) at a specific velocity. Both Cockatiels and Ring Turtle-doves switch gaits at 7 m/s. (b) The shift is associated with a phase delay in the peak angle of attack of the proximal wing section from downstroke to upstroke. Adaptation of Fig. 2 in Hedrick et al. (2002). Reproduced with permission of the Company of Biologists.

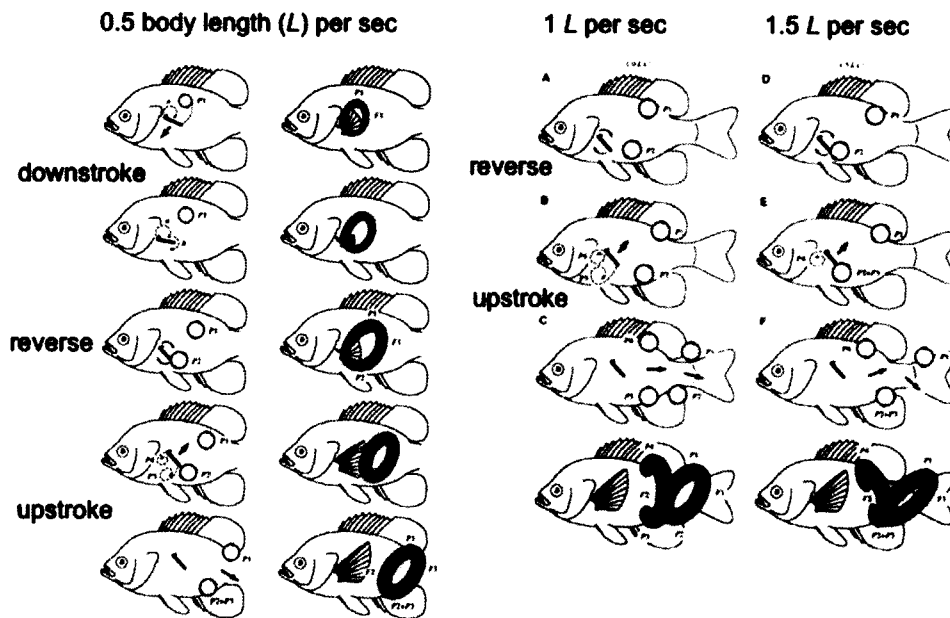


Fig. 7. Fish have gaits revealed as downstream vortex structures that differ at different speeds (measured in body lengths  $L$  per second). Figures for each speed depict formation of the vortex ring wake over the course of the pectoral fin-beat. Combination of Figs. 8 and 9 in Drucker and Lauder (1999). Reproduced with permission of the Company of Biologists.

### 3.3. Effector-independent principles

Identifying symmetries and bifurcations is a hallmark characteristic of the model-independent approach to natural systems. The approach explores regularities of phenomena at any given scale and strives to optimize those lawful properties into principles (Stewart & Golubitsky, 1992). Its application to the level of articular-links or synergies in the sections above brings to the forefront the general notion of abstract organizational principles that are invariant with respect to the effectors involved and the specifics of their modes of operation. Furthering appreciation and eventual understanding of the level of synergies follows from recognizing other abstract relations.

#### 3.3.1. Shannon's universal juggling equation

Juggling is a rhythmic synergistic activity with leading levels of space and action. It abides by Shannon's universal juggling equation. The qualifier "universal" refers to the stipulation that, regardless of the nature of the juggler (human, animal, and robot), the number and types of effectors, and the number and types of objects, the act of juggling requires satisfying the internal relations dictated by the equation.

Let  $T$  be the duration of a juggling cycle, beginning and ending with the same event: catching object  $i$  in hand  $j$ . Fig. 8 identifies how  $T$  is composed from the perspective of

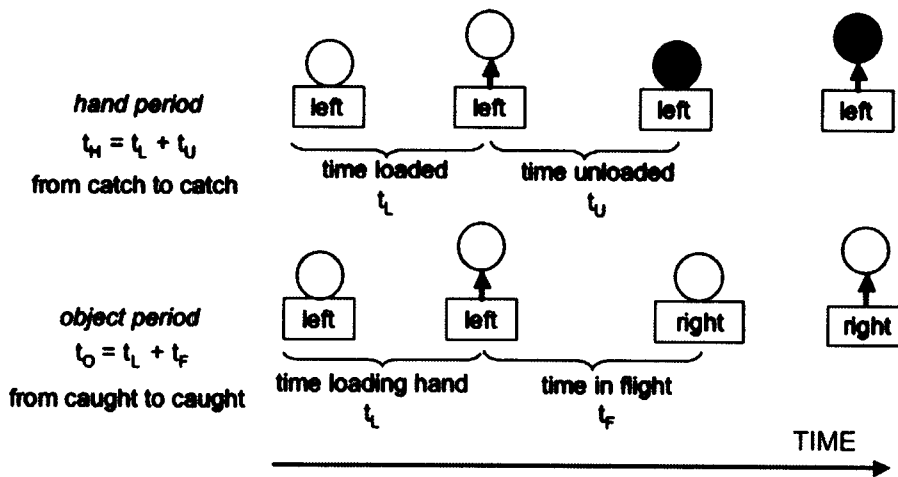


Fig. 8. The periods of hand and object in a three-object cascade juggle. See text for details.

a given hand ( $t_H$ ) and from the perspective of a given object ( $t_O$ ). Then, for  $O$  objects the total hand loop time is  $O(t_L + t_U)$  and for  $H$  hands the total object loop time is  $H(t_L + t_F)$  satisfying

$$O(t_L + t_U) = T = H(t_L + t_F)$$

or

$$t_O/t_H = O/H.$$

The latter is Shannon's universal juggling equation (Beek, 1989; Beek & Van Santvoord, 1996; Shannon, 1993). Imagine 8 hands (four jugglers) and 20 objects. Then, the ratio of the cycle time of any object  $i$  to the cycle time of any hand  $j$  would be  $20/8$  or  $5/2$ , meaning two object cycles for every five hand cycles. That is, during  $T$  – the interval beginning and ending with an instance of the catching of object  $i$  by hand  $j$  – object  $i$  is caught twice for every five acts of catching by hand  $j$ .

How does a juggler comply with the universal equation? Consider a single juggler performing, say, a cascade juggle with three objects. If the juggler fixes  $t_F$  by fixing the height to which the objects are thrown, then the remaining DF in the above equation are strictly those associated with the hand. One hypothesis is that  $k = t_L/(t_L + t_U)$  is the juggler's control variable, the proportion of hand-loop time that a hand transports an object (Beek, 1989; Beek & Turvey, 1992). The importance of  $k$  is in respect to the average number  $O^*$  of juggled objects in flight during  $T$ :  $O^* = O - Hk$ . For longer  $t_L$ ,  $k$  is larger and  $O^*$  is smaller; for shorter  $t_L$ ,  $k$  is smaller and  $O^*$  is larger.

The principal constraint on  $k$  may be a temporal stability requirement, specifically, how to mesh the dynamics of transporting an object,  $t_L$ , with the dynamics of the hand,  $t_H$ . Perhaps the principles of frequency locking apply: the two times must relate as a rational ratio of integers. For the cascade juggling of three objects, highly skilled jugglers tend toward  $k$  values of  $5/8$ ,  $2/3$  or  $3/4$ . When juggling five or seven objects, however,  $3/4$  seems to be the primary option (Beek & Turvey, 1992; Beek & Van Santvoord, 1996).



3.3.2. Fitts' law

For movements between two targets of width  $W$  and distance  $D$  apart, movement time  $MT$  satisfies the relation

$$MT \propto \log_2(2D/W).$$

This well-known relation is referred to as Fitts' law following its identification by Fitts (1954) in research directed at relating the mathematical theory of information transmission to human movement. The right-hand side of the relation is an index of difficulty in bits. There are a number of explanations of why Fitts' law has the form it has. Most are couched in effector-dependent terms (Latash, 1993).

Fig. 9 shows an arrangement in which a pointer can be moved rhythmically by hand between two stationary targets (the standard form of the Fitts' task) or conversely two targets can be moved rhythmically by hand to a stationary pointer. In Bernstein's terms, hand/object dexterity is entailed with the level of synergies in a background role. Mottet,

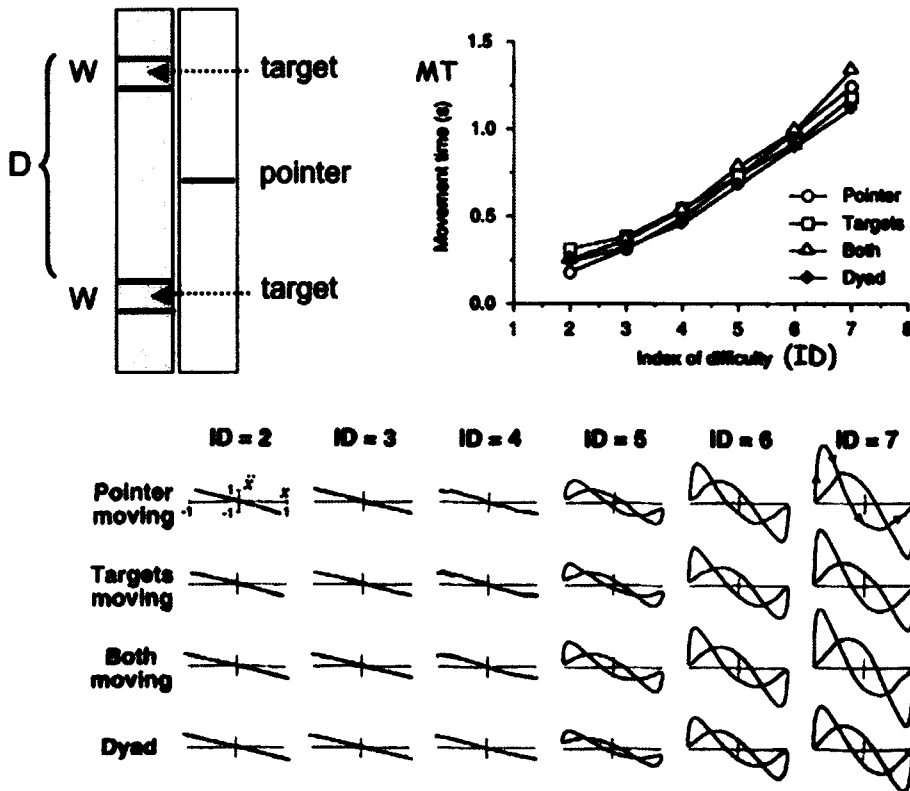


Fig. 9. Fitts' law is shown as an abstract relation in task space. Top left panel depicts the movable pointer and target. Lower panel depicts behavior of the pointer-target distance  $x$  in Hooke's plane for four conditions with "both moving" referring to one hand moving the pointer and one hand moving the targets and "dyad" referring to two people, one moving the pointer and one moving the targets. Results in Fitts' law format are shown in top right panel. See text for details. Adapted with APA permission from Mottet, D., Guiard, Y., Ferrand, T., and Bootsma, R. J. (2001). Two handed performance of a rhythmical Fitts' task by individuals and dyads. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 1275–1286.

Guiard, Ferrand, and Bootsma (2001) showed that Fitts' law is equally satisfied whether the participant moves the pointer to the targets or moves the targets to the pointer. They also showed that it is equally satisfied (a) if the participant moves the pointer with one hand and the targets with the other hand, and (b) if the pointer is moved by one participant and the targets are moved by another participant. The full set of results is shown in Fig. 9. In all four cases the rhythmic behavior as a function of index of difficulty (ID) exhibits the same pattern in Hooke's plane  $\ddot{x} \times x$ , where  $x$  is pointer-to-target distance. That is, in *task space* the Hooke's portraits are invariant over the four very different effector implementations. In sum, Fitts' law, like the universal juggling law, is an abstract relation in task space (Billon, Bootsma, & Mottet, 2000; Mottet et al., 2001).

### 3.3.3. Donders' law and Listing's law

A critical constraint on limb movements in three dimensions, such as reaching to grasp an object at any arbitrary location relative to the body, is the fact that three-dimensional (3D) rotations are *non-commutative* (Gielen, Vrijenhoek, Flash, & Neggers, 1997; Hestenes, 1994). The resultant 3D orientation obtained by combining two or more 3D rotations depends upon the order of the combination. In the aforementioned reaching task, positioning and orienting the hand so as to match the position and orientation of an object can be achieved through strictly synchronous or strictly sequential rotations at the arm's joints, or through a combination of synchronous and sequential rotations (Mitra & Turvey, 2004). In all cases, the non-commutative property introduces strong geometric constraints on the synergy or synergies enacting trajectory formation. It does so because changes in hand orientation produced in successive rotations are strongly dependent on previous rotations (Gielen et al., 1997). Non-commutativity means that, generally speaking, integrating rotational velocities does not yield cumulative rotational displacement in 3D unless the axis of rotation remains fixed (Tweed & Vilis, 1987).

Inquiry into rotational movements and the invariants that might underlie them has been anchored historically in the study of eye movements. The eye can rotate within its socket vertically, horizontally, and torsionally (in the direction perpendicular to both vertical and horizontal directions) by means of the simultaneous action of three pairs of muscles. This muscular system could, in principle, produce an indefinitely large number of eye orientations by which to achieve any one direction of gaze (Crawford & Vilis, 1995). In actual fact, for any one gaze direction the eye always assumes a unique 3D orientation regardless of preceding orientations and movements, a fact known as *Donders' law* (Crawford & Vilis, 1995). Another law confines the axes about which the eye rotates from a given central reference position to other eccentric positions. It confines them to a 2D plane. The confinement is known as *Listing's law* and the 2D plane is known as *Listing's plane*. The central reference position is the primary position, one at which the direction of gaze is perpendicular to the plane of the rotation axes. If the torsional component of eye rotation is defined as rotation of the eye about the axis perpendicular to Listing's plane, then Listing's law states that eye rotations only allow eye positions with zero torsion (Crawford & Vilis, 1995). Whereas all eye rotations away from primary position occur about axes lying in Listing's plane, rotation from any one arbitrarily chosen (eccentric) position to another is always about an axis that is tilted out of Listing's plane. The degree of tilt is such that the resultant eye-orientation could have been obtained by rotating to, and then from, primary position about axes lying on Listing's plane. In sum, Donders' law and Listing's law reduce the effective degrees of freedom for eye movements – while gaze direction picks the

horizontal and vertical components of rotation, application of Listing's law produces the axis of rotation (and hence determines the torsional component).

The question can be raised as to whether the two laws have analogues at the level of synergies. Do they identify a general, effector-independent principle for accommodating the non-commutativity of rotations of limbs and limb segments? Although there are suggestions that a positive answer might be forthcoming, the present degree of knowledge gives reasons for circumspection.

In a study of the orientation of the arm during throwing, **Hore, Watts, and Tweed (1994)** noted that, in close approximation to Donders' law, the arm adopts a single angular position for every throwing direction. Additionally, studies of the movements of the head (e.g., **Ceylan, Henriques, Tweed, & Crawford, 2000; Straumann, Haslwanter, Hepp-Reymond, & Hepp, 1991**), the upper arm (e.g., **Hepp, Haslwanter, Straumann, Hepp-Reymond, & Henn, 1991; Medendorp, Crawford, Henriques, Van Gisbergen, & Gielen, 2000**), and the forearm (**Hore, Watts, & Vilis, 1992**) have found that the axes of rotation in each case lie in 2D surfaces. The surfaces are not planes, however; they have a twist and require a fifth-order polynomial for their description (**Hore et al., 1992; Miller, Theeuwes, & Gielen, 1992**). Such surfaces may reflect upon the necessity of the arm and head rotation systems to accommodate different regional requirements of the workspace (**Ceylan et al., 2000; Medendorp et al., 2000**).

There are indications that, in rotating the arm for pointing in 3D, the synergies of the shoulder might behave abstractly as a Fick gimbal. That is, they behave as a system of nested rotations in which the horizontal axis is mounted on the vertical axis, as in earth-fixed telescopes. The advantages of such a system include abiding Donders' law, absence of torsion accumulation, shortest-path vertical movements (hence minimization of work against gravity), and constant-work horizontal movements. Generalization of the Fick gimbal principle is restrained however by observations that Donders' law may not be satisfied in arm pointing tasks that allow changes in elbow angle (**Gielen et al., 1997; Soechting, Buneo, Herrmann, & Flanders, 1995**).

#### 3.3.4. *A rotation law beyond Donders' and Listing's?*

The everyday tasks most commonly performed by the arm are not pointing-like tasks of the kind discussed for arm and eye but the grasping-like tasks introduced at the beginning of this section. At a minimum such tasks require that the palm of the hand be brought into alignment with a surface in a given location and at a given orientation in task space. Alignment is achieved (typically) through a synergic process of rotations at the shoulder, elbow, and wrist. As a class, oriented reaching movements will ordinarily impose stiffer requirements on the initial and/or final orientation of the hand than pointing, and will involve all seven of the arm's rotational degrees of freedom. Studying the smoothly transforming synergy of oriented reaching may well reveal organizing principles that are more robust and of wider scope than Donders' and Listing's laws.

Oriented reaching is not reserved for arm–hand. In games such as football (soccer for American readers) it is manifest in leg–foot and body–head activities; kicking requires 3D alignment of foot with ball and heading requires 3D alignment of head with ball. For racket and bat sports, oriented reaching is realized in 3D arm(s)-racket and arm(s)-bat activities. The ultimate significance of end-surface orientation (as contrasted with end-point location as in pointing-like tasks) raises the question of whether the leading invariant in oriented reaching is an invariant of transformations of hand (foot, head, racket, and

bat) *orientation* rather than transformations of hand (foot, head, racket, and bat) *position* (Mitra & Turvey, 2004). If the hand's change in orientation is constrained systematically and consistently, then the nature of the constraint should be revealed by a geometric analysis of the trajectory traced by successive values of the instantaneous hand orientation  $\mathbf{R}(t)$  in an  $(R_1, R_2, R_3)$  rotation-vector space. In this space,  $\mathbf{R}(t)$ 's direction gives the rotation axis and the axis's length gives the rotation magnitude.

Fig. 10 summarizes the primary outcome of experiments in which oriented reaches were conducted with the right hand from a fixed starting position to three different oriented surface locations under variations of load and speed (Mitra & Turvey, 2004). Inspection of Fig. 10 shows that hand orientation was constrained to 2D planar motions. The invariant planarity means that two rotation coordinates sufficed to capture the hand's orientation at

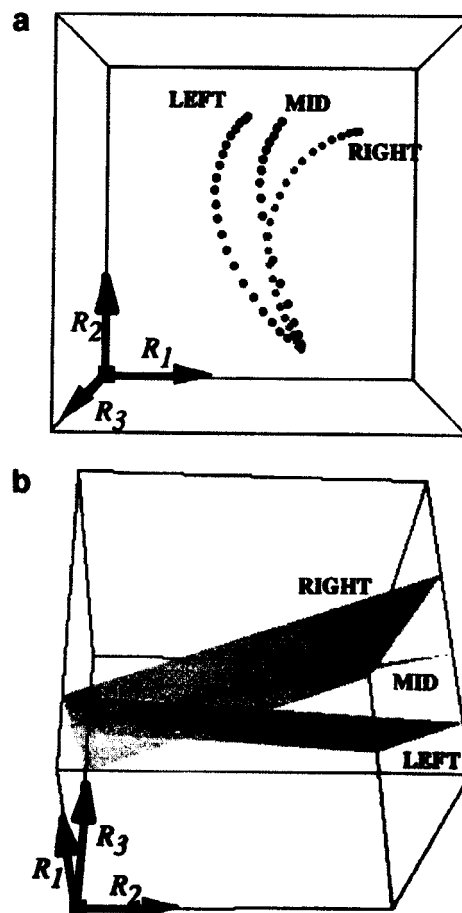


Fig. 10. Pronation-rotation planarity as a specific constraint on changes in hand orientation during 3D-reaching movements. (a) Trajectories of  $\mathbf{R}(t)$  for three movement directions in the  $(R_1, R_2, R_3)$  rotation-vector space viewed from above the workspace. (b) The same trajectories viewed from near the floor to the right of the workspace with invariant planes depicted. Reprinted with APA permission from Mitra, S., and Turvey, M. T. (2004). A rotation invariant in three-dimensional reaching. *Journal of Experimental Psychology: Human Perception and Performance*, 30, 163–179.

all points in its movement trajectory. Of particular theoretical value is the trajectory of the  $\mathbf{R}$  that rotates  $\mathbf{R}(t)$  to  $\mathbf{R}(t + 1)$ , that is, the trajectory of the rotor-of-rotation vectors  $\mathbf{RR}(t)$ . The outcome portrayed in Fig. 10 suggests that the rotor is either null or lies along the normal to the plane at the origin. Synonymously, it suggests that the axis about which the instantaneous axes of rotation rotate does not change during the course of oriented reaching. In contrast to the invariant axis of hand rotation, the parameters of hand translation (relative timing of velocity components, trajectory linearity) were found to be variable, changing systematically with the experimental manipulations. The challenge for the level of synergies of managing the 3D rotations of an end-surface to execute grasping-like tasks may well take priority over, or subsume, the synergic processes characterized by Donders' and Listing's laws. If so, then one would expect this policy to hold for all variants of oriented reaching regardless of the effectors involved.

### 3.4. Resonance

In common with material objects, the body and its segments have resonant frequencies (Walsh, 1992) – frequencies at which they are most inclined to vibrate relative to other frequencies. There are indications that the resonant frequency bestows special benefits upon rhythmic coordination, be it of multiple joints or of a single joint.

The skill of hula hooping provides a multiple-joints example. Balasubramaniam and Turvey (2004) investigated this task performed in the manner depicted in Fig. 11a. In

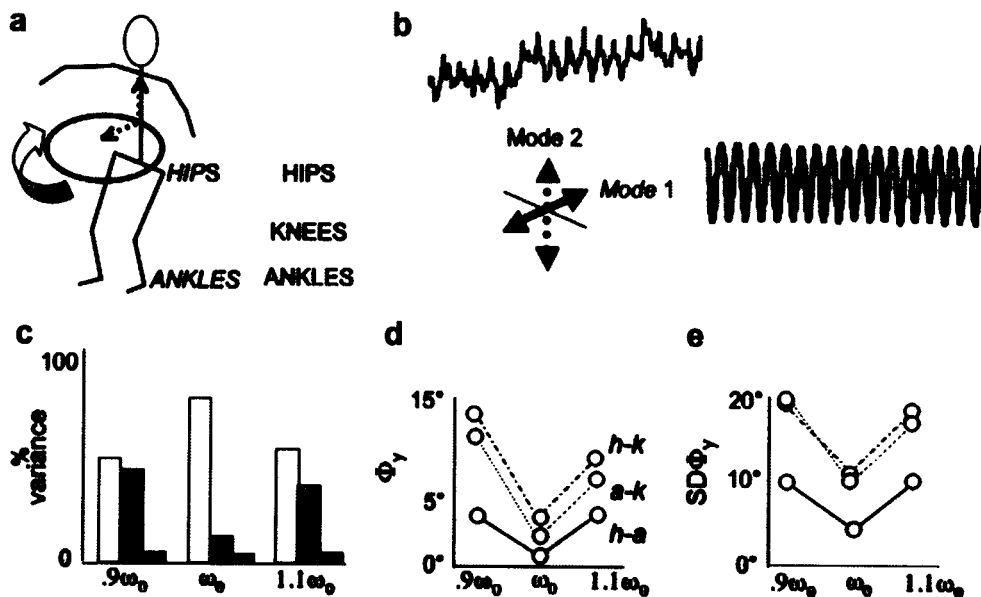


Fig. 11. (a) The hula-hooping task studied by Balasubramaniam and Turvey (2004) indicating the two impulse directions needed to sustain stable hoop oscillations. (b) The time series of the two coordination modes (eigenmodes), with Mode 1 defined over hips–ankles and Mode 2 defined over hips–knees–ankles. (c) The relation between Mode 1 (white bar) and Mode 2 (gray bar) as a function of resonance (preferred) frequency,  $\omega_0$ . (d and e) The relative phase ( $\phi$ ) in the  $y$  direction and its standard deviation (SD) for hip–knee (h–k), ankle–hip (a–h) and hip–ankle (h–a) as a function of resonance (see text for details).

order to sustain cyclic rotations of the unstable hoop, the actor must impart timely impulses to maintain the hoop's angular momentum in the horizontal plane. The question asked in experiments with moderately skilled performers was how the lower limbs organize to meet the challenge.

The initial experiment allowed the performers to hula hoop at the tempo they found most comfortable for the given hoop, a tempo at which, presumably, the body's oscillations were tuned to the hoop's oscillations – in short, the resonant frequency for the task. The time series for each of the  $x$ ,  $y$ , and  $z$  coordinates of the ankle, knee, and hip of both lower limbs were subjected collectively (18 of them) to a Karhunen–Loève or principal components analysis. Two coordination modes proved sufficient to accommodate most of the variance (Fig. 11c): Mode 1 was revealed as a synergy of ankles and hips controlling the horizontal to-and-fro motion and Mode 2 was revealed as a (concurrent) synergy of ankles, knees, and hips controlling the up and down motion. The time series for the two coordination (or eigen) modes are shown in Fig. 11b. Computation of the Hilbert relative phase of the two coordination modes revealed that they operated close to in-phase.

In a second experiment, a metronome paced the performers at the operationally defined resonant frequency  $\omega_0$  and at frequencies of  $0.9\omega_0$  and  $1.1\omega_0$ . As shown in Fig. 11c, the relative contributions of the first two modes depended on the resonant frequency. The contribution of Mode 1 decreased and the contribution of Mode 2 increased for the two non-resonant conditions relative to the resonant condition. The mean Hilbert relative phase of the modes was closest to in-phase ( $0^\circ$ ) for the resonant condition. Figs. 11d and e schematize the results at the level of the individual joints as represented by the relative phase of motions in the  $y$  direction for the hip–ankle, ankle–knee, and hip–knee. For each pair of joints, the relative phase at the resonant frequency was closest to  $0^\circ$  and least variable. For all three frequencies, involvement of the knee was associated with larger displacements from an in-phase relation and greater variability of relative phase. The task-specific lesson learned is that for a hoop of a given diameter, resonant frequency entails (a) a minimal vertical component of angular momentum, and (b) most nearly synchronized first and second modes (Balasubramaniam & Turvey, 2004).

In principle, resonance tuning should be expected to occur for kinematic chains whatever the number of their spatial degrees of freedom. Although they did not recognize it as such, Carson and colleagues (Carson, Riek, Byblow, Abernethy, & Summers, 1999) provided evidence for resonance behavior in the arm oscillating as a kinematic chain with two spatial degrees of freedom. The motion equation for such a system (mechanically exemplified by a double pendulum or two mass-springs with a coupling spring) yields two resonant frequencies, with the antiphase frequency higher than the in-phase frequency (e.g., Den Hartog, 1985). In the research of Carson et al., simultaneous rhythmic movements about the elbow and wrist exhibited the expected resonant pattern, namely, two self-selected frequencies with the frequency for the antiphase condition (elbow and wrist angles changing simultaneously in opposite directions) higher than the frequency for the in-phase condition (the two angles changing simultaneously in the same direction).

The promised single-joint example expands our insights into the advantages of resonance. A handheld pendulum can be oscillated by motions about the wrist at its resonant frequency as determined by  $\omega_0 = \sqrt{g/l}$ , where  $g$  is the constant acceleration due to gravity and  $l$  is the simple pendulum length. Alternatively it can be oscillated at frequencies above and below the resonant frequency. Goodman and colleagues (Goodman, Riley, Mitra, & Turvey, 2000) applied phase-space reconstruction with time-delay embedding (Abarbanel,

1996) to metronome-paced oscillations produced by six participants at  $\omega = \omega_0$ ,  $\omega < \omega_0$ , and  $\omega > \omega_0$ . There were three main observations. First, the number of active degrees of freedom required to capture the dynamics of the rhythmic behavior was three for the resonant frequency and four for each of the nonresonant frequencies. Second, the residual high-dimensional noise was similarly lowest for the resonant frequency. Whereas 33% and 20%, respectively, of the vectors in the phase spaces of the dynamics higher and lower than resonance were unpredictable, only 12% were unpredictable at resonance. Third, the predictability of the evolving dynamics extended further into the future for oscillations at the resonant frequency. At resonance, the prediction horizon was 5 times further than the prediction horizon for the higher than resonance behavior and 2.5 times further than that for the lower than resonance behavior.

A bias toward resonance confers distinct advantages on the level of synergies. At resonance, pendular rhythmic movements are more energy efficient (e.g., Holt, Jeng, Ratcliffe, & Hamill, 1995) and more stable (e.g., Rosenblum & Turvey, 1988). At resonance, the number of variables to be controlled is fewest, the movements are least noisy (most deterministic), and the trajectories are most predictable (Goodman et al., 2000). Considering the advantages of resonance, it is not surprising that locomoting animals typically tend to adopt movement frequencies that match the resonant frequencies of their pendular limbs (Turvey, Schmidt, Rosenblum, & Kugler, 1988; see also Greenewalt, 1960). It is also not surprising, perhaps, to respond to the persistent question of what the cerebellum addresses with the answer that it addresses the limb resonances and their implications for the control and coordination of movement (Walsh, 1992).

In concert with the above, Hatsopoulos, (1996; Hatsopoulos & Warren, 1996) has provided an explicit demonstration that the details of limb oscillations (e.g., issues of energy injection and dissipation, restoring forces, etc.) emerge from the mutual and reciprocal influences of neural and physical (limb) dynamics. He modeled the pattern-generating dynamics of the nervous system as a Van der Pol oscillator and the rotational dynamics of a pendular limb as a linearized spring-pendulum system (Kugler & Turvey, 1987; Turvey et al., 1988). Hatsopoulos coupled these two oscillators (simulating the coupling of neural and limb dynamics through proprioception), and found that the coupled system tuned into the resonant frequency of the pendular limb and did so over different endogenous frequencies of the central pattern generator. Complementary investigations by Williamson (2003) have demonstrated the plausibility and value of resonance tuning in robotic systems.

### *3.5. Collective variables and metastability*

Whatever might prove to be the specifics of its definition, the notion of synergy is cognate with notions of organization, cooperative activity, and collective behavior. It is also cognate with notions of low-dimensionality and metastability. Synergy is cognate with low-dimensional dynamical process because of a synergy's primary theoretical role, namely, to simplify control by reducing the number of variables that must be independently specified. Synergy is cognate with metastable organization because, in the most general case, the synergic tendency of the involved degrees of freedom toward dependence (integration) is complemented by their anti-synergic tendency toward independence (segregation). The relating of synergy to metastability follows from the facts that the same muscles, the same joint complexes, can realize different synergic functions, and that they

must be prepared to do so at an instant. A synergy, therefore, must be a kind of stable organization whose components are always ready to participate in other stable organizations.

In very many respects the best model system for promoting a detailed understanding of synergy is 1:1 frequency locking of two limbs or limb segments (Kelso, 1995; Kugler & Turvey, 1987). It provides experimental and conceptual access to the aforementioned and difficult notions of collective behavior, low-dimensionality, and metastability. It also facilitates connection with the symmetry-group principle of Section 3.1.

Investigations of the phase- and frequency-locking of the fins of *labrus* and related species by Von Holst (1939/1973) primed the conception of coordination as reflecting complementary tendencies. Using the notions of maintenance tendency (the tendency for each individual fin oscillator to continue at its own preferred frequency) and magnet effect (the tendency of each fin oscillator to force its preferred frequency on the other), Von Holst interpreted absolute coordination as the organization attainable when the maintenance tendencies were not too disparate and the magnet effect was strong. When the competition was equal to or greater than the cooperation (that is, the maintenance tendencies successfully countered the magnet effect), then the coordination was relative, with the rhythmic units moving at different tempos. Despite the absence of a fixed phase relation and a common frequency, fins in relative coordination nevertheless exhibited an attraction to some phase relations more than others. These attractive phase relations were proximate to those of absolute coordination. Thus, a change in the phase relation on each successive cycle, so-called phase wandering, gave way to a hovering in the vicinity of the preferred pattern of absolute coordination for several cycles, which then gave way once again to phase wandering, and so on in a repeating pattern.

Fig. 12 shows the insights of Von Holst as they are currently expressed in the well-known and well-studied Haken–Kelso–Bunz (HKB) equation (Haken, Kelso, & Bunz, 1985). The equation has several virtues that are embodied in the sequence of three plots of  $\dot{\phi} \times \phi$ . First, it gives expression to the notions of a collective variable (here, the relative phase  $\phi$  between the two segments), a primary control parameter ( $b/a$ ), and an imperfection or detuning parameter ( $\Delta\omega$ , the difference between the natural frequencies of the segments). Second, Fig. 12 gives expression to fixed-point attractors (zero crossings with negative slope), the co-existence of two such attractors (in-phase and antiphase), the shift of attractors due to symmetry breaking by  $\Delta\omega \neq 0$ , and the notion of bifurcation (a change in number of attractors from two to zero with increase in  $\Delta\omega$  from the first to the third plot). Third, Fig. 12 gives expression to how an imperfection parameter in conjunction with the control parameter can change the quantitative and qualitative aspects of the dynamics. Across the three plots of  $\dot{\phi} \times \phi$ , the control parameter is fixed and the imperfection parameter  $\Delta\omega$  is magnified. Fourth, Fig. 12 gives expression to metastability and, perforce, relative coordination. The attractors in the first two plots of  $\dot{\phi} \times \phi$ , with their associated negative slopes, will pull  $\dot{\phi}$  back to them for any small deviations of  $\phi$  from the attractive value. In the third plot of the sequence, the contribution of  $\Delta\omega$  to the collective dynamics is equal to or greater than the contribution of the cooperativity function. There are no zero crossings, no negatively sloped trajectories. There are only the “ghosts” of the previous attractors creating co-existing tendencies to coordinate and to separate (Kelso, 1995; Kelso & Engstrom, 2006). The “ghosts” are metastable points, presumably the places in phase space to which the trajectories are drawn in the relative coordination observed originally by Von Holst.



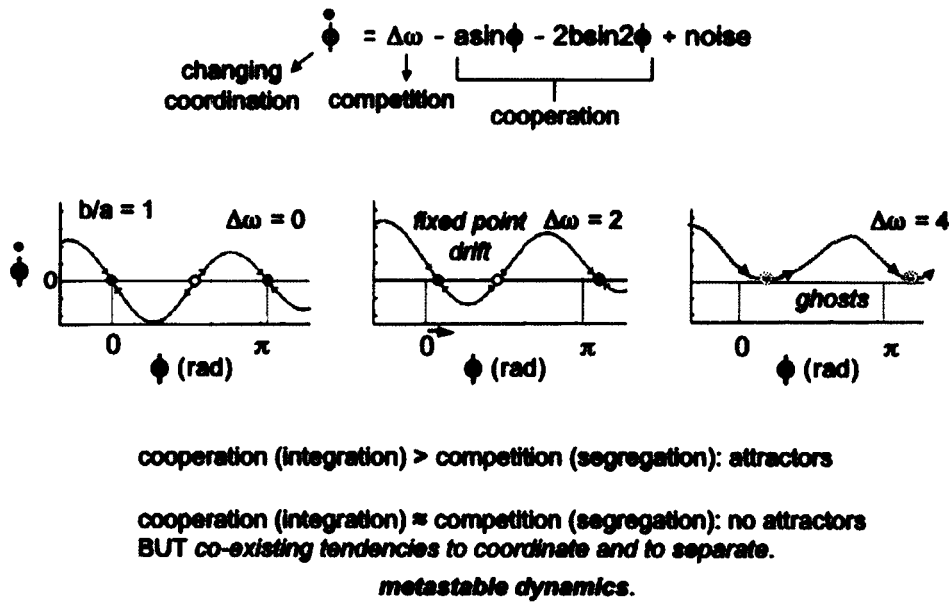


Fig. 12. The Haken–Kelso–Bunz equation (top row), its solutions (middle panels) and the concept of metastability (see text for details).

### 3.5.1. The general synergy equation

Taking the HKB equation (Fig. 12) as the model, the general form of a synergy  $S_i$  is

$$\dot{\zeta} = S(\zeta, c, \delta_1, \dots, \delta_k).$$

In this dynamical system,  $\zeta$  is the collective variable (or order parameter),  $c$  is the control (or primary bifurcation) parameter and the  $\delta_k$  are imperfection parameters. The nature of  $\zeta$  can differ from  $S$  to  $S$  but for the most general functioning of the level of synergies,  $\zeta$  is likely to be relative phase. When there are no imperfections,  $S$  is perfectly symmetric. This latter property and its implications can be appreciated through the HKB equation.

In the formulation of the HKB equation with  $\phi$  the collective variable, the sine functions derive from the phase derivative ( $dV/d\phi$ ) of the potential function  $V(\phi) = -a\cos\phi - b\cos 2\phi$ . This potential function underlying HKB dynamics possesses symmetry, that of reflection,  $V(\phi) = V(-\phi)$ , and that of time-translation (periodicity),  $V(\phi) = V(2\pi + \phi)$ . The symmetry breaking of  $V(\phi)$  (and, hence, of HKB dynamics) due to the primary bifurcation parameter is *spontaneous*. The symmetry breaking occurs as the bifurcation parameter (frequency inversely related to  $b/a$ ) is scaled up to a critical value. The symmetry breaking due to adding imperfection parameters is *induced*. The symmetry breaking is manifest quantitatively as soon as the parameters are in place (e.g., second  $\dot{\phi} \times \phi$  plot in Fig. 12) and manifest qualitatively when the parameters assume specific values conditional upon the primary bifurcation parameter (e.g., third  $\dot{\phi} \times \phi$  plot in Fig. 12).

Building on the foregoing details of HKB dynamics, the bifurcation diagram of  $S$ , that is, the full complement of changes in the number and/or types of its fixed points, is the product of  $c$  and  $\delta_k$  in combination and at specific values. In short,  $S$  is productive or

generative. The unfolding of  $S$  dynamics through its parameters automatically generates, in a context-dependent manner, a wide variety of quantitatively different and qualitatively distinct functional organizations. The unfolding is a model for the challenges raised in Sections 1.2.2 and 1.2.3.

### 3.5.2. Co-dimension and the degrees-of-freedom problem

Although experimental inquiry into HKB dynamics has focused on movement frequency as the primary bifurcation or control parameter, situations have been identified in which control is via changes in amplitude (movement excursion) (e.g., Ryu & Buchanan, 2004). A certain degree of task dependency must be expected in respect to the nature of  $c$ . Imperfection parameters must also be expected to be task dependent. Indeed, their number and their forms are potentially very large and  $k$  in the  $S$  equation can frequently be expected to exceed 1 (for a review see Park & Turvey, in press). Patently, the number of parameters required to flesh out all context-dependent variants of  $S$  is part and parcel of the degrees-of-freedom problem. Suggestions as to the minimal number can be found in the theory of normal forms and its deployment in the group-symmetry perspective (Golubitsky & Stewart, 1985, 2000) of Section 3.1.

A pitchfork bifurcation is the hallmark of a dynamical system with reflectional symmetry. In respect to the symmetric HKB dynamics, with increase in  $b/a$  the repellor at  $\pi/2$  (open circle) in the first  $\dot{\phi} \times \phi$  plot of Fig. 12, and another repellor (not shown) at  $3\pi/2$ , collide with the attractor at  $\pi$  converting it into a repellor (Kelso, 1995). Three fixed points converge and become one, an inverse or subcritical pitchfork bifurcation. Locally, the pitchfork is equivalent to the normal form (Strogatz, 1994)

$$p(x, c) = \pm x^3 \pm cx.$$

The prototypical unfolding of the pitchfork is given as

$$P(x, c, \alpha, \beta) = x^3 - cx + \alpha + \beta x^2$$

with  $\alpha$  and  $\beta$  as imperfection parameters (Ball, 2001; Golubitsky & Schaeffer, 1985).  $P$  informs that a minimum of two imperfection parameters along with the primary bifurcation parameter are needed to encompass the bifurcation possibilities of a given system with reflectional ( $x = -x$ ) symmetry. The dynamics of  $P$  are said to be co-dimension 3 dynamics. A working hypothesis could well be that (a) synergies are co-dimension  $n$ , where  $1 \leq n \leq 3$  and (b) for most realizations of a synergy, as represented by  $S$ ,  $n = 1$ .

## 4. Understanding the perceptual basis of the level of synergies

Although the effects of losing one's sight or one's hearing are easily imagined and simulated, the effects of losing haptic perception, are not. Near complete peripheral neuropathy provides helpful insights. Peripheral neuropathy is the absence of afferentation from the large myelinated fibers with other neural functions essentially intact (e.g., motor nerves are normal). One major documented case has no sense of the body and attachments to the body below the collarbone (Cole, 1995; Cole & Paillard, 1995). His purposeful movements rely on vision and require considerable concentration and intellectual effort. Loss of coordination accompanies a momentary loss of concentration or an ancillary intellectual effort (e.g., sneezing when standing, or note-taking while sitting, produce severe imbalance). The neuropathy has compromised the level of muscular–articular links, the level of synergies.

Because of the intimacy of haptic perception and coordination that defines this level, it alone can ensure movements involving hundreds of muscles, the internal coherence and harmony of coordination, and the persistence of coordination in the face of perturbations. For a person with peripheral neuropathy, standing, walking, reaching and manipulating are challenging if not impossible tasks and the ability to perceive by eye proves to be a poor substitute for the inability to perceive by deformable tissue.

Comprehending perception at the level of synergies, therefore, seems to be very much a matter of answering questions of the following kind. (1) How are deformable tissues organized to function collectively as a medium that can coordinate, globally and locally, information about mechanical disturbances occurring at nested length and time scales? (2) What precisely are the properties of the muscular–skeletal linkages that are perceptible by a system based in the receptive function of deformable tissues? (3) What is the nature of the variables to which the system is sensitive? The foregoing questions are the issue raised in Section 1.2.5 in expanded form.

#### 4.1. Force balance within the cell: A model mechanical system

Although it is commonly viewed as a composite of independent chemical subsystems, the cell has recently been described as a unitary organization of integrated mechanical components (Ingber, 2003a, 2003b). Fig. 13 depicts a tensegrity structure – interconnected tension-supporting components and isolated compression-bearing components. A tensegrity structure distributes stresses to establish a force balance and to stabilize itself against shape distortion. Said differently, the components of a tensegrity structure are constantly in balance with their external and internal force environments. (*Tensegrity* is a contraction of *tension–integrity*.)

Arguments can be given that the cell's internal structure consists of both kinds of stress bearing components depicted in Fig. 13. If the cell is a mechanical structure, with the hallmark tensegrity property of forces in balance, then any stresses imposed externally will propagate throughout the cell's interior. A potential benefit would be a basis for coordinating the local activities occurring at multiple cellular sites (Hu, Chen, Butler, & Wang, 2005; Wendling, Canadas, & Chabrand, 2003). The change in the shape of the cell as a unit and the changes in force distribution among the cell's stress bearing components constitute a kind of rapid (speed of sound) information propagation that can, in principle, support a mechanically based regulation and coordination of the cell's processes. Where regulation and coordination by electro-chemical transduction is slower, localized, and

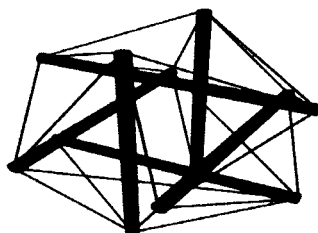


Fig. 13. A tensegrity structure. Thick rods are compression elements (e.g., bones) and thin strings are tension elements (e.g., fascia).

context-independent, regulation and coordination by mechanical force distributions would be faster, both global and local, and would occur in a context-sensitive manner.

#### 4.2. Appreciating fascia

The architectural organization of the cell proposed and defended by Ingber and colleagues (e.g., Ingber, 2003a, 2003b) can be taken as a model for the level of muscular–articular links (Fonseca & Turvey, 2006; Turvey & Fonseca, in press). The development of a tensegrity hypothesis of the level of muscular–articular links begins with an appreciation of the involvement of fascia in muscular coordination. There is a need to consider a fascia network alongside the neural network.

##### 4.2.1. Myofascial transmission

Fascia in different forms connect muscle fibers to muscle fibers, muscle to muscle, and muscle to bone, to yield possibilities for intramuscular, intermuscular, and extramuscular force transmissions, respectively. The essential point is shown in Fig. 14a. The figure highlights the fact that force transmission is not solely myotendinous as implied by textbooks. Although measures of force at a muscle's proximal and distal attachments are presumed to be equal, differences observed between proximal and distal forces indicate (a) muscle dependence on surrounding tissues and (b) modes of force transmission additional to the myotendinous route (Huijing, 2003). Of particular significance to the principles behind the resolution of the problem of degrees of freedom is the additional fact implied by Fig. 14b that the muscle force generated for a given muscle length depends on the muscle's position relative to neighboring muscles and compartment connective tissues (Huijing, 2003; Huijing & Baan, 2002).

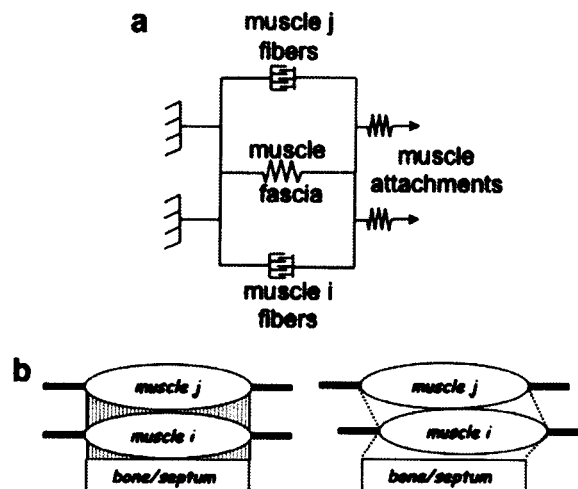


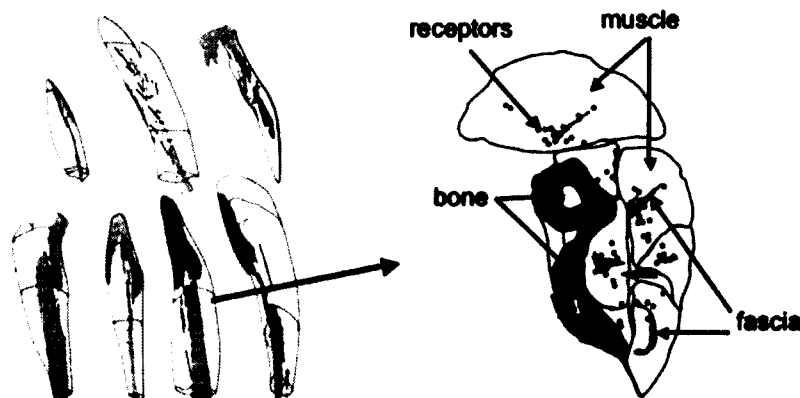
Fig. 14. (a) A schematic of myofascial transmission accompanying myotendinous transmission. (b) Fascia connecting muscle to muscle and fascia connecting muscle to bone are depicted. Because of the connective tissue, movement of muscle *i* affects the tensile state of muscle *j*. (b is adapted from Fig. 7, Huijing, 2003) (see text for details).

#### 4.2.2. Organization of afference via fascia

Theorizing about the afference that underwrites the functioning (expertise) of the level of synergies is traditionally, and not surprisingly, restricted to the neural network. The sensory basis of the level's accomplishments is viewed from the perspective of local signs. In the standard depiction, signals from mechanoreceptors – referring to the states of individual muscles, tendons, and ligaments – are conveyed to spinal neurons and then to brain by non-interacting linear pathways. The challenge for the standard depiction in respect to implementing the expertise of the level of synergies is that of identifying how spatially and temporally separate signals can become organized (see Section 1.2.5) so as to inform about the states of the body as a whole, segments of the body, segments of the body relative to each other, and segments of the body relative to the body as a whole.

Although dominant, the standard depiction has long been confronted by data that suggest a necessarily more cooperative and molar organization of afference (e.g., **Loofbourrow & Gellhorn, 1948, 1949**). A different depiction is suggested by the three-dimensional spatial distribution and orientation of mechanoreceptors in relation to muscle and fascia (e.g., **Strasmann, Van der Wal, Halata, & Drukker, 1990; Van der Wal, 1988**). The heterodox depiction begins with the observation that muscles do not seem to be the proper architectural units for understanding the organization of muscle spindles and Golgi tendon organs. Rather, the functional architectural units seem to be connective and muscular tissues organized in series (e.g., **Van der Wal & Drukker, 1988**).

**Fig. 15** displays the arrangement of muscle spindles and Golgi tendon organs for the antebrachial extensor muscles of the rat (see **Van der Wal & Drukker, 1988**, for human parallels). There seems to be no common organizing principle when considered from the perspective of individual muscles but such a principle is suggested when a perspective is taken relative to connective tissue. **Fig. 15** shows a strong spatial correlation between the morphological substrate of proprioception and the muscle–connective tissue architecture (**Van der Wal, 1988**). As the figure reveals, the primary location of the mechanoreceptors is the transitional zones between collagenous connective tissue and muscle.



**Fig. 15.** Mechanoreceptors align with fascia in the antebrachial extensor muscles of the rat. The shaded areas of the muscles on the left indicate the arrangement of muscle spindles and Golgi tendon organs. The base of the arrow identifies the outlined cross-sectional area that is pointed to and shown in detail on the right. See text for details. (Adapted from Figs. 6.13 and 6.7D4 in **Van der Wal, 1988** with author's permission.)

### 4.3. Biotensegrity and the level of muscular–articular links

The facts expressed in Figs. 14 and 15 provide a foundation for the hypothesis of a fascia network, a network of connective tissue, operating in partnership with the neural network. In relation to the tensegrity model of the cell, the tension elements in the tensegrity model of the body are those of the fascia net, the compression elements are those of the skeleton. On this model, afferent signal processing and integration (to use the conventional language) could proceed at the whole unit level. That is, mechanical regulation of posture and transformations of posture would be in reference to activity at the level of the whole system, the level at which the force balance is established. The many aspects of the fascia net act in unison. Importantly, given the issues raised in Section 1.2, muscles would be seen as acting together as a unit rather than acting antagonistically given that all muscles are part and parcel of the tensegrity structure's continuous tension (Levin, 2004).

In respect to the primary challenge facing the level of muscular–articular links, the force balance property of a tensegrity organization invites the image of rapid contraction of a very high-dimensional space of distributed mechanoreceptor activity to a very low-dimensional information space. Understanding the nature of the information space, the variables that it comprises, would most likely rest upon understanding the geometry of tensegrity structures. Once again issues of symmetry would come to the forefront of discussions on the level of synergies.

The potential commensurability in dimensionality of afference and efference, the same small number of degrees of freedom for both, is a likely consequence of tensegrity organization. From an engineering perspective, tensegrity structures are a special class of flexible structures whose members can perform, concurrently, the functions of strengthening, sensing, actuating, and feedback (e.g., Sultan & Skelton, 2004). They are structures potentially capable of implementing the intuitions conveyed in Fig. 1. Of equal significance, they are structures that can be tuned, an adjustment of the continuous tension that has consequences for the aforementioned functions. In the literature, the tuning of a tensegrity is referred to as *prestress* or *pretension* (Hu et al., 2005; Sultan & Skelton, 2004), a global state that is akin to *tonus* and, therefore, of special relevance to understanding Bernstein's level of tone, the background of all backgrounds (see Fig. 2).

In ways that must await theoretical development, there is a strong correspondence between tensegrity and its prestress property and the concept of preflex (Brown & Loeb, 2000). It is typically presumed that muscles respond to perturbations by means of active neural reflexes. The response time to perturbation can be dramatically reduced, however, during rapid locomotion. A more immediate response, one that precedes the reflex, is implied. The hypothesis is that this pre-reflex response results from the intrinsic force–length and force–velocity properties of muscles. Its zero-delay (Brown & Loeb, 2000; cf. Van Soest & Bobbert, 1993) is the manifestation of large and immediate restoring forces provided by the mechanical impedances from a rhythmically moving limb's stiffness and viscosity.

The larger significance of preflexes for comprehending the level of synergies lies with the broadening role assigned to an animal's mechanical coupling to the environment. Models of multi-limbed animals suggest that passive, dynamic stabilization from a feedforward, tuned mechanical system can dissipate the many and variegated fast-time mechanical perturbations encountered in rapid locomotion (Dickinson et al., 2000; Full & Koditschek, 1999). Preflexes, and the general organizational principle that underwrites them (perhaps

tensegrity), constitute a means of simplifying control – of helping solve the problem of degrees of freedom.

#### 4.4. Inertial properties and the accomplishments of effortful (dynamic) touch

Still unexamined in this coverage of the perceptual foundation for the level of synergies are the issues of the kinds of variables that the haptic system is sensitive to and the kinds of properties that are perceived by means of it. Useful answers have followed from inquiry into effortful or dynamic touch (Gibson, 1966), specifically inquiry into the non-visual perception of spatial and other properties of firmly grasped and manually wielded rigid objects (e.g., Carello & Turvey, 2004; Turvey & Carello, 1995; Van de Langenberg, 2007). This inquiry has involved experimental objects that were varied widely in shape, size and material composition, and of either uniform or non-uniform density. Fig. 16 is a reasonable summary of what is known. First, the non-visual perceptions of a wielded object's spatial and other properties are based upon the moments of the object's mass distribution. The three moments, namely, the 0th (mass), 1st (static moment), and 2nd (moment of inertia), are invariant over the variations in the forces brought to bear on the objects and on the body's tissues during wielding. Second, the perceived properties of a wielded object seem to be perceived independently from one another (e.g., Cooper, Carello, & Turvey, 2000; Shockley, Carello, & Turvey, 2004). The perceived properties as shown in Fig. 16 include the whole length of a rod, the partial lengths fore and aft of the hand, the center of percussion, the orientation (of the L bar) relative to the hand, the grasping hand's position relative to the rod, and the heaviness of the rod. Given an instruction to perceive property  $P_i$  the participant seemingly assembles the haptic system into a specific subsystem  $h_i$  such that

$$P_i = h_i(\text{moments}).$$

Collectively, the mechanoreceptors and the attendant neural and fascia nets seemingly implement a function ( $h_i$ ) on the moments that delivers the intended perception (of  $P_i$ ) (Turvey, 1988).

The study of effortful touch is one important way in which the perceptual capabilities underwriting the level of synergies can be approached. For present purposes this particular

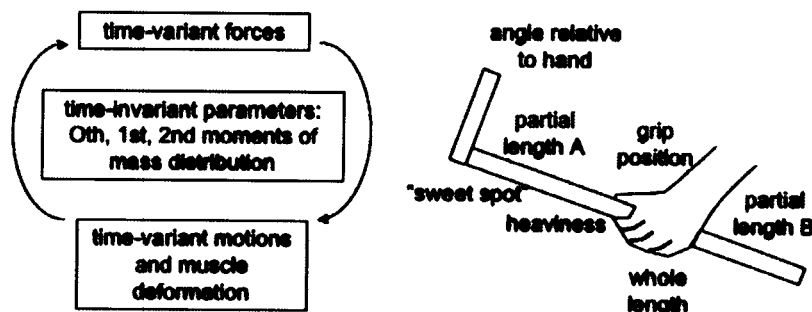


Fig. 16. Left panel identifies the variant and invariant aspects of wielding an object by hand in the manner shown in the right panel. The right panel identifies object properties that seem to be perceived independently of one another by dynamic (effortful) touch.

line of inquiry into the haptic perceptual system can lead to a deeper appreciation of the abstractness of (a) the system's capabilities and (b) the variables to which it is sensitive. The recommended strategy is that of identifying the various  $h_i$ .

## 5. Concinnity through allometric scaling

Bernstein's functional levels that have given impetus and shape to the present chapter are suggestive of a possible hierarchical ordering. The intuitive interpretation of hierarchy is a flow of control from higher to lower levels with the higher as the primary sources of constraint and the lower alleviating the control burden by assuming responsibility for more elementary computation and processing. On first blush the intuitive interpretation would seem to be appropriate for the division into levels of action, space, synergy, and tone.

Despite the intuitive appeal, dissecting a system into functional levels is not sufficient reason for identifying the system as a hierarchy. The pure form of a control hierarchy is a net with two or more levels of control constructed from divergent elements (e.g., node A dominates nodes B and C) and no reciprocity of control (B and C cannot dominate A) (e.g., Turvey et al., 1978). Bernstein's levels more closely approximate a heterarchical rather than hierarchical organization. A heterarchy abides by a control principle of circular transitivity: if A modulates B and B modulates C, then not only does A modulate C but C modulates A and B modulates A (Turvey et al., 1978).

One way to approach patterns of circular transitivity/control reciprocity is via the conjunction of (a) modern developments in mathematics and physics with respect to fractal processes (Mandelbrot, 1983) and (b) experimental results that point to fractal processes in coordinated movements. Key experimental results are of long-range correlations in step-to-step fluctuations in human gait (e.g., Hausdorff et al., 1996; West & Griffin, 1998), center-of-pressure fluctuations in prolonged quiet standing (Duarte & Zatsiorsky, 2001), and period fluctuations in finger tapping (Chen, Ding, & Kelso, 1997). The meaning of such correlations, the fractal meaning, is that any one event (a step adjustment, a postural wobble) in the time series, regardless of its size, exerts an influence of some magnitude on all subsequent events and, in like fashion, is influenced by all preceding events. In each of the above data sets, plotting the logarithm of a variance measure against the logarithm of a quantity equivalent to frequency yields an inverse power-law relation. In each case, the specific dependence of the variance measure on frequency (the resolution used to obtain the measure) defines a scaling relation. Together, the long-term memory carried in the fluctuations of the synergic processes of walking, standing and tapping, and the scaling relation common to these fluctuations, provide insight into the concinnity of neuromuscular and other events expressing the special expertise of the level of synergies.

The insight, specifically, is in regard to the notions of stability and control: homeodynamics rather than homeostasis, allometric rather than (local, instantaneous) negative feedback (West, *in press*).

### 5.1. Allometry and power laws

In the biological sciences, the term allometry (from the Greek *allos*, "other", and *metron*, "measure") typically refers to size-correlated variations in animal form and process that are typically expressed as power laws, that is, relations of the type  $y = f(x) = x^a$ .



The significant features of something (a process, a system) abiding by power-law behavior are that it has no characteristic measure (no defining mean) and that it is scale invariant (same dynamics at every scale) (see Fig. 5). It is worth elaborating the second feature. Let a particular value of  $x$  be multiplied by  $k$ . Then,  $f(kx) = k^a x^a$  and the relative change in the dependent variable from  $x$  to  $kx$  is given by  $f(kx)/f(x) = k^a x^a / x^a = k^a$ . That is, the relative change in  $f(x)$  is independent of  $x$ , independent of scale. Consequently, the identification of an allometric law – for example, one relating a characteristic metabolic or temporal variable to body mass (Calder, 1984) – is the disclosure of a relation between biological properties that is invariant over variations in mass, length, and time scales. Limb frequency and metabolic cost are both found to scale as power laws of body mass implying common size-independent mechanisms for timing and energy use.

In summary, the typical allometric law reflects a general fractal (or scale-invariant) ordering principle that correlates species nearby and species far apart on the dimension of body size. There are good reasons, however, to suppose that the fractal ordering principle applies more widely. In particular, it might be expected to apply to the multiple allometric laws that span the spectrum of processes operating *within a single animal*. The scaling of biological times (Linstedt & Calder, 1981) suggests that the allometric laws governing biological functions of different durations exhibit interrelated scaling exponents. The suggestion raises the question of whether power-law scaling is a mechanism at the level of the individual animal that ensures the integrated function of the component biological structures and functions. That is, it raises the question of whether the concinnity introduced in Section 1.1 reflects a control regime modeled on the allometric principle (West, 1999, in press).

### 5.2. *The hypothesis of self-organized criticality*

A theoretically illuminating power law is one that relates the size of earthquakes to their frequencies, the Gutenberg–Richter law. There are many more small quakes than larger quakes and although the energy of an earthquake of magnitude 8 on the Richter scale is ten million times that of an earthquake of magnitude 1, the covering power law suggests that the processes responsible for the quakes of magnitude 8 and magnitude 1 are the same. No special role separates the large earthquakes from the small. Whatever the theory of earthquakes it must address earthquakes of all sizes – it must address on equal terms barely noticeable tremors and catastrophic land shifts (Bak, 1996).

The Gutenberg–Richter law illuminates a challenge that has parallels in the achievements of the level of synergies. The challenge is that of understanding the principle by which very complicated processes (e.g., those of the earth's crust, with all of its geographic and geological features at many spatial scales, and their dynamics at many time scales) can be condensed into an extremely simple relation (e.g., for earthquakes, that between frequency and size). One much-discussed perspective on this challenge suggests that the system as a whole is in a delicately balanced state in which direct interactions limited to nearest neighbors effectively reach across the entire system (Bak & Chen, 1991). In this balanced or critical state any given component can affect any other component. In the search for viable formulations of the concept of synergy (and its simple relations as identified, for example, in Section 3.5), the notion of self-organized criticality is deserving of attention.

A model system, the sand pile (or some facsimile of it), highlights that the balance is between two processes at distinct time scales and that the separation of time scales is owing

to a threshold (Jensen, 1998). The sand pile grows from pouring sand onto a region of a flat surface, like a tabletop. Static friction, which sticks the individual grains together, makes the upward growth possible. As the height increases and the slopes become steeper, the continuous addition of more sand, and the consequent increase in slope, overcomes the friction, causing some grains to move down the pile but not to an extent that the pile can grow no further. At some point, however, a limit (the “threshold”) will be reached. The amount of sand added to the pile is matched on the average by the amount of sand that leaves the pile. The sand pile has organized itself into a state in which mean height and slope are time invariant. In this state, the avalanches (sand falling off at the edges of the pile) that preserve the constancy of the sand pile under continued adding of sand occur in varied sizes that order as a power law of frequency, resembling the Gutenberg–Richter law.

### 5.3. Component-dominant dynamics and interaction-dominant dynamics

A major conceptual consequence of pursuing the sand pile metaphor is schematized in Fig. 17. Conventionally, one thinks “horizontally” about movement control. That is, one thinks in terms of a number of distinct components, for example, regions of the brain or information-processing devices, whose internal dynamics, when integrated, account for the observed performance. The convention can be referred to as *component-dominant dynamics* because the intrinsic activities of the components are held to be much more influential, much more dominant in determining the observed performance, than the interactions among the components. In Fig. 17 (top), the idea of component-dominant dynamics is envisaged in its most basic form as links in a causal chain – as a linear (or horizontal) sequence of encapsulated devices, each a source of efficient cause.

The metaphor of self-organized criticality promotes consideration of an alternative dynamics and an alternative way of thinking about the level of synergies. The alternative dynamics is *interaction-dominant dynamics* (Jensen, 1998; Van Orden, Holden, & Turvey, 2003). The alternative way of thinking is “vertical”. In the dynamics of a system that has self-organized to a critical state the intrinsic dynamics of the components matter less than the mutual interactions among components. These mutual interactions occur at multiple embedding time scales, as Fig. 17 (bottom) highlights. The causal structure of interaction-dominant dynamics is less like the links of a chain and more like the legs of a table (it provides the *support* for the critical state) (Turvey & Moreno, 2006).

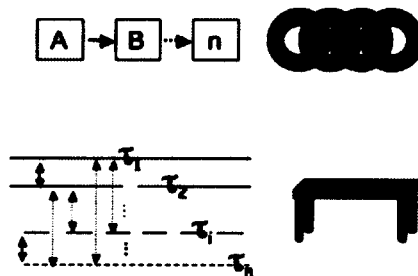


Fig. 17. Schematics of component-dominant dynamics (top) and interaction-dominant dynamics (bottom).  $A$ ,  $b$ ,  $n$  refer to components;  $\tau$ , refer to the time scales.

The vertical thinking is that any synergic activity nests processes at faster time scales and, in turn, is nested within processes at slower time scales. The inverse power-law behavior of stride intervals in walking is an expression of many processes interacting over a multiplicity of interdependent scales. In locomotion, a variety of proprioceptive loops act concurrently and interactively with a variety of optical flow and vestibular functions that are, in turn, concurrent and interactive with muscular, respiratory, and metabolic functions. The interdependence of temporally nested processes, such as those just identified, is required of the delicately balanced critical state: the behavior of any one process at any one time scale must be susceptible to, and reflective of, the behaviors of all processes at all time scales. This massive multi-scaled interdependence among components, processes, and their fluctuations is the concinnity property of the level of synergies and the essential outcome of allometric control.

## 6. The impredicative challenge of synergies

The appeal of allometric control is tempered by the larger challenge that it is heir to: comprehending the logic of circular entailment, the logic of a synergic process. A repetitive theme in this discourse on the level of synergies has been synergy as a process in which very few controls manipulate a much larger number of degrees of freedom. In the paragraphs that follow, this theme is taken a step further. Synergies are identified as impredicative organizations. If impredicativity (defined below) is the benchmark quality of complex systems, as argued by Rosen (1991, 2000), then synergies are not to be understood as mechanisms under constraints, as often assumed, but rather as primary indicators of complexity.

Inherited from the machine perspective on biology is the direction of entailment in regards to components and functions. The term entailment designates *causality* when discussing natural systems and *strict implication* when discussing formal systems (Rosen, 1988). From the machine perspective, entailment flows from component  $C$  to function  $F$ ,  $C \rightarrow F$ . In logical discourse, the primary property of an entailment is that it propagates “truth” hereditarily;  $X \rightarrow Y$  means that  $Y$  inherits the “truth” of  $X$  (Rosen, 1991, 2000). If  $X$  is assumed to be “true” (whatever “true” might be in a given context), then it must likewise be the case that  $Y$  is true. Thus, in the case of an anatomical, neural, or physiological component,  $F$  is inherited from  $C$  analogous to the  $F$ s of the mechanical  $C$ s that make up a clock or an automobile (Turvey, 2004).

The approximations to a definition of synergy identified in Section 1.2, and the hypothesized principles of the level of synergies identified in Sections 3 and 4 suggest that the entailments of a synergy are not of the kind  $C \rightarrow F$ . The two defining characteristics of a synergy of  $C_k$  components are: (1) the role or function of any component  $C_i$  is dependent on the synergy and (2) the synergy’s function  $F$  is dependent on the larger system of which  $C_i$  is a part. This closed loop of entailment can be diagrammed as  $F \rightarrow C_i \rightarrow F$  and it can be read, in the perspective of logic, as saying that “truth” propagates hereditarily in both directions. In a synergy,  $C_i$  is inherited from  $F$  and  $F$  is inherited from  $C_1, C_2, \dots, C_i, \dots, C_k$ . In the speech production results of Section 1.2.2, the lips respond to jaw perturbation in the case of “bab” but not in the case of “baz”. In the latter case, it is the tongue that responds adaptively. The parts inherit their functions from the whole that they compose. In more general terms (paralleling Rosen, 1991, p. 121), a component at the level of synergies can by its very nature have no completely inherent, invariant description that

entails its function; on the contrary, its description changes as the synergy to which it belongs changes. The results from *in vivo* work loops summarized in Section 1.2.3 may be reflective of the implied strong synergy-dependence of a component's description. An explication of the term *impredicativity* is now in order.

Entailments that are closed loop, such as those of a synergy, are identified as non-predicative or impredicative. Whereas a predicative definition of something is context free, an impredicative definition of something is in terms of (dependent on) the totality to which it belongs. Knowledge of the larger system is required in order to characterize the smaller system; the larger system, however, cannot be known in the absence of a characterization of the smaller system. The *vicious circle principle* has been traditionally used in the development of formal systems to filter out impredicativities (Chemero & Turvey, 2007; Turvey, 2004). The principle disallows any whole (or, mathematically, any set) that may contain parts that are definable only in terms of that whole (no set can include itself). In system terms, the vicious circle principle disallows consulting a larger system (here, a synergy) when attempting to understand a given subsystem (here, a muscle or muscle-joint complex). Only simpler subsystems can be invoked, in particular those whose defining properties and behaviors are context-free. The assumption motivating the principle is that any definition or description of a thing in a collection is suspect – not “objective” – if it relies on the use of the collection itself (Chemero & Turvey, 2007; Rosen, 2000).

The concept of synergy, therefore, presents an impredicative challenge: coming to terms with a circular entailment in which a set of things  $C_k$  (muscles, fascia, joints, neurons, etc.) composes a collective, cooperative thing (a synergy) with functional role  $F$  that comprises and constrains  $C_k$ . The guiding intuition governing the organization of the present article is that a thoroughgoing understanding of the level of synergies will depend on the degree to which the impredicative challenge is met.

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