A mobility gradient in the organization of vertebrate movement: The perception of movement through symbolic language

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Abstract: Ordinary language can prevent us from seeing the organization of whole-animal movement. This may be why the search for behavioral homologies has not been as fruitful as the founders of ethology had hoped. The Eshkol-Wachman (EW) movement notational system can reveal shared movement patterns that are undetectable in the kinds of informal verbal descriptions of the same behaviors that are in current use. Rules of organization that are common to locomotor development, agonistic and exploratory behavior, scent marking, play, and dopaminergic drug-induced stereotypies in a variety of vertebrates suggest that behavior progresses along a "mobility gradient" from immobility to increasing complexity and unpredictability. A progression in the opposite direction, with decreasing spatial complexity and increased stereotypy, occurs under the influence of the nonselective dopaminergic drugs apomorphine and amphetamine and partly also the selective dopamine agonist quinpirole. The behaviors associated with the mobility gradient appear to be mediated by a family of basal ganglia-thalamocortical circuits and their descending output stations. Because the small number of rules underlying the mobility gradient account for a large variety of behaviors, they may be related to the specific functional demands on these neurological systems. The EW system and the mobility gradient model should prove useful to ethologists and neurobiologists.

Keywords: amphetamine; apomorphine; drug-induced stereotypies; exploratory behavior; gestalt perception; language; motor development; movement notation; play; quinpirole; ritualized fighting

1. Introduction

In following the tradition of comparative anatomy, Heinroth (1910), Whitman (1919), and Lorenz (1937) conceived of behavior as an extension of anatomy and applied the methodology of comparative anatomy to the study of its structure. Lorenz (1981) considered the discovery that movement patterns may be homologous "the Archimedian point from which ethology marks its origin." Beer (1974) cites two major issues that concerned comparative ethology: homology and adaptation. How is it, then, that the search for common patterns of behavior across the vertebrates (i.e., homologies in the pre-Darwinian sense, without implying common descent) has not been as fruitful as anticipated by the founders of ethology? Could it be that the present-day shying away from the comparative morphology of behavior reflects the limitations of the informal vocabulary that has been available for such studies?

In a paper on "gestalt perception as a source of scientific knowledge," Lorenz (1959) explained why gestalt perception is an indispensable step in the establishment of behavioral homologies; he suggested that this process is basically intuitive and subconscious and therefore cannot be taught. What Lorenz did not consider was the role that language – any language – plays, in creating a disposition for perception and thought and in organizing experience (Vygotsky 1965; Whorf 1956). The gestalt perception of movement is programmed by the language used by the observer, and the terms and words of a language are the vehicles and tools of perception and thought.

Everyday terms obscure both what is common and what is different in the structure of behavior. Consider, for example, "play bowing" in canids and "looking (at one's partner) between one's own legs" in primates, which are described as two unrelated "play signals" (for a review see Fagen 1981, p. 416). The label attached to the first focuses on the orientation of the trunk; the label attached to the second focuses on the presumed function (looking) and the relationship between the animal's head and hindlegs. A kinematic analysis would reveal that the two postures share a common orientation of the trunk in relation to the

substrate (diagonally down) and a common orientation of the face in relation to the playmate (facing). They differ in the orientation of the trunk in relation to the playmate (toward in one, away in other) and in the orientation of the head in relation to the ground (in the second posture the head is upside-down). The opportunity to compare the structure of these two composite configurations is impeded if the data are composed of whole-animal categories of behavior labeled by everyday terms such as bowing and looking between the legs. These labels obscure the fact that in looking between its own legs the primate bows as well.

Even such straightforward terms as "up" or "forward" are equivocal because they leave room for interpretation: For example, "up" in relation to what – the animal's own body? gravity? the substrate's orientation? The undisciplined use of ordinary words in describing movement may carry the attention of the observer haphazardly from one aspect of movement to the next, impeding systematic analysis. In the representation, "female approaches male, then rears on hindlegs, then performs a neck bite," the observer describes the movement in reference to the male, then in reference to gravity, and finally in reference to contact between the parts of the body of the two interactants. The shift in attention every time a new movement has been performed excludes a continuous monitoring of movement in relation to any or all of these frames of reference.

In this target article I show how a behavioral gestalt can be revealed in a variety of situations and species using a consistent description of movement in a single coordinate system. This is illustrated with two variables from a specialized language for the analysis of vertebrate movement, the Eshkol-Wachman geometrical movement notation (EW) (Eshkol 1980; Eshkol & Wachman 1958).

The two variables that are specified systematically whenever a behavior is analyzed in this article are (i) the base of support: the part, or parts, of the animal's body that are in contact with the substrate and bear the animal's weight, and (ii) the orientation of the animal's trunk in relation to a spherical coordinate system whose center is attached to the joint linking the trunk and the base of support. Focusing on this description of movement turns out to be fruitful because all movement must be physically – and hence neurologically – organized in relation to the base of support.

Attention to the changes that take place in trunk orientation in relation to the base of support and temporary disregard of other kinematic and functional aspects reveals a morphological continuum that pervades a variety of seemingly unrelated behaviors.

2. Methodological considerations

2.1. Trunk orientation is described in relation to the base of support

A detailed exposition of the use of EW in the analysis of vertebrate behavior is given elsewhere (Eilam & Golani 1988; Golani 1976; Golani et al. 1979; Szechtman et al. 1985; Yaniv & Golani 1987). The verbal accounts presented in this article are transcriptions of EW motor scores.

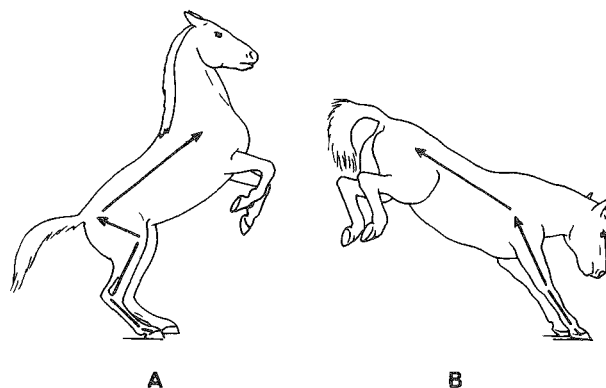Of the versatile descriptive tools available in EW, only

Figure 1. Arrows indicate the mechanical interdependence among the parts of the horse's body. In A, the base of the body is in the hindlegs and the orientation of the trunk is to be viewed accordingly, from pelvis to shoulders. In B, the base is in the forelegs and the orientation of the trunk is to be viewed from shoulders to pelvis.

two are used extensively in the present review: the base of support and the orientation of the trunk in relation to that base. These conceptual tools are illustrated in Figure 1: In A the horse's weight is shifted to the hindlegs; the mechanical interdependence between the segments of the horse's body entails that its trunk should be viewed as oriented diagonally upward from hips to shoulders. When weight is shifted to the forelegs, as in B, the forelegs become the base of the body, and the mechanical interdependence entails that the trunk should be viewed as oriented upward as well, but this time from shoulders to hips. In A the trunk moves on the hip joints; in B, on the shoulder joints.

3. The mobility gradient as an integrating model in the organization of vertebrate movement

3.1. Support and the orientation of the trunk in relation to gravity

The "neck bite" of the wolf in Figure 2A and the "hip thrust" of the dog in Figure 2B seem unrelated. In the EW system, one is more likely to see that the two are symmetrically opposed to each other. In the "neck bite," most of the animal's weight is shifted to the hindlegs and
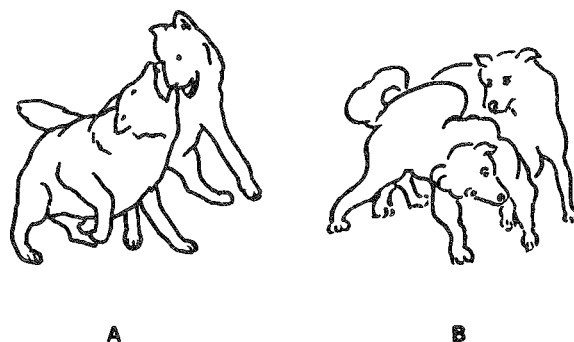

Figure 2. The "neck bite" performed by the "inferior" wolf on the left in A and the "hip thrust" performed by the "superior" dog on the left in B constitute symmetrical opposites. (A: from Moran et al. 1981; B: from Fischel 1956, illustrated in Schenkel 1967.)

the animal's trunk is oriented upward from hips to shoulders; in the "hip thrust," most of the animal's weight is shifted to the forelegs, and the trunk is also oriented upward, but this time from shoulders to hips.

In describing the orientation (position) of the trunk within a spherical coordinate system, one is more likely to realize that the two positions of the trunk represent two values *along the same interval scale* (top circles, Figure 3; bottom circles are explained in conjunction with Figure 4).

This in turn directs the attention of the observer to the whole range of positions between the two extremes. during "hip thrust" interactions (see Moran et al. 1981) in canids, for example, the "superior" or dominant animal *exploits the whole range* between the two extreme positions, rearing up on either its hindlegs (Figure 4A, jackal on left) or its forelegs (Figure 4B, jackal on left). The "inferior" or subordinate animal *exploits only half the range*, by shifting only between a horizontal and an upward position of the trunk from hips to shoulders (Figure 4A and B, jackal on right). In this interaction, the difference in status between the jackals (*Canis aureus*) is manifested in a difference in their range of movement in the vertical plane. This difference in range is schematically illustrated in Figure 3 (bottom circles).

Attention to morphology and temporary disregard of function direct the attention of the observer to similar behavior performed in other, seemingly unrelated contexts. For example, if one labels the three scent-marking postures of the jackals in Figure 5 A–C as "squatting," "leg

A   **B**

Figure 4.   Illustration made from film of ritualized fighting between two male jackals. "Superior" animal (on left in both A and B) alternates between a hindleg (A) and a foreleg (B) base, thus doubling the range of its vertical movements; "inferior" does not use the foreleg base and rears only on hindlegs (A & B). The range of its vertical trunk movement is reduced by half compared to that of "superior."

lifting," and "jumping on forelegs" (Golani & Mendelssohn 1971), no heed is given to the relatedness between the postures nor to the behavior described earlier in this section. Gradation is suggested when trunk orientation in the three postures is examined in relation to a spherical coordinate system attached to the base of the body: In Figure 5A the weight of the body is shifted to the hindlegs, and the trunk is oriented diagonally upward from rear to front; in 5B, weight is distributed between the forelegs and one hindleg, and the trunk is oriented slightly above the horizontal, from front to rear; in 5C, all the weight is shifted to the forelegs, and the trunk is oriented diagonally up from front to rear. Furthermore, the change in these two variables ("weight" and trunk orientation) is related, as in the previously described agonistic behavior, to the social status of the animals. Young and subordinate canids urinate by shifting weight to the hindlegs; with age, increasing status, or later stages in the estrus cycle, weight is increasingly shifted to the forelegs and the trunk changes its orientation respectively. A similar transition from squatting on the hindlegs in young and "inferior" animals to a hand stand in "superior" animals is seen in male canid posture during defecation. Because urination and defecation are often performed near vertical objects, superior animals end up
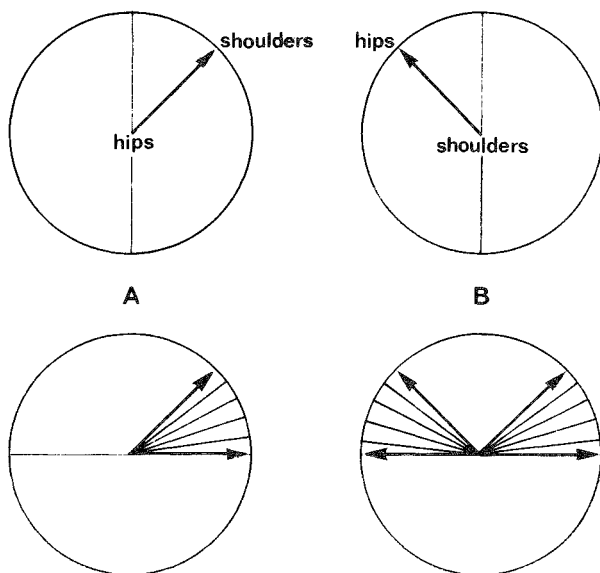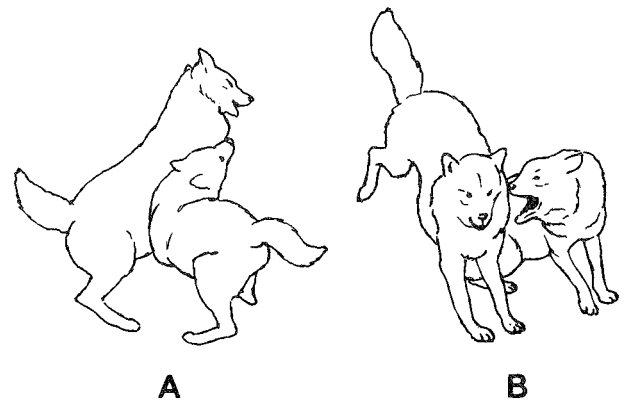

A   **B**

Figure 3.   Top two circles: Schematic illustration of trunk orientation in relation to a spherical coordinate system centered at joints closer to base. Arrows indicate trunk orientation. Center of circles represents the joints that are closer to the base. The orientation of the trunk is read from these joints out and up. A: Trunk orientation during rearing on hindlegs. B: Trunk orientation during rearing on forelegs. Bottom circles are explained in conjunction with Figure 4. A: Arrows indicate trunk orientation in two extreme positions. Lined section between arrows indicates angular range covered by trunk of "inferior" animal during rearing (on hindlegs only). B: Angular range covered by trunk of "superior" during rearing (on either hind- or forelegs).

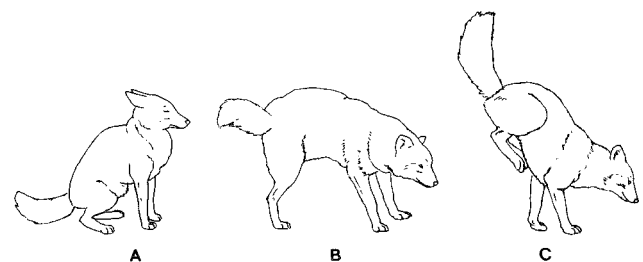**A**   **B**   **C**

Figure 5.   Trunk orientation in postures assumed during urination in golden jackals. A: squatting of female, B: leg lifting of "superior" male, C: jumping on forelegs by "superior" female. Shift of weight to forelegs and respective change in trunk orientation are associated with increasing status. (Adapted from photographs presented in Golani & Mendelssohn 1971.)

scent-marking higher than inferior ones. This way, social status, which is manifested in fleeting stance on a spherical coordinate system, is mapped by durable scent marks onto a vertical metric scale.

In situations of extreme immobility, such as an introduction to a new environment or the proximity of a superior rival, all four legs of quadrupeds are flexed, weight is evenly distributed between them, and the trunk is in contact with the ground in a horizontal position. This posture and the gradual transition out of it are schematically illustrated in Figure 6, 1–4. The forelegs extend first and the hindlegs later, carrying the trunk first to a diagonal (from hips to shoulders) upward position then to a horizontal position, this time *away* from the ground. Sometimes, before darting forward, a canid, for example, may freeze and flex its forelegs. In this "ambush" or "play bow" posture (Fagen 1981), which may precede fast forward running, weight is shifted to the forelegs and the trunk assumes an upward position from shoulders to hips.

The shift of weight from hind- to forelegs and the corresponding change in vertical orientation of the trunk occur in the examples described so far in contexts that involve some form of buildup. In the transition from (1) inferiority to superiority between and within animals (as defined by, e.g., Schenkel, 1948, in terms of other relatively independent variables); the transition from (2) nonestrus to estrus as well as in the process of sexual maturation (the postures assumed during scent marking); and in the transition from (3) relative immobility to extensive locomotion.

3.2. "Weight" and the orientation of the trunk in the horizontal plane (pivoting)

The label "hip thrust" (Golani & Mendelssohn 1971; Schenkel 1948), which has been used to describe the behavior of the superior wolf (e.g., in Figure 7, left wolf, frames 20 – 57) is useful because it directs the attention of the observer to the action and to the part of the body of the superior that imparts this action onto the inferior. (In rodents the same type of behavior has been labeled "lateral posture" [Grant & Mackintosh 1963], "lateral walk," or "lateral attack" [Blanchard et al. 1977]). The label "neck-bite" (Schenkel 1948) is similarly useful because it encapsulates in two words the action imparted by the inferior onto the superior and the part of the body of the superior to which this action is applied (Figure 7, right wolf, frames 57–91). These labels would have been even more useful, however, had there been an awareness that both direct attention to the free end of a linkage of moving segments, both provide a functional interpretation for the
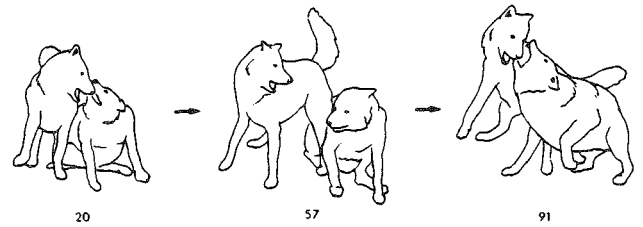
Figure 7. "Hip thrusts" during ritualized fighting in wolves. Numerals indicate frame number on a 24 f/s film. "Inferior" (on right) pivots on hindlegs (frames 57–91), "superior" on forelegs (frames 20–57) (from Moran et al. 1981).

movement (description by consequence), and both veil the movements of the parts of the linkage that connect the free end to the base. Ordinary perception of movement is based on a strategy that is useful in everyday life: For example, one attends to the tip of a finger that traces a movement in the air, and one tends to ignore the movements of the upper arm, the lower arm, the hand, and the finger that carries this tip. Indeed, many descriptions in the literature of, say, rat movement, include moving snouts and heads – but hardly ever a moving chest or pelvis, which actually induces the movement of the snout.

If the horizontal movements of the two wolves during "hip thrusts" are examined in reference to the base of the body, however, one is bound to see that the inferior animal pivots exclusively around its hindlegs (Figure 7, wolf on right, frames 57–91), whereas the superior animal performs the hip thrust either by pivoting around its forelegs (Figure 7, frames 20–57) or its hindlegs (not illustrated). As with vertical movement during "hip thrusts," so with horizontal movement: The inferior uses one base, whereas the superior alternates between two, thus doubling the range of its movement.

"Hip thrusts" are but one of several configurations of interactions constituting ritualized fighting in wolves (Golani & Moran 1983; Moran et al. 1981). This type of interaction was systematically analyzed in honey badgers (*Mellivora capensis*) where it was found to be composed of parts termed – in analogy to wrestling – rounds (Yaniv & Golani 1987). A badger initiates a round by establishing contact with the partner, either by forward progression or by pivoting toward it. As in wolves, pivoting is performed either around the hindlegs (Figure 8A) or around the forelegs (Figure 8B).

Whereas the inferior pivots toward the partner only around its hindquarters (Figure 9, left badger, frames 1320–1359) the superior pivots toward it *either* around its hindquarters (Figure 9, right badger, frames 1413–1423)
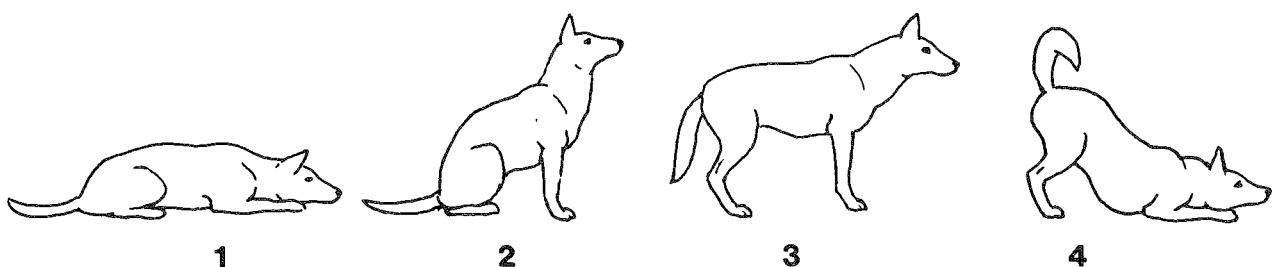

Figure 6. Transition out of immobility is associated in canids with a change in vertical trunk orientation. 1: crouched immobility, 2: rearing on (flexed) hindlegs, 3: standing, 4: readiness for extensive locomotion, as in play bow.
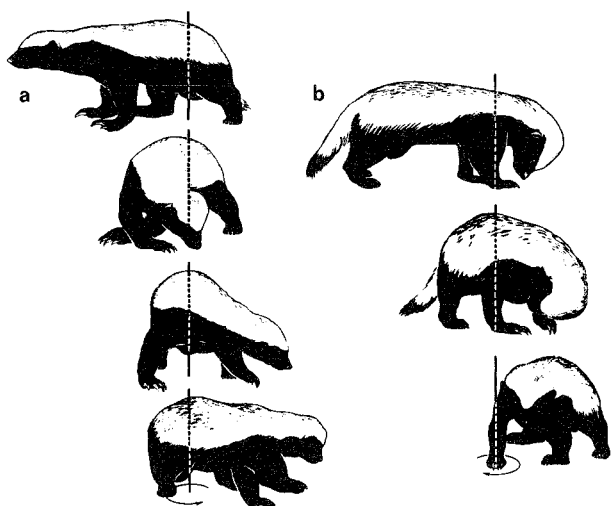
Figure 8. Pivoting in a honey badger. A: on hindlegs and B: on forelegs. Pivoting is illustrated from top to bottom and proceeds in the direction indicated by the arrows. Interrupted vertical lines indicate location of axis of pivoting (Illustrations made from film; in Yaniv & Golani 1987).

or around its forequarters (not illustrated). Contact is released by pivoting away from partner (Figure 9, right badger, frames 1413–1423). Whereas the inferior pivots away from partner on its forequarters only at a late stage of the interaction, the superior pivots away from partner on its forequarters right at the start. Examining all the interactional contexts in which pivoting is performed, we have shown that *the superior shows a higher overall*
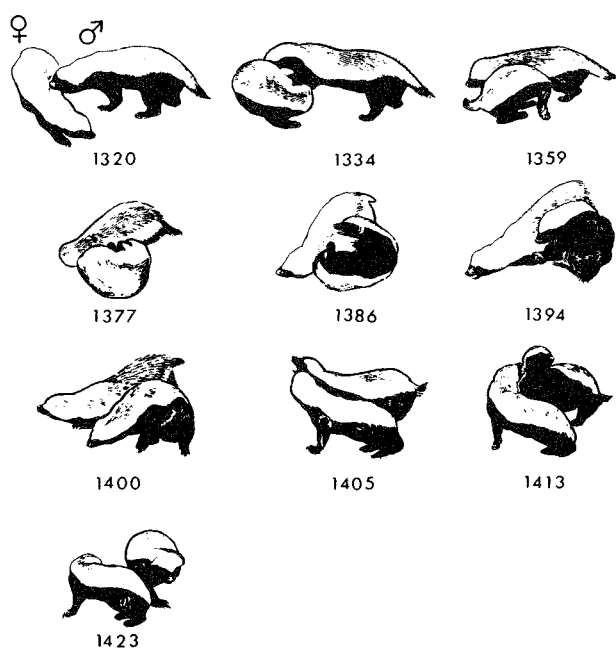

Figure 9. A "round" in a ritualized fighting interaction of a pair of honey badgers. Drawings were made from a 24 f/s film. Numerals indicate frame number. Drawings illustrate horizontal pivoting on hindquarters of "superior" (male, frames 1320–1334; 1413–1423); and "inferior" (female, frames 1320–1359). Tumbling forward (see later in text) is performed in inferior only around hindquarters (frames 1386–1400).

tendency to pivot around its forelegs (Yaniv & Golani 1987).

3.3. Stimulus-bound versus free behavior

To study the visual and tactile effect of a moving badger on the behavior of its partner, we notated continuously the parts of the bodies of the two interactants that touched or almost touched each other. In the language of EW, this relationship is called "opposition" (Eshkol 1980). A record of this relationship is analogous to the retinotopic description of eye movement commonly used in the study of oculomotor behavior. It indicates the initial point of contact or opposition with the partner on the body surface of one interactant and then the path of opposition on the body surface to a new point. This way we specified the interactional environment of each of the partners. Next, we examined each of the partners' choices of base during pivoting in relation to each of the initial interactional configurations observed. For example, when the snout of the superior establishes opposition with the hindquarters of the inferior, the inferior pivots on its hindlegs toward the superior (thus shifting the point of opposition with the superior to its own snout; Figure 9, frames 1334–1359). The snout-to-hindquarter opposition between the partners provides a specification of the visual (and/or tactile) environment that elicits the pivoting.

A systematic comparison of the relations of opposition preceding pivoting showed that in the superior, a snout opposing its hindquarters elicited any of the four physically possible types of pivoting (on fore- or hindlegs, toward partner or away). In contrast, in the inferior, a snout opposing its hindquarters elicited only one type of pivoting toward partner (on hindlegs) throughout the round, and only one type of pivoting away (on forelegs), which was performed only late in the interaction.

This held true for all the other configurations of interactions and response types associated with them. The inferior responds to each of the configurations immediately, mostly with one specific response. The superior appears to be free, because it responds with several response options and variable latencies to the same configurations. On the assumption that a configuration of the interaction represents the stimulus situation confronting a badger, one may conclude that the increase in the tendency to pivot around the forelegs is associated with an increased freedom of response (Yaniv & Golani 1987).

3.4. Ontogeny

3.4.1. Movements on the caudal base of support develop early. The terms "head turning," "trunk flexure," and "pivoting" (Altman & Sudarshan 1975) have been used to describe three types of movement appearing successively in the ontogeny of rat locomotor behavior. These terms are hardly helpful in highlighting the intrinsic relationship among the three movement types: Only "head turning" implies a change in the orientation of the head in relation to both the environment and the body; "trunk flexure" disregards the changes in orientation in relation to the environment; and "pivoting" ignores the changes of relation between the parts of the body. The tacit change of frame of reference every time a new term has been used

blurs the intrinsic affinity of the respective movement types to each other. When viewed within the framework of the present review, however, it can readily be seen that the three movement types, which appear in ontogeny one after the other, are horizontal movements performed on progressively smaller caudal bases (Figure 10, left column): In head movement, the base of support includes pelvis, torso, and all four legs; in chest movement it includes pelvis and hindlegs and in pivoting only one hindleg. The base is reduced in the same cephalocaudal order in the development of forward and vertical movement (Figure 10) (Golani et al. 1981; Eilam & Golani 1988).

3.4.2. Movement on anterior base of support develops later.

Horizontal movements of head, chest, and pelvis (pivoting) on caudal joints are performed in some rats (*Rattus rattus*) as early as postnatal day 3. Vertical movement appears later: raising the head in the air on day 12; sitting up accompanied by release of foreleg contact on day 16; and rearing up on the hindlegs on day 25 (Eilam & Golani 1988). The same developmental order has been described in a variety of mammals (Golani et al. 1981).

Use of forelegs as the base of support and pivoting on forelegs appear still later in ontogeny, during playful and

Figure 11. Falling back is performed by wolf pups during combative activity on being grasped on the dorsal side of the neck. Numerals indicate frame number on film (from Havkin & Fentress 1985).

aggressive interactions (personal observation). The later appearance of these behaviors has been documented in the ontogeny of social play of wolf pups (Havkin & Fentress 1985): From 40 days of age onward, when grasped by a partner in the dorsal side of its neck, a pup may drop to sitting, raise its trunk to a diagonally upward position, and then fall back (Figure 11). From day 53 on, however, the same stimulus situation may elicit either falling back or "lowering of the shoulders and full extension of the hindlegs" followed by tumbling forward head on (Figure 12). When this combative technique is examined from a pure geometrical point of view one can see that in tumbling head-on, the wolf pup "exhausts," so to
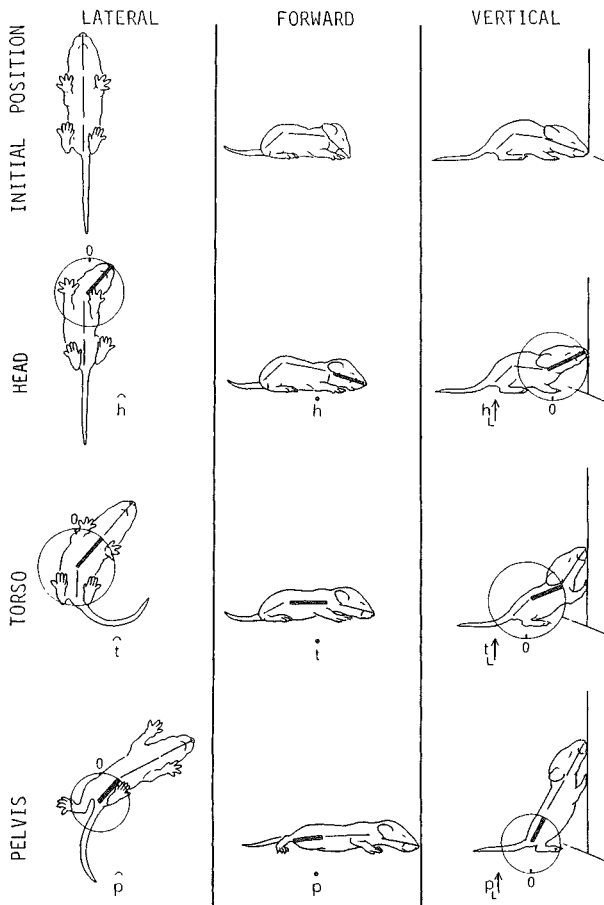

Figure 10. Shoulder-to-hips reduction of base of support during movement seen in infant rats in the process of transition out of immobility. Columns represent the three spatial component-variables. Horizontal lines represent the moving part of the trunk closest to base. The axis of the moving part of the trunk closest to the stationary base is represented by a thick barline.
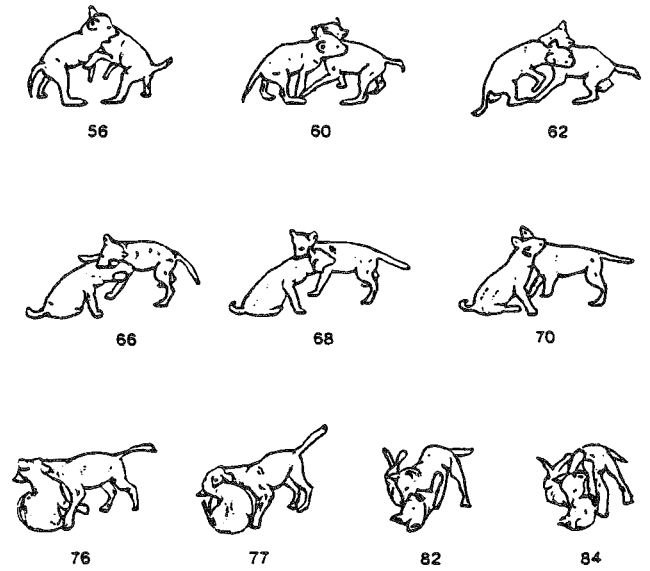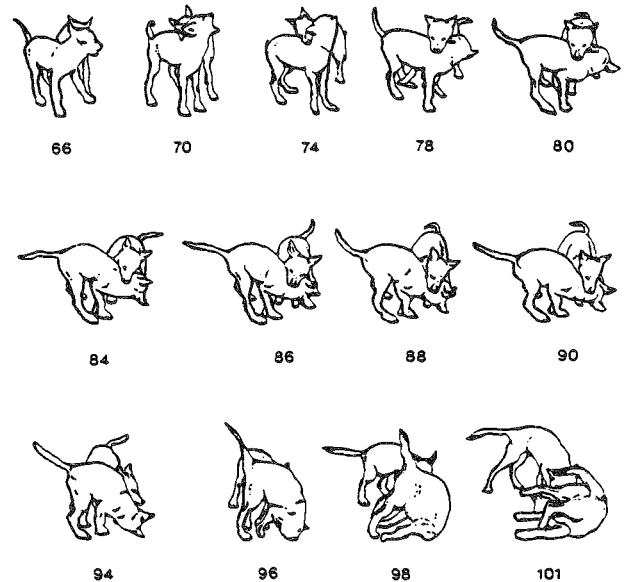

Figure 12. Tumbling head-on is performed by older wolf pups on being grasped on the dorsal side of the neck (from Havkin & Fentress 1985).

speak, the vertical plane, thus culminating the development of movement along this dimension.

In several carnivores tumbling head-on has been termed "forward fall" (Havkin & Fentress 1985) or "rolling over" (Fox 1971; Henry & Herrero 1974; Hinton & Dunn 1967; Leyhausen 1979). In wolf pups it has been described as a combative strategy having the advantage of forcing the top pup to release contact with the bitten scruff of the pup that tumbles (Havkin & Fentress 1985). Once again, as correct as this interpretation may be, premature attention to the functional significance of this behavior might distract us from seeing its intrinsic relatedness to other vertical movements. More important, the terms used to represent this movement obscure the fact that it takes place in the vertical dimension. To reveal, that is, perceive, the growth of movement along the vertical, it would be helpful to be equipped a priori with a "search image" that includes the concept of a *vertical* dimension.

3.5. Fighting roles and developmental age of movement types

After having established the developmental order of movement types we may now return to ritualized fighting in canids (Figures 2, 4, 7). Whereas the repertoire of the inferior *is restricted to movements that appear early in ontogeny* (shift of weight to the hindquarters, pivoting around them, and raising of trunk upward on hips), the superior exhibits *the whole developmental range* (showing also shift of weight to the forelegs, pivoting around them and raising of trunk upward on shoulders). Note that in ritualized fighting in honey badgers the inferior tumbles only on a caudal base: In tumbling forward from supine to standing position (Figure 9, frame 1386–1400, badger in foreground) and in tumbling backward from standing to supine (reversed movement to that illustrated in Figure 9, frame 1386–1400) the base is at the hindquarters (Yaniv & Golani 1987).

3.6. Serial order

3.6.1. In moment-to-moment behavior: "Warmup" in development and "shutdown" with the direct dopamine agonist apomorphine. Lacking a technique of behavioral description that could match sophistication at the neurochemical level, behavioral pharmacologists had to devise their own methods for scoring behavioral events. Their categories of rat open field drug-induced behavior often focus on the movement of the free end of the animal, sometimes also attributing to it a functional significance, for example, side to side head movements, biting, gnawing, licking, and sniffing. Several parts of the body that contribute substantially to whole animal movement – legs, pelvis, and torso – are practically absent in the representations of drug-induced behavior. Based on the categories commonly used in this field, rats injected with the prototype stereotypy-inducing drugs apomorphine and amphetamine have been reported to display a behavioral syndrome consisting of enhanced locomotion and a subsequent growing tendency to stay in one place accompanied by perseverative "focused stereotypies": circling, rotating, side to side head movements, sniffing, licking, and gnawing (Cooper & Dourish 1990; Costall & Naylor

1973; Kokkinidis & Anisman 1979; Schioring 1971; Thomas & Handley 1978). Based on such reports it has been impossible to explain "why certain responses dominated the drugged animal's behavior at any given point in time since injection," and "why some responses are repeated at length while others are not" (Lyon & Robbins 1975). Once the behavior has been partitioned by the initial act of perception into a sequence of unrelated response types, it is difficult to reveal any underlying continuity; and in the absence of a systematic mapping of normal behavior, it has been impossible to say why certain response types dominate the stereotyped behavior at the expense of others.

A more abstract *geometrical* analysis reveals that most open field behavior with apomorphine (1.25 mg/kg, s.c.) consists of only two movement types: forward progression and change of orientation in the horizontal plane (horizontal movement). In the course of the drug's action there is a gradual transition from the first to the second (Figure 13, Szechtman et al. 1985). The interaction between these two components generates the large number of patterns of behavior observed with this drug. The rat starts with pure forward progression along straight paths (Figure 14A, stage I) and ends with pure horizontal movement ("pivoting" on hindquarters (Figure 14A, stage V) followed by side to side forequarter movements (not illustrated). In the period when the two components overlap, the changing proportion between them generates progression along paths of increasing curvature (i.e., "circling", Figure 14A, stages II–IV; Figure 14B refers to amphetamine induced behavior, described in sect. 3.10).

Once this behavioral transformation is pointed out, it is difficult to see how it failed to be perceived earlier (see, e.g., Huntingford 1984, p. 44). It appears that the vocabulary of ad hoc terms used by behavioral pharmacologists to describe movement, distracted them from seeing this transformation. In particular, the ad hoc term "circling" (or "rotation") obscures the gradual transition from pure forward to pure horizontal movement because the behavior represented by it is seen as a discrete pattern rather than a composite of two overlapping kinematic variables. The disadvantage of the term is that it impedes the perception of continuity between circling and all the other pattern types. By analogy, in carpet-weaving the term "flower," the pictorial end result, will not show the process of thread composition that generates the flower pattern on the carpet.

Similar long bouts of repetitive pivoting and "side to side head movements" that were described as perseverative or aimless in rats with apomorphine were interpreted in infant rats as a "search automatism" for the mother (Lorenz 1981; Prechtl & Schleidt 1950; 1951). Once again, as correct as it may be, the functional interpretation of this behavior in only one of the situations camouflages the similarity between the two behaviors. Furthermore, in the absence of an abstract (geometrical) formulation of the transformation that the behavior undergoes in at least one of the situations it is almost impossible to see that the transformation in the second is *a mirror image of the first*.

Thus, after pronounced immobility there is in infant rats a gradual transition from pure horizontal to pure forward and then to pure vertical movement and a *cephalocaudal* (head-to-pelvis) spread of movement along
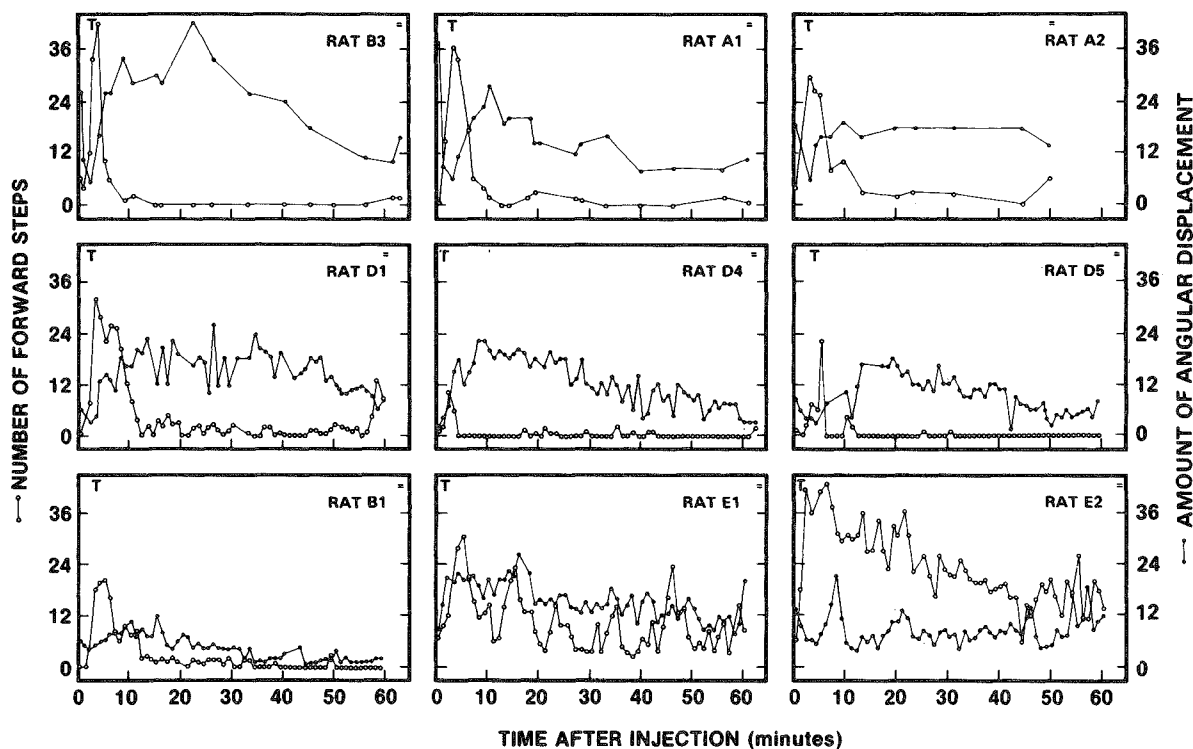
LONGITUDINAL AND LATERAL MOVEMENTS

Figure 13. Time course of forward progression and of horizontal movement (amount of horizontal angular displacement of head) in individual rats injected with 1.25 mg/kg of apomorphine. Forward progression was measured in terms of forward steps of both hindlegs. Horizontal angular displacement was measured in units of 45° (1 = 45°). For each component, every data point represents the value in the minute interval at the indicated time. The position of the sign "T" indicates the time at which vertical movements disappeared, and the position of the sign "=", the time at which they reappeared. If they reappeared after 65 min. the sign "=" was positioned at the extreme right end of the graph (from Szechtman et al. 1985).

the body within each spatial dimension separately (Figure 10; [Eilam & Golani 1988; Golani et al. 1979]). An infant does not move a part of the trunk within a spatial dimension unless that part has already moved within the dimension preceding it in the prescribed "program" (horizontal, forward, vertical) and unless the part anterior to it has already moved within that dimension. This constraint generates the infinite combinations of movement types observed in infants. In moving out of immobility the infant performs the nine types of movement (consisting of movements of three parts of the trunk within three spatial dimensions) one after the other, reverting in between to movement types already performed earlier on. In later stages of this process, when the whole body is already recruited, this constraining principle is expressed in the following way: The infant pivots repeatedly before walking forward. Once it has walked forward, it alternates repeatedly between pivoting and forward walking. Finally, after the first performance of whole body vertical movement, it alternates unpredictably among movements along the three spatial dimensions. Performance of each new type of movement reaches an exaggerated rate before subsiding to normal. Because the amplitudes of the movements show an overall increase as well, the result is a process of motor expansion termed *warmup*. This process was originally described in rats recovering from severe bilateral lateral hypothalmic damage (Golani et al. 1979). Warmup sequences are culminated day by day by increasingly "advanced" types of movement;

hence the parallel order of emergence of new types in moment-to-moment behavior and in development and recovery.

There is with apomorphine a process in which the same movement types appear, increase in rate and amplitude above normal levels, and are finally eliminated in an order opposite to the one seen in warmup (vertical movements are typically eliminated at the onset of drug action, however, without being exaggerated first). The movements also show an overall decrease in amplitude in the course of this process (Figure 13). This process of motor constriction, which consists of a reduction in the number of degrees of freedom for movement, has accordingly been termed "shutdown" (Szechtman et al. 1985).

3.6.2. Compression of warmup and shutdown sequences in normal adult behavior. Because of repetition and reversion to earlier movement types, the expansion of movement during warmup is interrupted, slow, and *spread out*. With age, or with increasing familiarity with the environment (which, in turn, reduces the initial immobility), repetition and reversion are diminished and may even be eliminated. After pronounced immobility adult rats do not rear unless they have already moved forward. Nor do they move forward unless they have performed a horizontal movement. They may do so in a compressed fashion, however: from immobility to a short amplitude pivot, to forward stretching, and to rearing (Eilam & Golani 1988). *Compressed* transition from arrest to pivot-
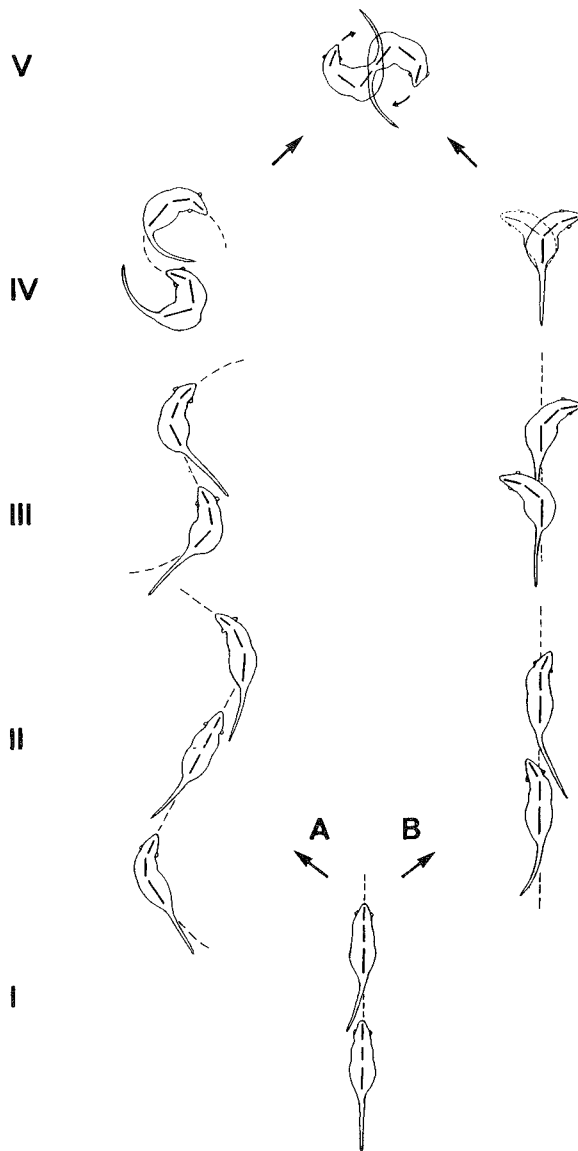
Figure 14.   Schematic representation of stages in rat spontaneous locomotor behavior under the influence of apomorphine and amphetamine. Stages are labeled by Roman numerals. The first and last stages are observed with both drugs. The left column, A, represents three transitional stages observed with apomorphine. The right column, B, represents three transitional stages observed with amphetamine. Each stage is illustrated by dorsal view of two or three successive positions of rat. Interrupted line represents path followed by rat during progression at that stage. Solid barlines represent longitudinal axes of pelvis, chest, and head. The orientation of the axes should be viewed from back to front. Angle between each of the trunk's segments and its next caudal neighbor should be noted. With both drugs there is an overall transition from pure forward (stage I) to pure horizontal (stage V) movement. With both there is a progressive superposition of phasic horizontal movements that gradually increase in amplitude, on forward progression. There is also gradual elimination of forward progression. With apomorphine (left column, A), however, horizontal movements of the head from the outset involve recruitment of chest and pelvis in horizontal movement. This generates progression along paths of increasing curvature. In contrast, with amphetamine (right column, B) the caudal part(s) are not recruited in horizontal movement during stages II–IV.

ing to forward walking is also a feature of the behavior of the inferior wolf during ritualized fighting. Such sequences may be interpreted as *compressed* versions of infantile warmup. In the same vein, the tendency of canids to pivot in the course of the transition from forward locomotion to arrest might be interpreted as a compressed sequence of shutdown (Golani & Moran 1983).

3.6.3. Warmup, shutdown, and ritualized fighting unfold along one behavioral manifold: The mobility gradient.
Because warmup and shutdown take place along roughly the same behavioral continuum, and because a shift along this continuum implies a change in the number of movement types available to the animal at that moment (in terms of spatial dimensions and body parts), this continuum has been termed "the mobility gradient" (Eilam & Golani 1988; Golani & Moran 1983; Yaniv & Golani 1987). The most advanced movement type performed by, say, an infant or a drugged rat, marks the animal's position on the gradient, thereby defining the repertoire of movement types available to it at that time.

Animals also differ in the number of movement types available to them during ritualized fighting: The inferior animal is seemingly unable to shift the weight of its body to the forelegs during part of the interaction, using only half of the range used by the superior in the horizontal and vertical planes (wolves, Figure 4; Yaniv & Golani 1987). We have also shown that in badger interactions, the difference across roles – from inferior through two intermediate roles to superior – consists of a progressive change from predictable to unpredictable behavior. The hindlegs of the inferior are flexed throughout the round whereas the superior appears to be free to flex or extend the hindlegs at all times. The inferior does not walk forward, whereas the superior appears to be free to do so at all times. Inferiority consists of pivoting around the pinned down hindquarters. Forward progression is seen only when the inferior is "pulled" forward by maintaining its snout in contact or opposition with the partner that is moving away. Superiority consists of an unpredictable sequencing of movements that cover the whole range of the horizontal and forward dimensions. Finally, during ritualized fighting the inferior wolf shows an "obligatory" transition from arrest to forward progression and from forward progression to arrest through pivoting on hindlegs (Golani & Moran 1983).

The movement types of the mobility gradient thus appear in the behavior of the inferior during the transition out of immobility in the order described for warmup; during the transition into immobility they appear in the order described for shutdown. In the behavior of the superior these movement types appear unpredictably, together with movement types performed around the forequarters. The gradual buildup in status across roles is thus associated with an addition of the foreleg base (and the movement types performed on it), a gradual addition of nonstimulus-bound forward progression, and a gradual reduction in the predictability of sequences of movement. The two interactants therefore occupy two different positions on the same mobility gradient. Social status may be defined in this situation by the movement types available to the animal, the predictability of their sequencing, and the degree to which the animal is stimulus-bound (Yaniv & Golani 1987).

3.7. A summary of the mobility gradient model

A systematic examination of the orientation of the trunk in relation to the base of the body in rodents and carnivores reveals a structure characterized by motor expansion or, when performed in reverse, motor constriction. In its constricted state, the animal's weight is on its hindlegs and it is immobile. Expansion consists of cephalocaudal recruitment of the parts of the trunk in movement within each of three spatial dimensions separately. Movement builds up first in the horizontal plane, then in forward transport, and then in the vertical plane. During these stages, the parts of the trunk move around their respective *caudal* joints. Next, the weight of the body can also be shifted anteriorly, and the parts of the trunk can now also move in the horizontal and vertical planes around their *anterior* joints. Expansion is culminated with pivoting around the forelegs and, sometimes, with tumbling forward, head-on. The transition along this gradient may be prompt and compressed or interrupted, involving many repetitions and reversions to earlier types of movement. In the interrupted version, it also involves an interrupted increase in amplitude. In this last version, once a new type of movement has been performed the animal reverts to it time and again. As a result, there is a gradual increase in the number of types of movement available to the animal at any one moment: In the process of expansion there is a transition from relatively stereotyped sequences consisting of few types of movement to relatively rich and unpredictable sequences (Eilam & Golani 1988). Sometimes expansion is also accompanied by a transition from stimulus-bound to relatively free behavior. Precisely reversed sequences unfold in the course of behavioral constriction.

This structure appears in such contexts as locomotor development, agonistic and exploratory behavior, and scent-marking. It can serve as a geometrical model or search image in the examination of other contexts and species. If it is a general one, it should help the observer see or even predict features of behavior that might be overlooked otherwise. In establishing a continuum, one becomes sensitized to its missing portions and can recognize them promptly, or even look for them (e.g., the "missing links" in phylogeny).

3.8. The extrapolated features of the hypermobile portion of the gradient

Does mobility expand *beyond* the limits outlined so far, and if so, what would the properties of the hypermobile end of the gradient be? These properties can be extrapolated from the continuum established so far. They should include several elements:

1. Deliberate shifts of weight back and forth between hind- and forelegs, with respective release of hind- and foreleg contact with the ground, and a respective transition of the axis of pivoting between hind- and forequarters.

2. Exhaustion of the three spatial dimensions of movement – horizontal, forward, and vertical. This might in turn lead to the incorporation of *additional* dimensions of movement, such as rotations around the longitudinal axis of the body (as in "barrel-rotation") and rotations around

axes that are external to the animal's body (as in running in a circle and in swinging around a bough).

3. In development, and in the shutdown of mobility (with apomorphine), the appearance of movement along a new dimension involves temporary exaggerated repetition of movement along that spatial dimension; it is therefore expected that rotations around the newly added axes will prevail, and that there should be frequent rolling, tumbling, circling, and swinging.

4. There should be frequent and unpredictable *switching* between movements around the respective axes.

5. Stimulus-boundedness (sect. 2.3) should be reduced to a minimum. There should be minimal dependence on the immediate surrounding tactile and visual stimuli. In interactions, the location and movements of the partner should play a minimal role in shaping movement.

6. Finally, because pinning down to the ground is characteristic of the immobility end of the gradient, frequent release of contact of all four legs (as in jumping) should prevail at the hypermobile end; in other words, the animal should be minimally bound to contact with ground.

3.9. "Exuberant" locomotion and play

It has long been established that exploratory behavior often builds up into "exuberant" locomotion (Lorenz 1981), play (Fagen 1981; Meyer-Holzapfel 1956a; Welker 1971) and "fright" behavior (e.g., Wilson & Kleiman 1974). It is not surprising, therefore, that all of the above extrapolated features seem to be present in these behaviors. The "play bow" and the "hand stand," involving a shift of weight to the forelegs and a shoulders-to-hips upward orientation of the trunk, are frequent in play, as are lateral swaying of the hindquarters (involving a rotation around the fixed forelegs), tumbling forward, "back flips," somersaults, rolling on the ground and in the air, swinging around boughs, locomotor-rotatory movements, and running in a circle (for an extensive review, see Fagen 1981).

The prevalence of rolling and tumbling in the supposedly constricted behavior of the inferior badger during ritualized fighting (Yaniv & Golani 1987) seems to result from blocking of forward locomotion: Perhaps because of hindquarter immobility, mobility spreads to other spatial dimensions. Indeed, tumbling is performed only backward from standing to supine, and forward from supine to standing. It never involves a shift of weight to the forelegs, and it never occurs in the absence of contact or opposition of the animal's snout with the partner's body.

In contrast, in the full blown forms of play and in exuberant locomotion, these and all the other rotation types may be performed solo or in the air (Fagen 1981). In other words, performance is not contact or opposition bound. In asymmetric playful interactions, the animal whose mobility is relatively constricted may roll or tumble backward, but the performance of these behaviors should always involve contact or opposition with the partner; the animal whose mobility is expanded should roll or tumble forward also when at a distance from its partner, regardless of contact or opposition.

The relative imperviousness to weight, contact, and

close visual stimuli is reflected in the play literature by descriptions that include such adjectives as "light," "free," "inattentive," "nonfocused," and "easy to interrupt" (Fagen 1981). The frequency and ease with which foot contact with the ground is released, and the fast shifts of weight between hind- and forelegs are, perhaps, reflected by the variety of verbs used to describe jumping and bounding gaits during solo and pursuit/play: stotting (jumping in place), cavorting, capering, gamboling, bucking, bolting, lolloping (proceeding by clumsy bounds), frisking, prancing, and so forth (Fagen 1981). Finally, play is characterized by a fast rate of *switching* between movement types. This involves an unpredictable transition from one movement type to the next (e.g., Meyer-Holzapfel 1956b; Symons 1978). The amplitude of the movements is also reported to be larger than usual ("exaggerated" e.g., Bekoff 1974). Because some of the expanded features also appear in "fright" behavior, it is sometimes difficult to distinguish fright from play and exuberant locomotion (Wilson & Kleiman 1974).

To establish the hypothesis that there is a continuity between exploration and play and that play and exuberant locomotion constitute the most expanded portion of that continuum, it will be necessary to specify the order in which the building blocks of play are incorporated into the stream of this behavior. If my hypothesis is correct this order should form an extension of the order already established for the less mobile portions of the continuum, and it should be manifested in moment-to-moment behavior and in ontogeny. As pointed out by Bohm (1969), random behavior is often erroneously equated with disorder, whereas in reality it might reflect a more complex level of order. Precisely because of the apparent disorder observed in the hypermobile portion of the continuum, it is necessary to work one's way up to this portion from its more stereotyped and therefore easier to analyze precursors. In the absence of a concept that would tie together the seemingly unrelated features of play – the large repertoire of movement types, the unpredictable switching between types, the supernormal amplitudes, the lightness, the inattentiveness – play appears paradoxical and enigmatic. If the present hypothesis is correct, then the principles established in the less mobile portions of the gradient of buildup, spread of activity, and the gradual reduction in predictability and in stimulus-boundedness make the features of play behavior unsurprising.

3.10. The mobility gradient, drug induced behavior, and basal ganglia function

After having provided a zoological perspective, it should now be interesting to compare several patterns of behavioral shutdown induced by dopaminergic drugs, while at the same time examining the vocabulary commonly used to describe them. As pointed out earlier, the study of behavior induced by dopaminergic drugs is based to a large extent on a limited set of distinct response categories: locomotor activity, stereotypy, gnawing, grooming, and a few other categories. When detailed response categories are used to distinguish among the behavioral effects of different manipulations, such use is based on personal (tacit) familiarity with the animal's movements. For example, what is common and what distinguishes the

following behaviors: sniffing, head waving, head weaving, head checking, and side-to-side head movements? Unless defined geometrically, they can be used neither for comparison across manipulations (unless such comparison is based on personal familiarity), nor for the establishment of behavioral continuity (such as among horizontal head-, chest-, and whole body movement).

As has been suggested by several workers, the study of basal ganglia/behavior relations should include not only selective manipulations of central mechanisms, but also more refined means of assessing the effects of these manipulations on behavior (Dourish 1987; Kuczenski & Segal 1988; Rebec & Bashore 1984; Waddington et al. 1990). These workers indicate that the prevailing classification of a large variety of drug- and lesion induced whole-animal movement into "locomotion" and "stereotypy" is much too broad compared to the intricate and refined distinctions already established on the neuroanatomical and neurochemical sides of the brain-behavior interface. The terms "locomotion" and "stereotypy" are clearly based on some perceived common morphological features, but what are these features and how do the behaviors so labeled vary across manipulations? This question can be examined in the articulated framework offered by the mobility gradient model.

The mobility gradient is composed of such kinematic distinctions as the base of support for movement, the three parts of the trunk, the three spatial component-variables, a distinction between spatial and body-related horizontal movement (to be elaborated next), movement amplitudes, and in addition, gradients of stimulus-boundedness and of the number of degrees of freedom for movement available to the animal at any given moment. The generality and economy of description obtained by using these distinctions makes them suitable candidates for the kinematic quantities controlled by the brain. (A controlled kinematic quantity is used here in the sense of Powers [1973], to mean a kinematic variable corresponding to a perceptual signal that is affected and controlled by the outputs from a controlled system's output function. A detailed example of such a variable is presented in sect. 4.2.).

3.10.1. Behavioral assessment of drug action. To compare the prevailing method of behavioral assessment of drug action to that performed in the context of the mobility gradient model, movement material commonly categorized as "locomotion" and "stereotypy" will be examined across drug treatments with apomorphine 1.25mg/kg (APO), (+)-amphetamine 5mg/kg (AMPH), and quinpirole 0.5mg/kg (QUIN). All observations were conducted over the first hour after injection, in a large simplified environment (a 1.60 × 1.60m glass platform with no objects or walls; for considerations relating to the structure of testing environment, see Szechtman et al. 1985). Whereas APO and AMPH are nonselective dopaminergic stimulants, QUIN acts selectively on the D-2 subtype of dopamine receptors (Kebabian & Calne 1979; Waddington et al. 1990). Unlike APO and QUIN, AMPH is also known to affect other neurotransmitter systems, for example, serotonin (Ernst 1967; 1969; Kuczenski & Segal 1989). By comparing the effects of these drugs on behavior, I illustrate the usefulness of the

mobility gradient model for establishing hypotheses about brain/behavior relations. This section ends with a discussion of the potential value of the model for the neurophysiological study of basal ganglia function.

3.10.1.1. Apomorphine induced behavior. As APO starts to take effect, the rat progresses along straight paths, both along and away from edges (Figure 14, stage I). For a period of seconds or a few minutes, turning is observed only at corners. Then horizontal movement sets in, being superimposed on forward progression, thus producing turning, even when the rat is a distance away from corners and cliffs. During a phasic horizontal movement the head moves laterally on the chest, the chest then joins it by moving laterally in the same direction on the pelvis, and the pelvis then joins the chest by moving laterally in the same direction on the hindlegs (Figure 14, stage II). Because lateral bending of the head is maintained for some time, the rat progresses along a curved path during this interval. Then head orientation becomes fixed in relation to the environment, and as the rat progresses forward in the new direction established by the head, the chest and the pelvis align in a straight line with it.

During the time interval when head, chest, and pelvis are aligned along a straight line, the rat progresses along a straight path. Progression along a curved path is resumed as soon as the rat performs a new lateral movement of the head and then of the chest and pelvis (Figure 14A, II). In the course of the drug's action the rate and amplitude of lateral head movements (and hence also of chest and pelvis movements that join it) increase. Concurrently, there is a gradual reduction in the amount of forward progression. This generates an increase in the rate of progressions along paths of increasing curvature and a gradual shortening of continuous progressions along straight paths (Figure 14A, III–IV). In the full blown version of this process, forward progression is eliminated, and the rat pivots in place in alternating directions (Figure 14, V). Finally, horizontal movements of the pelvis disappear as well, and the rat is left with a residue of "side to side (chest and) head movements" (not illustrated).

3.10.1.2. (1)-Amphetamine induced behavior. It has been realized for quite some time that the behavioral effect of APO on open field behavior is quite different from that of AMPH. Nevertheless, the only major differences that have been established so far on the basis of available methods of behavioral assessment have been the absence of gnawing with AMPH, and, at lower doses of both drugs, the much lower amount of locomotor activation with APO (Fray et al. 1980; Geyer et al. 1987; Robbins et al. 1990).

Movement notation analysis of rat (+)-amphetamine (5mg/kg; s.c.) induced behavior reveals that under this drug too there is a process of behavioral shutdown. Unlike shutdown with APO, however, where vertical movements are eliminated at the onset of drug action, with AMPH, they are first exaggerated and only then eliminated. Shutdown with AMPH thus includes the orderly appearance, then exaggeration, and finally elimination of all the three spatial component variables (vertical first, forward next, horizontal last (Adani 1990; Adani et al. 1991; Eilam 1988).

With both APO and AMPH there is an orderly transition in the course of drug action from pure forward

(Figure 14, stage I) to pure horizontal movement (Figure 14, stage V). With AMPH, however, the stage of relatively pure forward progression sets in much later (10–28 min. after injection; n = 8), and last much longer (12–18 min.). The spread of side to side horizontal movement along the parts of the trunk takes place with AMPH in a qualitatively distinct way (Adani 1990; Adani et al. 1991). With APO, as soon as horizontal head movements set in, the chest and pelvis join as well, and the rat progresses along curved paths. With AMPH, horizontal head movements first set in without recruiting the chest (Figure 14B, II). Next, chest horizontal movements join the head movements without recruiting the pelvis (Figure 14B, III–IV). Finally, the pelvis is recruited as well (Figure 14, V). Thus, in contrast to APO, during movement away from edges, the caudal parts of the trunk are constrained during stages II–IV from performing horizontal movements. While the anterior part(s) perform(s) side to side movements, the hindpart(s) trace(s) a straight path in the environment.

With AMPH, as with APO, horizontal movement sets in before the elimination of forward progression, gradually increasing in rate and amplitude. With AMPH, however, forward progression is eliminated in some rats *before* horizontal pelvis movements set in. Such rats first perform side to side chest and head movements while staying in place (Figure 14B, IV), and then they pivot in place in alternating directions (Figure 14, V). In other AMPH treated rats, forward progression is eliminated *after* the onset of horizontal pelvis movements. Such rats first show superposition of whole body horizontal movement on forward progression, that is, progression along curved paths (not illustrated), and then pivoting in place (Figure 14, V). Thus, progression along curved paths is *not* an invariant feature of AMPH induced behavior, appearing, if at all, at a late stage of this drug's action. In contrast, it *is* an invariant feature of (1.25 mg/kg) APO induced behavior, appearing in all APO treated rats at an *early* stage of drug action (Figure 14A, II–IV). Therefore, if the term "circling" is to be interpreted *sensu strictu* as progression along a curved path, then circling is not an invariant feature of the behavioral shutdown observed with AMPH.

3.10.1.3. Comparison of behavior under the effects of apomorphine, amphetamine, and quinpirole. In Figure 14A, stage II, the chest and the head of the APO-treated rat alternate between being aligned in one straight line with the midsagittal plane of the pelvis (henceforth "the midsagittal plane") and being laterally bent to the right or left of it. The three drugs generate three distinct profiles of organization of movement in relation to this plane (Einat & Golani, in preparation). With AMPH, the anterior parts of the trunk first show an increasing tendency to stay in the midsagittal plane and then an increasing tendency to cross it from side to side without staying in it. With QUIN, the anterior parts of the trunk show throughout the course of drug action an even stronger tendency than during the early phase of AMPH's action to stay in the midsagittal plane. With APO, except for an extremely brief period of alignment in this plane at the onset of drug action (Figure 14, I), the tendency to stay in it is moderate, and similar to that observed in intact rats. These three distinct profiles of organization also prevail during the intervals in which the rats stay in place.

Seven relatively independent measures of trunk movement in relation to this plane characterize these patterns of organization. For example, the cumulative time of staying in the midsagittal plane per 5-min. intervals, relatively stable across the session in both intact and APO-treated rats, is first augmented and then drastically reduced with AMPH, and is only augmented with QUIN (Figure 15).

In normal and APO treated rats, the anterior parts of the trunk typically stay in the midsagittal plane on reaching it, for both brief and long time intervals. With QUIN, the anterior parts stay in this plane for only brief intervals (the long cumulative time of staying in this plane with QUIN is obtained through frequent intervals of staying in this plane). Crossings of this plane without stopping are rare and sporadic in normal and APO rats and almost absent with QUIN. In contrast, with AMPH, such crossings become the most frequent response in the course of the second half of the session (Figure 16).

Differential behavior in relation to the midsagittal plane is also manifested in the mode of progression on curved paths and in the mode of turning in place. Intact rats typically proceed from one place to another along a straight path; progression along curved paths, involving a simultaneous change of orientation of, for example, 90° and three forward steps (arcs) are rare and sporadic and involve various degrees of lateral bending of the trunk. With APO, arcs are strictly limited to the first 10 minutes of the session (Figure 14A, II) and are performed with a

Figure 16. Number of transitions of the anterior parts of the trunk from one side of the midsagittal plane to the other, without stopping at that plane, out of the total number of transitions. Top panel: pooled data. Bottom panels: across the session. N = 4 in each group. Note opposite effects of amphetamine and quinpirole during second half of session.
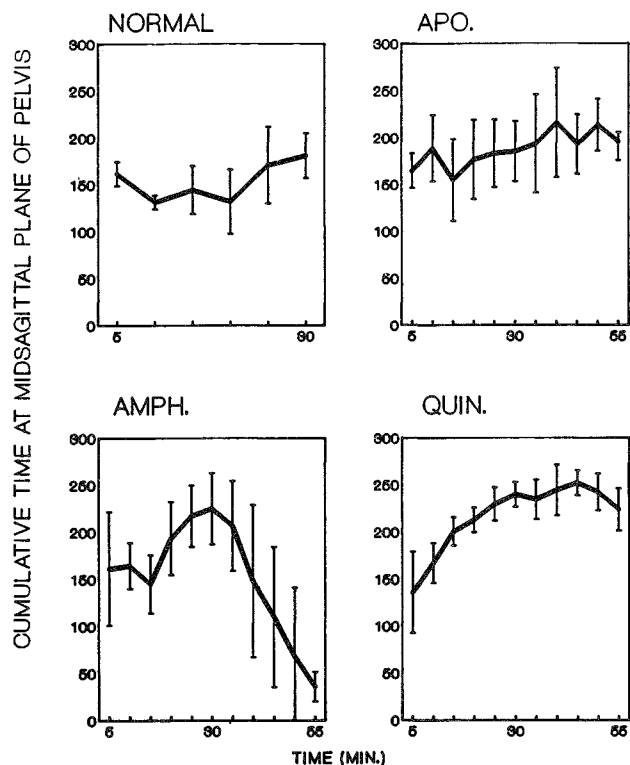

Figure 15. Cumulative duration during which chest and head were positioned along midsagittal plane of pelvis during rat spontaneous locomotor behavior, per 5 min. bins, across the session. N = 4 in each group. Note relative stability in normal and apomorphine treated rats, augmentation and subsequent drastic reduction with amphetamine, and only augmentation with quinpirole.

laterally curved trunk. During the last third of the one-hour session, with AMPH all the arcs are performed with a laterally bent trunk, whereas with QUIN, 80% of the arcs are performed with a straight trunk, and another 18% with pelvis and chest forming a straight line. Turning in place with an altogether straight trunk is performed only with QUIN. The prevalence of this peculiar type of horizontal turning in place has been demonstrated in infant rats under acute and in adults under chronic QUIN treatment (Eilam et al., submitted). These authors have further found that with QUIN, rats often substitute the horizontal turning in place with vertical turning consisting of rearing in place and then landing facing in the opposite direction. During such turns, the horizontal plane is not traversed at all.

In summary, at the doses used, APO and AMPH induce two distinct patterns of shutdown and spread of horizontal movement along the parts of the trunk. With QUIN there is an enhancement of vertical, forward, and

horizontal movement and no overall transition from forward to horizontal movement, even under chronic treatment (Eilam & Szechtman, personal communication). Thus, with APO and AMPH the three spatial component variables replace each other in the course of the session, whereas with QUIN they co-exist throughout at a very high intensity. The only constriction observed with QUIN is in body-related horizontal movement (lateral movement of anterior parts in relation to midsagittal plane of pelvis). The frequent crossing of the midsagittal plane by anterior parts without stopping there is idiosyncratic to AMPH.

3.10.1.4. The potential role of EW analysis in the study of brain/behavior relations. Movement notation analysis has so far been applied only to the locomotor effects produced by systemic administration of a single dose of three drugs. It is too early, therefore, to offer a model that would link the rules of behavioral transformation described with underlying physiological mechanisms. It should also be emphasized that we used drugs to highlight aspects of the organization of the mobility gradient, and not to study brain mechanisms. Nevertheless, a few examples might provide some guidance on how the mobility gradient model could fit into current neurophysiological thinking.

The main neural systems implicated in the production of dopamine-mediated behavior are the mesostriatal, the mesolimbic, and the mesocortical dopaminergic systems (Creese & Iversen 1974; Kehne et al. 1981; Kelly 1977; Kelly & Iversen 1976; Kelly et al. 1975; Sessions et al. 1980; Swerdlow et al. 1986). The mesostriatal system, originating in the substantia nigra pars compacta and terminating in the caudate-putamen (dorsal striatum) has been shown to mediate mainly stereotypy, whereas the mesolimbic system, originating in the ventral tegmental area and terminating in nucleus accumbens (ventral striatum), mainly mediates locomotor enhancement (Creese & Iversen 1974; 1975; Kelly et al. 1975; Moore & Kelly 1978; Pijnenburg et al. 1975; Staton & Solomon 1984). It has been suggested that with AMPH the two systems are partly in competition. Initially, AMPH-induced behavioral activation is mediated by dopamine release in both caudate and accumbens, thus permitting complex behavioral sequences including both response types. As the AMPH effect increases, greater activation of caudate occludes the locomotor response arising from the accumbens (Robbins et al. 1990). This is a neural counterpart of the Lyon-Robbins hypothesis (Lyon & Robbins 1975), which suggests that the rat's behavioral repertoire becomes restricted in the course of AMPH activation because of competition between response categories.

From the vantage point of the present analysis, these hypotheses raise several questions. Consider, for example, the structure of APO and AMPH induced behavior described above (Figure 14A and 14B). If "locomotor activity" is to be equated with forward progression, and "stereotypy" with horizontal movement, then it could be postulated that forward progression is primarily subserved by mesolimbic mechanisms whereas horizontal movement is mediated primarily by the mesostriatal system. This possibility allows one to re-examine the question of whether there is intrinsic competition among the three spatial component variables and hence between the putative underlying structures that mediate them.

With APO and AMPH the three spatial variables replace each other in the course of the behavioral shutdown process. This observation supports the hypothesis that these variables compete with each other. With QUIN, however, these spatial variables are enhanced simultaneously without subsequent reduction in any of them. In particular, there is no shutdown of *spatial* horizontal movements with this drug (horizontals are performed with a relatively straight trunk). The only shutdown observed with QUIN is in body-related horizontal movement. Thus, without ruling out the possibility of neural competition between the caudate and the accumbens, the QUIN preparation demonstrates that the three spatial variables may be enhanced *without* inhibiting each other. Moreover, this preparation suggests that there is separate neural control of spatial versus body-related horizontal movements.

In addition to the established neuroanatomical distinctions between brain dopamine systems, there is now ample evidence that dopamine receptors exist as a number of subtypes, the most accepted division being the D-1:D-2 scheme (Kebabian & Calne 1979; Waddington et al. 1990). APO is a potent D-2 agonist and a partial D-1 agonist, QUIN is a selective D-2 agonist, whereas AMPH releases dopamine, which acts on both receptors (Waddington et al. 1990). With simultaneous administration of such nonselective dopamine agonists as APO and selective D-1 blockers, or selective D-2 agonists and selective D-1 antagonists, it has been shown that stimulation of D-2 receptors is required for the induction of locomotion and stereotypy, but dopaminergic activity at D-1 receptors exerts a necessary "enabling" or "permissive" influence over these processes (Pugh et al. 1985). Thus, for example, a selective D-1 antagonist, R-SK&F 83566, blocks stereotyped behavior induced by either APO or RU 24213, a selective D-2 agonist (Molloy & Waddington 1985; Waddington et al. 1990). The administration of selective D-2 agonists to otherwise intact rats is believed to induce locomotion and stereotypy because of the presence of endogenous dopamine, which acts on D-1 receptors (Waddington et al. 1990). In addition, it is now suggested that D-2 receptors also exist as a number of subtypes (e.g., Andersen et al. 1990).

The fact that APO and AMPH induce spatial shutdown whereas QUIN does not suggests that spatial shutdown requires D-1 stimulation. In contrast, D-2 stimulation appears to be necessary for the prolonged shutdown of body-related horizontal movement (turning with straight trunk) observed with QUIN. Another selective D-2 agonist, RU 24213, has been reported to induce stereotyped behavior characterized by sniffing and locomotion with no consistent rearing (Pugh et al. 1985). In contrast, rearing is a consistent response with QUIN (Eilam et al. 1989). This difference could serve as a clue that these D-2 agonists induce *different* behaviors, perhaps distinguishing between two subpopulations of D-2 receptors. Reexamination of the behavior with RU 24213 within the framework suggested here might show what is common and what is different in the effects of these two selective D-2 agonists.

Whereas APO and QUIN are specific dopamine agonists (Ernst 1967; 1969; Waddington et al. 1990), AMPH promotes a complex pattern of biochemical change, not only in dopaminergic systems, but also in noradrenergic,

serotonergic, and, presumably, many other systems (Kuczenski & Segal 1988; 1989). It is possible that the avoidance of the midsagittal plane, observed only under AMPH during the later stages of the session, reflects the involvement of other systems in addition to the dopamine system. Note that true circling behavior (i.e., progression on curved paths) is first observed with AMPH toward the end of the shutdown sequence in only some of the rats (after stage III in Figure 14, not illustrated), whereas with APO it is seen in all rats at an early stage (Figure 14A, stage II). This distinction might prove useful in studies of the neurochemical basis of circling behavior. These studies presently group together under the category "turning in circles": continuous unidirectional progression along the edge of the testing enclosure, true circling, and pivoting in place (Glick et al. 1976).

3.10.1.5. *Correlations between mobility gradient variables and some central functions.* Ample evidence indicates that the striatum serves as a sensorimotor integrator receiving information from a wide variety of brain regions via cortical afferents. Dopamine in turn appears to modulate this input in a variety of ways (Albin et al. 1989; Alexander et al. 1990; Carlsson 1988; Rolls & Williams 1987; Swerdlow & Koob 1987). The striatum and other parts of the basal ganglia along with their connected cortical and thalamic areas are presently viewed as components of a family of "basal ganglia-thalamocortical" circuits that are organized in a parallel manner and remain partly segregated from one another, both structurally and functionally (Alexander et al. 1986; 1990). It has recently been suggested that each of these circuits may contain a number of highly specialized channels that permit parallel and concurrent processing of a large number of variables. Within one of these, the "motor" circuit, a well defined somatotopy is maintained throughout all stages of the circuit, giving rise to clearly differentiated channels of the parts of the body (Alexander et al. 1990; Rolls & Williams 1987). Electrophysiological recordings in monkeys have shown that neuronal activity in some stations located along the subcircuits or channels belonging to the "motor" circuit are related to, for example, direction and amplitude of limb movement. Thus, neurons in the putamen appear to be grouped in multiple functional clusters that represent a single body part or a specific movement of that part (Alexander et al. 1986), and the firing rate of neurons in this structure tends to have a linear relation to the amplitude of movements (Crutcher & Delong 1984; Rolls & Williams 1987).

Thus, the "motor" circuit apparently mediates processes related to specific directions and amplitudes of movements of particular body parts. The rules of warmup and shutdown, which engage the parts of the body, the spatial component variables, and movement amplitudes within prescribed constraints, may prove useful in guiding the search for corresponding neurophysiological variables and constraints at the "motor" circuit level. Such variables and constraints may map smoothly onto their kinematic counterparts isolated at the motor level.

Another variable of the mobility gradient that appears to be mediated by the basal ganglia is the degree to which an animal is stimulus bound. As has been shown, inferior animals respond compulsively and stereotypically to particular stimulus situations whereas superior animals respond with varying latencies using a variety of response

types (Yaniv & Golani 1987). One of the functions of the basal ganglia is to regulate sensorimotor interactions in a way that determines which sensory stimuli are used to initiate motor action and which are disregarded (Albin et al. 1989). It has been suggested that the sensitivity to changing complex stimuli and the rate of habituation to patterned visual stimuli are mediated in monkeys by the caudal neostriatum (Rolls & Williams 1987). Damage to the neostriatum in cats and monkeys can lead to compulsive attention to stimuli with a failure to habituate normally (Denny-Brown, 1962; Villablanca et al. 1976). Cools has similarly suggested that the striatum determines the degree to which rats and cats are stimulus bound (Cools 1980; 1985). These findings might partly explain the correlation described in the present review between an animal's position on the mobility gradient and its degree of stimulus boundedness.

There is also evidence that the striatum is involved in the selection of behavioral responses, that is, in the switching between responses or different types of behavior (Cools 1980; 1985; Rolls & Williams 1987). The mobility-gradient model suggests that an animal's mobility is characterized by its ability to switch among a given number of movement types. Warmup is associated with an increase and shutdown with a decrease in the number of degrees of freedom for movement. The morphological complexity of behavior can thus be expressed in terms of the number of movement types among which an animal can switch at any given moment. During spatial shutdown the number of movement types among which the animal can switch is reduced, whereas the rate of switching among the restricted number of movement types still available to the animal may be increased. The present model thus offers an additional measure for an animal's switching capacity, the number of movement types among which the animal can switch and which can aid in elucidating the striatal involvement in response selection processes.

Bilateral lesions in primates, restricted to stations along the "lateral orbitofrontal" circuit, which belongs to the family of basal ganglia-thalamocortical circuits, appear to result in a perseverative interference with an animal's capacity to make appropriate switches in behavioral set (Alexander et al. 1986; Divac et al. 1967; Mishkin & Manning 1978). It is possible that this circuit is also involved in gating the number and identity of movement types among which an animal can switch. Because APO and AMPH reduce the number of such movement types whereas QUIN does not, it might be worthwhile to compare the effects of the three drugs in animals with lesions in this system.

When the information leaves the striatum via brainstem areas enroute to the spinal cord it is subject to further modifications along the way (Scheel-Kruger 1983). It is only reasonable to expect that differential manipulation of downstream structures, located beyond the dopamine receptor level, would generate behavioral transformations that reveal the hierarchically organized functions of striatal output stations (Cools 1985). It might thus prove useful to re-examine the effects of such manipulations on open field behavior using EW analysis. A geometrical analysis of behavioral output generated by selective stimulation and blocking of the cascade of striatal output stations might reveal the successive con-

straints imposed by these stations on the shape of rat locomotor behavior.

Finally, the generality of the mobility gradient raises the possibility that its main features are hard wired in the brain. The reticulospinal system is the final one in the cascade of striatal output stations (Cools 1985). It is among the most conservative networks in the brain, being part of the major brain stem systems that have been retained over the course of vertebrate evolution (for a review see Nissanov & Eaton 1989). The reticulospinal system provides a kind of "hard wired coordination" for such highly divergent motor responses as orientation activities requiring comprehensive coordination of the limbs and body (Peterson 1984). If trunk orientation and the order of changes in trunk orientation together with the associated stepping are hard wired in the reticulospinal system then it would not be surprising that the mobility gradient is widespread across the vertebrates and that a wide range of manipulations of central mechanisms generate various versions of it.

3.11. The limits of the mobility gradient

Clearly, a systematic establishment of the ground plan of vertebrate behavior will require no less effort than that which has been invested by anatomists in the establishment of the ground plan of vertebrate skeletal anatomy. Although the plan sketched here is based on patchy evidence limited to rodents and carnivores, it can be used as a "search image" in work on other vertebrate groups. How far does the mobility gradient extend across the vertebrates?

A shoulder-to-hips recruitment of trunk segments and a gradual transition from immobility to horizontal to forward movement has been described in the development of movement in the amphibian urodele *Amblystoma punctatum* (Coghill 1929) and in embryos of fish (Tracy 1926) and turtles (Decker 1967). Coghill reports that in the horizontal movement of *Amblystoma*, "individual performance recapitulates the history of its performance." Amphibian larvae have been reported to have two types of "starts" after arrest: S-starts, which precede predation and consist of pure forward swimming, and C-starts, which follow a startle response. C-starts consist of forward swimming preceded by pure turning (horizontal plane movement; Wassersug 1989). They were originally described as occurring in the same context in fish (Webb 1978), where they have been shown to consist of forward swimming preceded by a pure horizontal whole body movement (pivoting on hindpart), variable in direction and size, and propagating from head to tail (Weihs 1973). Could the C-starts, which are performed in the context of a stressful situation, be compressed versions of warmup? Nissanov and Eaton do suggest that the underlying circuitry of C-starts is widespread among the vertebrates (see sect. 3.10.1.5, last para.).

It is a coincidence that on being attacked inferior fish assume a head-upward position, whereas the territorial display of some male fish consists of the symmetrically opposite head-down posture (see frontispiece of territorial stickleback in Tinbergen 1951)? A similar head-down posture is assumed in some fish species on sighting a predator from a distance; this posture precedes fast swimming away (Fishelson, personal communication). Does it reflect enhanced mobility in fish, too?

Is the mobility gradient present in birds? If it is, then in this group, display must also mature along this gradient. A shoulders-down position of the trunk is seen, for example, in "nest-cooing," and at the end of "bow-cooing" in pigeons (Lehrman 1964), in "chocking" in gulls (Tinbergen 1959), and in "play bowing" in Arabian babblers (Puzis 1984). Because the bow is also seen in playful situations in lions, canids, and even monkeys (for a review see Fagen 1981; see also Introduction sect. 1), could this posture be homologous across the vertebrates? In other words, does it satisfy criteria such as correspondence of position in moment-to-moment sequences of movements or in the sequence of stages passed through in ontogeny (Lorenz 1981)? Is it a manifestation of the same state of motor expansion across the vertebrates? To show that it is, it would be necessary to show that in each of the species these bowing display postures mature *after* postures in which the trunk is raised on the hindquarters.

The primacy of horizontal movements over vertical ones in moment-to-moment behavior and in ontogeny begs the question of phylogeny. Progression by lateral undulation of the trunk, as in fish and primitive mammals (e.g., the otter shrew, *Potamogale velox*), is considered a primitive trait whereas progression by vertical undulation, as in whales (*Cetacea*), is seen as an advanced, specialized trait. If so, then perhaps movement unfolds along *self-similar* geometrical manifolds across the three different time scales of moment-to-moment behavior, ontogeny, and phylogeny. That horizontal movement appears in phylogeny first is not surprising, considering the bilateral symmetry of the skeletomuscular system and the investment involved in movement in the vertical plane against gravity.

4. Epilogue

4.1. Ordinary language versus EW

In this target article I have tried to illustrate how the linguistic resources available to an observer facilitate some ways of perceiving and thinking about movement and inhibit others. The hypothesis that perception and cognition are affected by one's language and one's stage of language development has been extensively studied (e.g., Basilius 1952; Fishman 1960; Lenneberg 1953; 1967; Piaget 1967; Vygotski 1965; Whorf 1956). It should be noted, however, that the similarity between the claim made in the present review and Whorf's rather vague linguistic relativity hypothesis is to be construed in a very limited sense. No claim is made here concerning any irreversible effects of language on human conceptual systems or about the existence of significant variations in the human conceptual system. Clearly, the use of a particular vocabulary does not *preclude* other perceptions nor does it impose an impenetrable barrier to the perception of other gestalts. Furthermore, as exemplified in the present article, once a pattern has been singled out by a specialized language, it can be formulated relatively easily in everyday speech either directly or in roundabout ways.

Ordinary language reflects the central role played by

objects in everyday life. "The use of ordinary language makes us look, all too often, for things, objects, where there are simply no things at all" (Wittgenstein, in Brand 1979). The classical ethogram – a product of perception shaped by ordinary language – reflects this process: It consists of discrete building blocks, much like an inventory of things or objects. Such an inventory is not very useful in the search for behavioral homologies described in terms of kinematic variables.

Like any other specialized language developed to cope with the intricacies of a particular field of study, EW is not better than ordinary language. Rather, it is a specialized part of it, an extension of a partial system of ordinary language (Brand 1979). The present article is aimed at showing that the reason EW is more powerful in the analysis of movement is not that it is richer, but, paradoxically, that it is "poorer" than everyday language. By restricting ourselves to a specification of trunk orientation in relation to the base of the body and suspending the use of other descriptive tools, we discipline attention, thereby gaining in generality.

4.2. Detail versus economy in description

Because it has been taken for granted in ethology that the stream of behavior should be partitioned into discrete units (e.g., Martin & Bateson 1986; Slater 1976), ethologists' efforts have been invested in the a posteriori justification of such units. Hence the notion that they are "modal action patterns" (Barlow 1977), often composed of several relatively variable components. Although emphasizing the variability of these units, this term has not called into question the initial partitioning. Is there any physiological reality to such units? In summarizing faithfully the state of the art, Barlow focused on their statistical properties "without presumptions about causation and control," describing them as "recognizable without a precise definition of what is meant by recognizable," and avoiding a prescription of "just how one extracts units of behavior." In other words, the problems of smooth reduction to physiology, of definition, and of method, were, and still are, carefully avoided. At the same time, there has been a concern among ethologists of being overwhelmed by the intricacies and detail of animal movement. Hinde (1966, p. 13) cautioned that when combined with insufficient rejection of data "variations in postures and relative positions of the interacting animals . . . may lead to a hopelessly confusing mass of detail, and divert attention from the essentials of the problem"; Slater (1976, p. 14) cautioned against "going into a greater degree of detail than is necessary to achieve the end in mind"; and Martin and Bateson (1986, p. 40) asserted that "inexperienced observers often err on the side of trying to record too much . . . the fewer categories used, the more reliably each will be measured."

Following Hinde, Martin and Bateson (1986, p. 39) proposed to overcome the problem of variation by using "description by consequence": "Describing behavior by its structure can sometimes . . . place demands on the observer's ability to make subtle discriminations between complex patterns of movement." But often the problem itself is how to determine what the "consequences" of a behavior are from the point of view of the animal. In other

words, within the framework of control theory (Powers 1973), what are the controlled variables? What are the kinematic quantities that have a physiological reality? Can the controlled variables be established a priori, on the basis of unexamined common sense?

It has been shown that during amphetamine-induced circling rats perform crossing steps with their forelegs (Figure 17D) whereas with apomorphine they do not (Cools et al. 1989). This observation has been used to argue that the two drugs produce their drug-specific circling by affecting different dopamine systems that in turn influence different parts of the body. What does this tell us about the kinematic variables that are actually controlled by these systems? Further analysis revealed that with amphetamine, for example, the forepaw establishes a fixed relationship of opposition with the head after releasing contact with the ground. This paw to head relationship is actively maintained until landing. As a result, the paw always lands under the head. If, during stepping, the head is positioned toward the side contralateral to the stepping leg – a crossing step ensues (Figure 17D). If the head is positioned toward the side ipsilateral to the stepping leg,
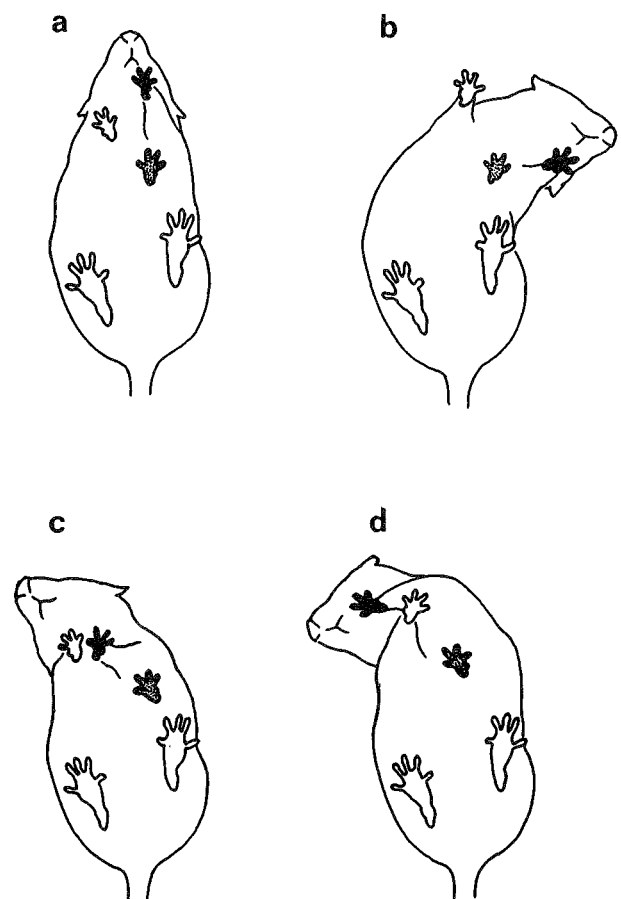
Figure 17. Types of foreleg stepping observed in intact and drugged rats. Bottom view: Gray paw represents location just before stepping and black paw represents location at the moment of landing. A: forward step; B: open step; C: closing step; D: forearm crossing step. With AMPH, forepaw always lands under head; open step (B), crossing step (D), and forward step (A) result because head location determines the location of landing (foreleg performs "catching-up" steps in relation to head). With APO, paw may land, for example, under neck (C).

however, an open step follows (Figure 17B). The controlled variable with amphetamine is thus the relationship of opposition between the forepaw and the head during the swing phase and *not* the relationship of opposition between the two forepaws (as implied by the categories "crossing" and "open" steps; Adani et al. 1991).

In contrast, with apomorphine head position does *not* determine unequivocally the place where the forepaw lands (e.g., Figure 17C; Kiryati, Adani & Golani, unpublished results). This example illustrates that one cannot take for granted that even such straightforward (and useful) categories as crossing and open steps are the controlled variables. Only by isolating the coordinate system that yields an invariant description can one establish the variable that is presumably controlled by the brain. Once such a variable is isolated, it has the potential of showing smooth reduction to the neurophysiological processes that mediate it and can be used in morphological studies that compare movements in terms of their controlled variables (for further examples see Golani 1981; Golani & Fentress 1985; Pellis 1989).

In contrast to the method advocated by Martin and Bateson (commonly used in ethological representations of whole-animal movement), work based on EW analysis derives a representation of behavior based on a few essential variables at the *end*, rather than at the beginning

of a study. Instead of starting with few categories and ending up with a practically unlimited list of categories, each belonging to the ethogram of a different species or situation, we start with a "mass" of detail and end up with relatively few variables suitable for several species and situations. Such variables as trunk orientation in relation to base are not established a priori but "distilled" out of the mass of recorded detail (e.g., Eilam & Golani 1988; Yaniv & Golani 1987).

A description of vertebrate behavior in terms of trunk orientation in relation to base reduces the apparent variability and reveals a shared pattern of organization across taxonomic levels, situations, and pathological preparations. As such, it also has the potential of serving as a specification of the demand made on the brain in terms of the kinematic variables the brain controls.

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Why Eshkol-Wachman behavioral notation is not enough

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Golani claims that EW movement notation is better than ordinary language at revealing commonalities and differences between behaviors. EW descriptions concentrate on the kinematic features of animal behaviors and clearly provide a means for identifying similarities and differences between behaviors with respect to such features as trunk orientation and freedom of movement mentioned by Golani.

What is the significance of these features for ethology? Golani argues that they are significant for understanding the neurological organization of behavior. I agree that this is an important goal, but would argue that it is not the sole goal of ethological research. Hinde (1982) claims that ethology shares with the rest of biology an interest in questions of "immediate causes" and development, but he identifies two further questions of special interest to ethologists: What is the function of behavior, and how did it evolve? Much of Golani's target article is concentrated on discussing neurological mechanisms and ontogeny, reflecting attention to the first two questions – the ones Hinde identifies as generic to biology. Although there is some discussion of phylogeny, there is little discussion of function. Golani's article, at least implicitly, plays down the significance of the questions

Hinde identifies as characteristically ethological.

To see the implications of this, consider the analogy Golani offers in section 3.6.1 where he says, "in carpet weaving the term 'flower,' the pictorial end result, will not show the process of thread composition that generates the flower pattern on the carpet." An examination of this analogy reveals what is missing in Golani's account of ethology.

I agree that one cannot guess weaving technique from a pictorial description alone, but there is much more to learn about a carpet than how it was woven. For example, one might want to know why the carpet has a flower on it and not some other design. Knowledge of weaving technique is not entirely irrelevant to answering this, if certain designs are not possible because they are too difficult to produce given existing weaving technology. But given what is feasible to produce, no amount of knowledge of weaving technology can explain why a particular pattern was produced. To see how this relates back to ethology, consider Golani's example from section 1, comparing canid "play bowing" and primate "looking between one's own legs." If primates can bow without performing a look between the legs, why do they use looking between the legs as a play signal rather than a simple bow? Understanding the neurological organization of these behaviors (at least at the rough level of analysis provided by EW) cannot answer this question because it ignores the functional role of the behavior.

EW descriptions also seem limited with respect to understanding the evolution and immediate causes of behavior. I agree that the notation provides one way of assessing similarity across the phylogenetic tree (as Golani illustrates in sect. 3.11). But, again, complete understanding requires more than EW can provide. To return to the carpet analogy, pictorial description of the carpet may help explain the development and use of a particular weaving technology. Demand for particularly intricate depictions of flowers can drive the development of weaving technology to allow the production of such designs. Such demand also explains the application of the technology in a particular instance. Relating this point back to ethology, functional

demands for a particular behavior can drive the evolution of neurological mechanisms to support that behavior as well as driving the use of the mechanisms in appropriate circumstances. Knowing that play involves maximum freedom of movement does not help us understand why the nervous system provides for such freedom, nor why animals play when they do play. A danger of EW notation is that it obscures the function-driven nature of both the evolutionary process and the moment-to-moment expression of behavior.

As a philosopher interested in functionalist theories of mind and in the insight that ethology can provide for understanding the mind, I find EW notation a useful tool and I am grateful to Golani's target article for drawing my attention to it. But it is important to realize that it is far from being a replacement for other means of describing animal behavior.

Is the mobility gradient suitable for general application?

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It is hard to quarrel with success. In Golani's hands, the Eshkol-Wachman (EW) system of describing overt behavior has become a powerful instrument. Using it, he has deduced the mobility gradient, so prominent in early development, and shown what a powerful vehicle it can be for analyzing the effects of drugs. And although he is cautious about extrapolating his findings on drug action to brain function, the approach promises to provide meaningful insights into the organization of the central nervous system. Golani's target article, however, goes beyond this productive application to reach some debatable conclusions.

He has written two essays in one. In the first, he has opened our eyes to a powerful way to investigate from a distinctive perspective a select group of problems, namely, ontogeny, dominance-subordinacy, and psychopharmacology. In the other, a statement of his philosophy of the correct way to describe overt behavior, he has overstated the generality of this approach. I comment critically on the fruitful part of his paper, mainly to give Golani an opportunity to elaborate his approach and to dispel my reservations. Then I will challenge his philosophical thesis.

The mobility gradient is obviously a powerful tool, constructively applied by Golani to a selected sample of mammals. I am impressed by the universality revealed, so much so that it gives me pause: To what extent is the universality just a matter of biomechanics? Would all terrestrial tetrapods conform, but not, say, whales? *"Fish gotta swim and birds gotta fly. . . ."* Would other kinds of animals with entirely different *Bauplans* fit into this scheme? Does depicting dominance relationships as front pivot and rear pivot offer any benefit over the turn toward and turn away or approach-avoid that pervades the literature?

The more absorbing general principle may not be the sequence from forward, to horizontal, to vertical, but the one from stereotyped or constrained to variable behavior. Can that be applied to systems independent of the constraining morphology of four limbs to, say, facial expressions in primates, feather postures in birds, or color change in cephalopods and fishes?

A problem I find throughout is an eagerness to persuade the reader. That is not unusual in science and hardly a sin. Nonetheless, we are supposed to try to disprove our favored hypotheses, or at least to present alternative hypotheses. Could other hypotheses explain the mobility gradient in Golani's examples? I suspect not. But the mobility gradient is overt only in certain circumstances, as in early development or in asymmetrical contests. Later in ontogeny, sequencing becomes highly variable. Golani then indulges in unconvincing hand waving to

incorporate that unrestrained behavior into the mobility gradient. The hypothesis becomes unfalsifiable. Other hypotheses must be more productive.

A productive hypothesis makes surprising predictions that lead to new insights. With specific reference to hypermobility, Golani offers six predictions. How were they deduced? Only prediction six contains an element of explanation. Lapsing into a skeptical mode, I assert that the predictions are all post hoc, that the observations, especially concerning play, were already known, and that the predictions were deduced from the observations.

The application of Golani's model to play behavior reveals more uncritical striving. If we take the mobility model seriously, play should be the end point because that is the culmination of development. But play is only a way-station on the path to complete development. Play wanes and the organism becomes less freely active, and not because of senescence. In addition, if development is so canalized that play must result, then it is inevitable in species with similar central nervous systems. Yet play is almost confined to mammals (some birds engage in object play). To explain why mammals play and other vertebrates do not, we need more research.

Another example of over-reaching is Golani's extension to C and S starts in amphibian larvae. Golani draws the parallel between S starts as "pure forward swimming" and C starts as "horizontal plane movement," key components of the development of the mobility gradient in mammals. This comparison misses the fundamental mechanics of swimming by elongate vertebrates. Swimming is achieved by initiating a wave at the head and passing the undulation to the rear (Alexander 1969), a good example of the mobility gradient. Both S and C starts begin with movement of the head laterally, although the movement is more obvious in C starts.

Similarly, the example of head-up and head-down orientation in fishes, for subordinacy and dominance, respectively, fails because it ignores the functional significance of such behavior (Golani implores us to disregard function). In support of Golani, sticklebacks and cichlids hold breeding territories on the bottom; escape from the territory holder is achieved by swimming up. But the generality of this conclusion is erroneous because the escape direction depends on ecology: On coral reefs, plankton feeders flee down into the reef, algal grazers flee upward.

Golani correctly points out that when two fish meet head on, the front end of the subordinate is apt to rise at the close approach of the dominant. That response, however, is explained by the downward vector of the obliquely inserted pectoral fins as they back-water, with no compensating paired fins at the rear end of the fish.

These are small points, however, raised to stimulate Golani to be more self critical when extending his thinking to other organisms. The bone I want to pick with him relates to his grander view of how to describe behavior. With the zeal of a convert, Golani seems to suggest that the EW method is not just the best way to describe motor output but the only way. He has persuaded me of its utility, but is it the only way, all things considered? I doubt it.

Golani criticizes the more traditional methods on a number of scores. The ethological approach is said to lead to a bewildering profusion of behavioral events, leaving the observer swamped. In contrast, the EW method resolves the behavior into just a few elements, which are the heart of the behavior. This statement inspires a number of retorts. First it misrepresents how ethologists proceed, a distortion achieved by a selective sampling of the literature. Ethologists (Moynihan 1970; Wilson 1972) have written that animals possess remarkably few displays. True, one can multiply the appearance of motor events through permutations of few elements (see especially Ohm 1959). Nevertheless, most ethologists quantify remarkably few behavioral events in an experiment to achieve an adequate test of the hypothesis in question.

Oddly, Golani then reverses field to fault ethologists for detecting too few behavioral events. Note, however, that these "ethologists" are now psychopharmacologists. In my limited experience with workers in that field, most, but not all, are untrained in ethological methods. They seem to strive for the simplest measure possible, perhaps to enable assistants to collect data for them with the least error. Golani shares that interest in simplification, but differs on the degree of streamlining.

Behavioral events do not exist as Platonian ideals. Rather, they are for astute investigators to select to test their hypotheses. Depending on the question, this might involve end points that are either functional consequences or such recognizably patterned motor output as modal action patterns (Barlow 1977).

Curiously, Golani seems to understand the relationship between the needs of the investigator and the question at hand only for the issues that concern him. His interest in homologies is an example of a stated concern but one whose utility he does not appear to understand. Golani proposes the mobility gradient in its simplest form as an example of how to find homologies. To get to that point, he uses as a springboard the comparative, evolutionary studies of ethologists and their struggles with the concept of homology. What he misses is that his oversimplification is useless in such evolutionary analyses. The parallel is to say that neurons are homologous in mammals and are therefore informative about the phylogeny of mammals.

To make evolutionary sense out of the course of evolution of behavior, one needs behavior that differs across species. Otherwise, one must conclude that evolution has stood still. Thus Lorenz (1941) tracked the changes needed to produce the differences in displays among extant anatid ducks to deduce how the displays evolved. That was enormously informative. By comparison, the mobility gradient is the height of sterility *for evolutionary studies*. To draw informative conclusions about the evolution of behavior, and thus about homologies, one needs behavioral events that strike an optimum between being diverse enough to reveal change and conservative enough to expose relationships. The mobility gradient is not optimal, at least as so far applied.

I was slightly amused by Golani's criticism that ethologists are mired in detail, whereas he has struck upon the untying of the Gordian knot, the ultrasimple mobility gradient. His first papers using the EW notation (e.g., Golani 1973) came to mind. The detail was overwhelming; one could not tell what he was looking for. It was like reading a newspaper with a microscope. Over the years he has backed off to ever lower powers of magnification until he detected a pattern: the mobility gradient.

Now Golani is like a boy with a hammer. Admittedly, it is a wondrous and fruitful tool. He does not need to hammer on everything with it, however. Having said that, I wish he would pound on some other areas of research in animal behavior. The mobility gradient might yield fresh insights into theorizing about combat (e.g., Hammerstein & Parker 1982). Applied to symmetrical contests, it might reveal more than conventional methods of describing fights. It might be useful, too, in assigning choice of mate, an often ambiguous determination in behavioral experiments. How would the model apply to such issues as altruism and territorial advertising? We need a richer, more reasoned attempt to extend this line of thinking. And Golani is the person best prepared to do that. I hope he can start in his *BBS* Response.

The environment modulates the mobility gradient, temporally if not sequentially

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Golani suggests that changes in the mobility gradient may be related to changes in reactivity to the environment as illustrated

in stimulus boundedness, switching between responses, and availability of responses (sect. 3.10.15). The following observations examine this conjecture and support the conclusion that the environment modulates the time course of the mobility gradient and may alter its sequential pattern.

A person's environment at the time of injection influences the topography of the behavioral response to amphetamine (Kokkinidis & Anisman 1980). Similarly, in rats, more amphetamine-induced stationary sniffing and headweaving was observed in a hole board apparatus than in an open-field (Pope et al. 1980); more rearing was seen in an enclosed maze than in an elevated maze (Mumford et al. 1979); and more sniffing of surfaces was noted in a small chamber than in an open room where looking away was more common (Ellinwood & Escalante 1972). Postures induced by amphetamine were similar to those exhibited initially by saline-treated rats in the same environment. Thus, saline-treated rats in a wire mesh cage thrust their snouts into the mesh, whereas rats placed on a small table exhibited little snout contact with the substrate, preferring instead to peer over the edge of the table (Beck et al. 1986). Rats given amphetamine in the cage incorporated snout contact into their stereotypy, whereas rats administered amphetamine and put on the table spent most of the time hanging over the edge. Although the amphetamine-treated rats persisted in these behaviors over the 90-min. session, the controls habituated, curled up, and went to sleep. Mobility, like square crossing, declined at the same rate in both groups over the time course of the drug, as predicted by Golani. Reanalysis of the data revealed that vertical head movements were eliminated before forward and horizontal movements in the caged group, again as predicted (Beck & Chow, unpublished data). In the tabled group, however, the vertical (and other) movements persisted over the 90-min. observation period as the animals continued to bob their heads while hanging over the edge of the table. Assessing the same measures over a longer time course would help determine whether the effect represents a violation of the vertical-forward-horizontal sequence of the mobility gradient or merely a skewing of its time course. The data have the important implication that the behavioral effects of amphetamine depend partly on the demand characteristics of the environment pertinent to orienting and are not simply the reflexive output of a hard-wired circuit (sect. 3.10.15, last para.). This threat to the validity of the cascade of the mobility gradient may be only an apparent one, because it is compatible with the view that compulsive attention to local details and a failure to habituate are adjuncts to the mobility gradient (sect. 3.10.15, para. 3).

The relation of the mobility gradient to the ability to switch responses has been illustrated by showing that the effect of changing the apparatus to permit a different form of amphetamine-induced orienting depends on time elapsed since the injection (Beck et al. 1986). Thus, altering the apparatus so that two sides were table edges and two were box walls produced appropriate enduring changes in the investigative behavior at 10 min. and 30 min. postinjection in animals treated with saline. Rats administered amphetamine, however, were unable to sustain a shift in orienting behavior to such a change at 30 min. and were only partially able to do so at 10 min. postinjection. Upon alteration of the environment at 30 min., the amphetamine-treated rats momentarily interrupted the ongoing investigative mode to explore the new apparatus features and then returned to their initial mode of responding. The abortive switch in investigative behavior was accompanied by a brief period of increased mobility; an observation consonant with Golani's hypothesis. Failure to habituate could account for the persistence of the investigative mode in the animals kept in an unchanging environment for 90 min. A deficit in habituation, however, could not account for the behavior of the rats exposed to a change at 30 min. postinjection. Rather, a reduction in response options and an inability to switch responses would appear to be the appropriate concepts.

We were unable to replicate this effect with acute doses of apomorphine. The animals showed an indiscriminate investigative response, simply maintaining snout contact, no matter what substrate they were placed on (Beck, unpublished). The environment present at the time of apomorphine administration was not preferred later in the acute time course. The influence of the environment has been demonstrated on substrains of rats, however. After injection with apomorphine, when given a choice, one substrain persisted in making non-oral snout contact with vertical surfaces, whereas another substrain preferred making oral contact with horizontal surfaces (Szechtman et al. 1982). Perhaps hard wiring is a better view of the apomorphine than the amphetamine mobility gradient.

The rat pup exhibits the mobility gradient in its postnatal development, first showing lateral movements (Day 0), then forward movements (Day 2), and finally vertical movements (Day 8) (Eilam & Golani 1988; target article, sect. 3.6.1, para. 5). These measurements were made on lone pups on a hard surface. When milk is squirted into the mouths of 1-day old rat pups, they exhibit trunk dorsiflexion, among other movements (Hall 1979). By Day 3, suckling rat pups make vertical probing movements with the snout against the dam's teat, into fur painted with salivary gland extract, and in response to milk odors (Pedersen & Blass 1981; Terry & Johanson 1987). Probing has been related to inhibition of the dam's limb movements and facilitation of milk letdown (Stern & Johnson 1990). The early appearance of probing may not represent a violation of the sequence of the mobility gradient. It may only be a temporal distortion, because the environment under the dam may be a temporal extension of the *in utero* environment where synchronous movements, including dorsiflexion of the trunk, are present by Day 17 of gestation (Robinson & Smotherman 1987).

Description and explanation: A plea for plurality

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A proper analysis of human and nonhuman animal (hereafter "animal") movements may be foundational for numerous fields, including ethology, psychology, comparative anatomy, biomechanics, neuroethology, physiological ecology, and dance. Philosophers are also concerned with the description of actions and their causes (Brand 1984; Brand & Walton 1980; Dretske 1988; Goldman 1970). It is therefore important to ask whether there is really a "best" way to describe and explain behavior? Or, does the way one describes and explains behavior depend on the questions one is asking and the goals of one's study?

Richard Dawkins (1991) has recently claimed that Charles Darwin's achievement, like Einstein's accomplishment (but unlike those of Freud and Marx), is universal and timeless. Others have made similar pronouncements for sociobiology. I get the feeling that Golani also views the Eshkol-Wachman (EW) movement notational system as being somewhat universal and perhaps even timeless; over the past 20 or so years he, and some of his associates, have written strong, sermon-like texts concerning the Eshkol-Wachman (EW) movement notational system and its central role in the proper and detailed description of animal movements.

Despite my concern that some of the limitations of EW Golani and others have noted may well preclude its use in many analyses of animal movement, even in the search for the ground plan of vertebrate behavior, Golani's target article is a very useful attempt to provide interdisciplinary strength for some of his claims. Here, the representatives of diverse disciplines meet one another in overlapping territories that none (or few) would have anticipated. For example, how language informs our views of the world is very briefly considered, and how classical ethograms *may* list things "where there are simply no things at all" (Wittgenstein, in Brand 1979; see Golani's sect. 4.1) is noted, but, unfortunately, not argued.[1]

Perhaps I am merely short-sighted or narrow-minded, but I still do not see clearly the light at the end of the EW tunnel. My concerns center on (1) just how universal the methodology of EW is, (2) the choice of words, terms, and sentences used to describe animal activity and justify the use of EW, and (3) how the many and diverse goals of comparative and evolutionary ethology can be incorporated into the EW paradigm. I also want to know why few have used EW other than those closely associated with Golani. I do not believe that the tedious effort required to use EW has necessarily been a stumbling block, because other methods can be equally tiresome. Rather, I think that the limited use of EW is related to the fact that we need to consider the questions at hand in any given study, and the goals of most studies, whether or not they are concerned with the description and explanation of movement, do not necessitate the use of EW.

Golani begins his abstract by claiming boldly (but without sufficient later argument) that "ordinary language can prevent us from seeing the organization of whole-animal movement." (It may be important to note that he uses the word "can" and not "does," leaving room for equivocation.) He then notes that this may be a reason why the search for behavioral homologies has not been as successful as early ethologists had hoped. It is not clear to me that Golani overcomes his objection to the use of ordinary language, for even the reductionistic EW system requires ultimately that an ordinary (and shared) language be used for transmitting information about description and explanation among interested parties. Golani seems to agree; he later writes (sect. 4.1) that "EW is not better than ordinary language." Because this statement is central to his argument, I would have liked to see it placed earlier in his essay and to have read a more highly developed argument concerning just why EW should replace other methods, all of which also depend to some extent on ordinary language.

Golani's implication that people have shied away from the comparative morphology of behavior does not reflect the fact that many *have* continued to stress the importance of accurately and reliably describing, interpreting, and explaining animal behavior (see Bekoff & Jamieson 1990); they have simply used methods other than EW. Furthermore, I do not agree that the purported lack of interest in detailed description "reflects the limitations of the informal vocabulary that has been available for such studies" (Introduction, para. 1). There are other movement notational systems available (Bekoff 1979; Hollenbeck 1971; Hutchinson-Guest 1970; 1984; Lyons 1959 and references therein) and Golani should have told us why their vocabulary is more informal and limited than that of EW. Hutchinson-Guest (1984, Chapter 21) compares three of the most established and widely used methods in dance, the Benesh, EW, and Laban systems. She reports that recording in EW was slower than in Laban, and that Laban was more practical than EW and more accurate than Benesh. Of course, this is not to say that EW *is* relatively useless. Rather, Golani needs to provide more comparative information concerning the state of the art of movement recording so that readers can make up their own minds about what to do in specific instances, even if they are looking for the ground plan of vertebrate behavior.

My concern with EW's acontextual and inconvenient notation is best instantiated in Golani's discussion of the shared elements of "play bows" (PB) and "looking between one's own legs" (LB). I have studied social play for years and this discussion really does not tell me much that I can use in my analyses of play.[2] It may be interesting and important that there are shared components in PBs and LBs, but I am uncertain whether this means anything to

the animals who have to read each other's signals; the animals may not see what human observers see. Furthermore, what an animal sees varies within and between encounters because of variations in relative spatial orientation between the participants, and, of course, differences in context, social and otherwise.

There are also many movements that *necessarily* incorporate other movements, because it may be impossible for an animal to move its trunk or part of one limb without moving another part of the same limb or other parts of its body. Furthermore, although it may be useful to note that when performing LB a primate *may* also be performing a PB, this is not necessarily the case; LB and PB each has its own unique components. At least in some canids, PBs are highly stereotyped (Bekoff 1977) and the high degree of stereotypy appears to be important in establishing or maintaining a "play mood."[3] PBs that are performed as part of other activities in other contexts might not be as stereotyped in form or in temporal characteristics as those performed during play. Furthermore, in asking whether a "generic bow" (GB, my terminology) is present across diverse taxa (sect. 3.11, para. 4), Golani is overlooking the probability that what look like "bows" may be something else in different contexts. A mere shoulders-down position does not warrant calling a GB a PB or any type of bow.

In solely concentrating on (1) the base of support and (2) "the orientation of the animal's trunk in relation to a spherical coordinate system whose center is attached to the joint linking the trunk and the base of support" (Introduction, para. 6), numerous other details are ignored. Where mere reductionistic description is necessary for the goals of a study, EW may be useful; where one may want to gain some understanding of, say, communication between animals, EW may not be useful.

I have some of the same concerns with Golani's discussions of the "neck bites" (NB) performed by the wolf and the "hip thrusts" (HT) performed by the dog,[4] actions that appear to humans to be symmetrically opposed. Golani's discussion of the utility of the terms "hip thrust" and "neck bite," when applied to the behavior of the so-called superior and inferior wolves (sect. 3.2, para. 1), instantiates why I have reservations about the acontextual use of descriptive or explanatory terms, no matter how they have been derived. Golani claims that these labels would be more useful if it were recognized that they "both provide a functional interpretation for the movement (description by consequence)." Many do realize this; however, while I agree that a functional interpretation *may* be more useful, this is not always the case, for many canids and other animals perform HT and NB in a variety of contexts where they probably serve diverse functions, notably during play, agonistic encounters, courtship, copulation (HT and NB), and predation (NB).

All in all, although there are some interesting and thought-provoking lessons to be learned from considering the use of EW to describe animal movements, I still find the reductionistic, acontextual, and inconvenient descriptions that flow from the system to be uninformative in many cases. In distilling a few essential variables that *may* represent more general patterns of behavior, needed descriptive detail is usually lost. Simplicity, while convenient and informative (Sober 1975) in some instances, is not always the best way to go. Where diverse interests inform and motivate inquiries into animal movement, plurality may be more informative.

Last, some of the reservations that Golani mentions at the end of his target article seem as damaging to the use of EW as they may be to other approaches describing animal movements. We really do not know this, however, because we are not told the relative merits of EW. In the beginning, we need to ask just what kinds of knowledge are being sought and what are the best methods for obtaining what we are after. Many people have made the transition from the description of animal movements to gathering information on neurobiological bases of action (for example) without using EW. It would be useful to know how

previous studies would have benefited from using EW rather than the methods that were used, and how EW would advance our knowledge where it counts.

NOTES
1. I emphasize these words because Golani, in my opinion, accepts this notion without sufficient argument.
2. Golani's later discussion (section 3.9), in which he infers, incorrectly in my opinion, that the features of play behavior have been "surprising" to those who study the activity that is called "play," likewise does not inform or motivate my own interests in play. People who have studied play comparatively, evolutionarily, and from more proximate perspectives, have looked for reasons why play has certain characteristics but they have not been "surprised" by what play looks like. A reductionistic, acontextual analysis of action may lead one to view the morphology of an activity as surprising.
3. Some other motor patterns that have been called "play-soliciting signals" in canids and other species also appear to be highly stereotyped, but none have been analyzed to the same extent as canid play-bows.
4. Golani often refers to "the x" (where "x" is a particular action) of *the* wolf or *the* dog or *the* "y." This is usually done because many studies in which EW has been used rely on very small numbers of what are assumed to be prototypical animals. It remains possible that a lot of individual variability, even among members of the same species, is overlooked because of small sample size.

The mobility gradient: Useful, general, falsifiable?

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Golani's target article has raised what are, for me, two important and neglected issues in behavior. First, how do we identify behavioral homology? Second, how do we identify biologically meaningful units of behavior? Unfortunately, I found that the substance of the paper really dealt with neither of these questions. After reading a summary of the EW system and some results from its use, I was closer neither to an understanding of how, exactly, I would decide whether two behavioral patterns were homologous, nor to an understanding of how I should go about defining behavioral units.

I have two comments. The first concerns the vast "mobility gradient model," which seemingly aspires to unite under a common causal umbrella the sequence of postures in behavioral ontogeny, the transition from resting to motion in adults, the postures used in agonistic behavior, and the sequence of postures used in scent marking. My second comment concerns Golani's claim that EW is necessary to extract us from the mire of inaccurate verbal description.

First, the "model." Here, I found some unexpected humor. You can have the same good laugh that I did if you will consult the illustration of the mobility gradient shown in Figure 6 and then imagine (you don't need EW to see this in the mind's eye) how a deer would look if it wanted to conform to this supposedly uniform vertebrate pattern. From a recumbent position, the deer would rear back onto its haunches, stretching its long front legs out in front of itself; then it would stand. Of course, this never happens and therefore the picture is comical. Deer and most other ungulates rise by first rocking forward to lean on the carpal joints, then gathering the hind feet under the hips, straightening the hind legs, then placing the forefeet, one at a time, onto the substrate. The orientation of the vertebral column, and hence the placement of "weight," as Golani would view it, first rocks forward, then back, exactly the reverse of what the mobility gradient prescribes. For further humor, try to picture a kangaroo, a bat, and a human attempting to follow the mobility gradient's demands.

Many mammals and many other vertebrates (all salamanders,

for example) simply do not launch into activity in the manner that Golani depicts as universal because their skeletal plans demand another sequence of postures. I view the sequence of postures that any animal adopts as it moves from recumbency to mobility as a reflection of its particular set of locomotor specializations (or lack thereof). Golani has detected a supposed universal sequence because he has focused on a few species (some carnivores and rodents) that share a conservative mammalian skeletal plan (Eisenberg 1981), with only slight locomotor specialization. If one considers either more specialized mammals, such as ungulates, or more plesiomorphic tetrapods, such as turtles, the "mobility gradient" that describes transition from recumbency to activity in Golani's species simply does not apply.

Perhaps Golani would respond to my challenging examples by claiming that I am seeing "compressed," or "interrupted," sequences. But then how, I wonder, does one distinguish between a "compressed" sequence and a real violation of the model? I do not see an answer in the target article; and, in addition to the fact that there seem to be so many obvious violations of the weight posterior/weight anterior rule, this is my main gripe about the mobility gradient model – it is not presented as a falsifiable hypothesis. Golani never makes it clear what sorts of data would refute the mobility gradient hypothesis. For example, if in some species we observe the same sequence of postures in behavioral ontogeny and in the transition from rest to activity but a different sequence in scent marking, is the mobility gradient model falsified?

Now on to Golani's suggestion that we need EW to clean up our description of behavior. I agree that description of behavioral acts varies in quality; function and consequence tend to creep into what should be pure description. And it is true that the reference frame is rarely constant. Before one resorts to the selective microscope of EW, however, one should first ask, "What is the question I am trying to answer?" I believe that for many kinds of behavioral questions, EW is either too detailed or simply inappropriate. I would never use EW, for example, if I wanted to know whether house mice showed sex- or individual-specific play partner preferences. Also, for some questions, such as the important one that Golani raises – the identification of units of behavior – EW is probably too coarse. As Golani has presented it EW emphasizes a sequence of postures. This is different from a sequence of muscle contractions that, for me, is a better way to define units of behavior. For example, Bekoff (1986; 1989) and Bekoff et al. (1987) have shown, using EMGs, that chickens use the same motor program in hatching and in walking. The postures in the two contexts are quite different and I doubt that EW would detect that in fact the same motor program is being played out in both instances.

Striatal structures, dopamine and the mobility gradient model

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Apart from providing an excellent, compressed introduction of the Eskhol-Wachman notation system (EW), Golani describes the so-called mobility gradient model, a completely new set of rules underlying the organization of behavior within and across species, each of which results from the careful assessment of the EW analysis. In the final part of his article (sect. 3.10) he argues that this mobility gradient model is a powerful tool for establishing hypotheses about brain-behavior relations. In this commentary I would like to underline the relevance of the latter point.

During the past years we have used Golani's mobility gradient model as a "search image" in our studies on the function of the dorsal striatum (DS), the ventral striatum (VS), and the olfactory tubercle (OT). As discussed in detail at the 21st International Ethological Conference in 1989 (Utrecht, The Netherlands: August 9–17, 1989), we have been able to trace large portions of the neural counterpart of the mobility gradient model. Because the overall hypothesis about the involvement of the OT, the VS, and the DS in this model will be published elsewhere in detail, I do not describe it here. Nevertheless, some of our findings and hypotheses are complementary to those put forward by Golani in his target article and are accordingly mentioned here. Because of space constraints I limit myself to the most illustrative examples, collected in our studies with rats challenged to display a full blown version of the "warm-up" and the "shut-down" (sect. 3.6.1) by novelty or dexamphetamine (1.0 mg/kg, i.p.).

A. Role of telencephalic, dopaminergic structures in movements permitted by distinct joints. (1) A blockade of dopaminergic receptors within the OT (local, bilateral injections of 10 ng/0.5 μl sulpiride) completely inhibits any expansion of cephalocaudal recruitment of body parts in movement in any spatial dimension: The animal remains in its constricted state, immobile, with its weight on its hindlegs. Stimulation of these receptors in drug-naive and habituated rats (local, bilateral injections of 10 μg/0.5 μl dexamphetamine) results among others in a full blown version of the mobility state, during which whole body vertical movement (pelvis rearing) dominates. (2) A blockade of dopaminergic receptors in the VS (see above) allows the rat to develop its motor expansion, but to a limited degree. The cephalocaudal recruitment of the body parts in movement in the vertical plane stops at the shoulder joint. Once the head has started to shift between a horizontal and upwards position in the vertical plane, progression of the normal "warm-up" stops: No more segments caudal from the shoulder joints are recruited. Thus, torso, pelvis, and all four legs continue to serve as base of support and remain immobile; the shoulder joints serve as the root of the only movements seen ("head rearing"). Stimulation of these receptors in the VS (see above) elicits an abnormal type of vertical movement: During a phasic vertical movement the rat's weight is shifted to the pelvis and the hindlegs, and the torso is oriented diagonally upwards from the hip joints to the shoulder joints. Remarkably, the head maintains a fixed angular relation to the moving torso. Thus, pelvis and hindlegs continue to serve as base of support and remain immobile, whereas the hip joints, but not the shoulder joints, serve as the root of the movements shown. (3) Finally, blockade of dopaminergic receptors in the DS (see above) allows a greater, but not yet complete, motor expansion. The cephalocaudal recruitment of the body parts for movement in the vertical plane goes on until the pelvis: Both head rearing and torso rearing are seen, whereas pelvis rearing remains absent. Thus, once "head rearing" (see above) is present, the torso is recruited. The rat's weight is shifted to pelvis and hindlegs, the torso starts to shift between a horizontal and an upwards direction in the vertical plane, and becomes ultimately oriented diagonally upwards from the hip joints to the shoulder joints. No segments caudal from the hip joints are recruited: Pelvis and hindlegs continue to serve as base of support and the hip joints serve as the root of the movements seen ("torso rearing"). Stimulation of these receptors in the DS (see above) does not elicit any vertical movement.

On the basis of these and related data we reached the conclusion that the neck, shoulder, and hip joints are subserved by the OT, the VS, and the DS, respectively (21st International Ethological Conference, 1989). In subsequent studies we found additional evidence: Movements (permitted by the shoulder joints, namely, lateral movements of the forelegs, are subserved by a subregion of the VS (the dorsomedial region of the nucleus accumbens), whereas movements permitted by the hip joints,

lateral movements of the hindlegs, are subserved by the DS (Cools & Jongen-Relo 1991), suggesting that the dopaminergic continuum consists of modules, each of them subserving the relation between particular body parts.

B. Role of telencephalic, dopaminergic structures in movements in three spatial dimensions. These conclusions suggest that each of these brain structures plays its own role in movement in the horizontal, forward, and vertical direction; each has its own function in movement in these spatial dimensions. Thus, the full expansion of movement in the vertical direction (pelvis rearing) involves a continuous recruitment of the head (permitted by the neck joint, viz., a function of the OT) but not necessarily of the chest and the pelvis, because the latter segments of the body can be "carried" by the head. The full expansion of movement in the forward direction (forward walking) involves the continuous recruitment of at least one foreleg (permitted by a shoulder joint, viz., a function of the VS). Concerning the full expansion of movement in the horizontal (lateral) direction (circling around axes that are external to animal's body), it is not yet known whether the horizontal pelvis movement (permitted by the hip joint, viz., a function of the DS) and/or the horizontal head movement (permitted by the neck joint) direct the curvature of the path.

These data clarify why a dominance of movements in the vertical direction is seen after dexamphetamine injections into the dopaminergic OT (Cools et al., unpublished data) and a dominance of movements in the forward direction occurs after injections into the VS (Pijnenburg et al. 1976). The involvement of the DS in controlling the hip joints clarifies why stimulation of dopaminergic receptors in this structure does not result in movements in the vertical and forward direction; to what degree the role of the DS in horizontal (lateral) movements (Kelly et al. 1975) has to be considered as the consequence of its function in controlling the hip joints remains open for discussion.

C. Role of telencephalic, dopaminergic structures in the ontogeny of movement. As described by Bayer and Altman (1987) there is evidence that large portions of the OT mature before the VS, and that large portions of the VS mature before the DS. Therefore, during the first stage of the ontogeny of these structures only movements subserved by the OT should appear, in the next stage movements subserved by the OT and the VS, and in the final stage movements subserved by the OT, the VS and the DS. According to the above-mentioned framework, this implies that movements permitted by the neck joint (namely, a function of the OT) appear in the first stage, movements permitted by the neck joint (OT) and shoulder joints (a function of the VS) in the second stage, and movements permitted by the neck joint (OT), shoulder (VS) and hip joints (a function of the DS) in the final stage. Since full motor expansion in the forward and vertical direction requires the recruitment of the shoulder joints (VS) and hip joints (DS), respectively, only head movements in the lateral direction (neck joint: OT) would be expected during the first stage of the ontogeny. By analogy, additional movements in the forward direction (shoulder joint: VS) would be expected during the second stage of the ontogeny, and movements in all three spatial dimensions during the final stage of the ontogeny of these structures. As described by Golani (sect. 3.4), the various types of movements indeed appear in the aforementioned order.

D. Role of telencephalic, dopaminergic structures in the mobility gradient. As described earlier (Cools 1987; Scheel-Krüger 1986), the OT, the VS, and the DS form part of one integrated unit of circuitry, which consists of feedback *and* feedforward loops, thereby providing the neurophysiological mechanisms required for the mobility gradient itself. In the above-mentioned framework, the "warm-up" seen during ontogeny, exploratory behavior, recovery from gross brain lesions, and so on would imply an activation of the feedforward loops, resulting in a successive recruitment of the OT, the VS, and the DS (the serial order seen during the maturation of these brain struc-

tures), whereas the "shut-down" seen during aging, habituation, progression of brain pathology, and so forth would imply an activation of the feedback loops, resulting in a successive inactivation of the involvement of these structures in the reversed order. According to this view, the most advanced stage of the warm-up, characterized by the highest degree of unpredictability and nonstimulus-boundness (Golani: sect. 3.6.2), would only appear, when the DS was fully recruited or activated.

As reviewed and discussed elsewhere in detail (Cools 1981; Cools et al. 1990), it is indeed the DS that frees the animal from external constraints: Enhanced dopaminergic activity in the DS allows the animal to switch behavior arbitrarily. In view of the recruitment of the OT, the VS, and the DS during the warm-up just described, it is intriguing to note that the function of the DS is indeed superior to that of the VS, which allows the animal to switch behavior with the help of cues, namely, external stimuli that are previously singled out originally neutral (irrelevant) ones (for review, see Cools 1990).

E. Role of the striato-nigro-collicular pathway in the hypermobile portion of the mobility gradient. Golani predicts that the hypermobile end of the gradient would include at least six elements; in section 3.8 he provides a detailed description of each of these elements. Given the notion that the most advanced stage of the warm-up only appears when the DS is recruited or activated, it can readily be seen that the hypermobile portion of the mobility gradient requires a "superactive" DS. Such a superactive DS is known to produce decreased GABA-ergic activity in the deeper layers of the colliculus superior (Scheel-Krüger 1986). Against this background it is no longer amazing that Golani's description of the hypermobile end of the gradient (sect. 3.8) appears to be an excellent summary of the behavioral effects seen in rats with a reduced GABA-ergic activity in the deeper layers of the colliculus superior (Cools et al. 1984 and references therein). Following the reasoning of Golani in sect. 3.10.1.4, not only the reticulospinal system (sect. 3.10.1.5), but also the colliculoreticulospinal and/or the colliculospinal system form part of the kind of "hard wired coordination" for the movements in question.

In summary, I have tried to illustrate how assessing the rules resulting from Golani's approach, as well as assessing the framework and descriptions provided by EW analysis, leads to completely new insights into brain/behavior relations.

Eshkol-Wachman movement notation and the evolution of locomotor patterns in vertebrates

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Golani argues that the Eshkol-Wachman (EW) movement notation system is especially useful for studying the neurobiological basis of behavior. I present a test of this assertion by describing the development of our neuroethological analysis of the fish C-start movement. To the extent that our recent kinematic notation method is similar to EW, our findings support Golani's claim. I suggest that such an approach may be an important tool for studying the evolution of locomotor patterns.

The C-start is a characteristic fixed-action pattern of fishes escaping from sudden attack by predators or from objects falling into the water (Figure 1A; Eaton et al. 1991). In 1978, Paul Webb and I agreed to use the neutral term *C-start* because the animal *starts* the movement from a resting position and acquires a *C-like* bending of the trunk during initial moments of the behavior (S1 profile, Figure 1A; Eaton & Bombardieri 1978; Webb 1978). Following the initial bend, the animal accelerates
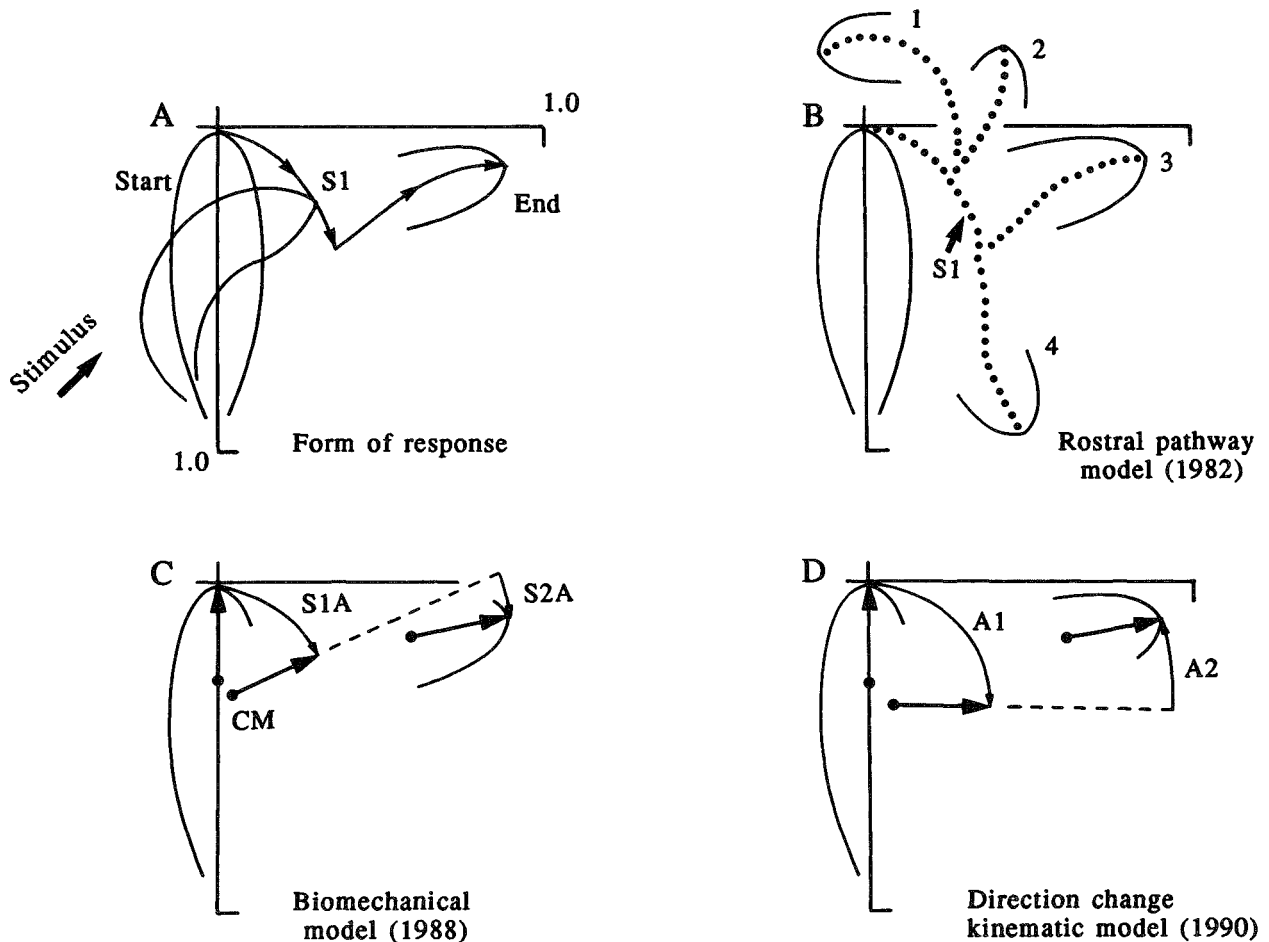
Figure 1 (Eaton). Development of the kinematic analysis of the C-start. A: Example of a response away from a stimulus approaching from the left-caudal direction. The position of the fish (start) is standardized at the time of the stimulus to a coordinate system in which the rostrum is at the origin. Axis units indicate distance moved in body lengths. The fish begins with a C-like bending motion of the trunk (stage 1, S1) followed by forward propulsion. For a 12-cm goldfish, the entire sequence moves the animal's center of mass about 4 cm in 80 ms (end, Fig. 1A). B: Final positions of four responses (1–4) analyzed according to the pathway taken by the rostrum. C: The response in A is here analyzed according to the biomechanical components of the behavior. During stage 1, the center of mass (CM) rotates so that the rostrum is oriented toward a new angular heading. Stage 2 begins when the center of mass begins forward propulsion and is displaced more than a criterion distance. At this point the angular heading is measured (S1A). The heading is again measured relative to S1A at the end of the response (S2A). D: Direction change kinematic analysis of the response in C. Here, the total initial angle (A1) is measured. As shown, this may be greater than the angle turned by the end of stage 1 (S1A in C). The angle of the second turn (A2) is analyzed relative to A1. These turns can be accounted for by the underlying pattern of trunk muscle EMGs. (Retrospective analysis of data originally published in Fig. 5C of Eaton et al. 1982.)

(end profile, Figure 1A) away from the direction of the aversive stimulus (arrow, Figure 1A). This behavior is mediated by neurons of the reticulospinal system. Reticulospinal neurons receive various sensory afferents and make mono- or disynaptic connections on spinal motoneurons.

For the C-start analysis, however, we need to modify the EW perspective. The *base of support* is the surrounding water. This is because of the buoyancy of the fish and the high viscosity of water compared with air (Webb 1988). The water is the physical medium against which the fish transfers its momentum in order to accelerate. Thus, we can ignore the animal's movement relative to the gravitational field that determines the base of support for terrestrial animals. Instead, all motion is described relative to the animal's starting position.

In the first studies of the C-start movement, we and others analyzed the kinematics by describing the path of the rostrum. The dotted lines in Figure 1B illustrate the rostral paths of four different responses. This *rostral pathway model* shows elements of the mobility gradient model of Golani. In different

trials, the animal seems to follow a similar, or stereotypic, pathway up to about 25 ms after the start of movement (arrow, S1). This is the average duration of a rotational movement before the center of mass begins forward propulsion. Once the fish begins to move forward, it can take a variety of trajectories (cases 1–3, Figure 1B), or it can continue in roughly the same heading determined by the initial turn (case 4). Thus, as described by Golani, the movement builds up in the horizontal plane, then in forward transport.

The rostral pathway model seemed to reflect a simple neurobiological concept. It was thought that the initial stereotypy of the behavior corresponded to the action of a single reticulospinal command neuron, the Mauthner cell, that fired only once to trigger postsynaptic followers whose action lead to the subsequent components of the behavior (Eaton & Bombardieri 1978; Kupfermann & Weiss 1978). Following the development of digital machine-vision technology for kinematic analysis, we realized that the rostral pathway model was inadequate (Eaton et al. 1988). Previously, the kinematic data set had been limited

in size by the cost and inconvenience of using high speed cinematography to record the behavior. Once we analyzed large numbers of responses using digital images we found that the initial turn angle of the C-start was a normally distributed parameter ranging from 20°–110°. How could the firing of a single Mauthner neuron code this variability? Thus, it seemed to us that in addition to the Mauthner cell, a population of reticulospinal neurons must be involved in controlling the extent of the initial turn. To address this issue, we used the *biomechanical model* illustrated in Figure 1C.

The biomechanical model is more sophisticated than the rostral pathway model. In the biomechanical model we analyzed the rotational and translational movements of the center of mass of the fish (CM, Figure 1C). The center of mass is the point about which the propulsive forces of the musculature are developed and the point probably targeted by predators. We looked at the extent of the initial turn (S1A) before the center of mass (CM) began forward propulsion and at how far the animal turned in a fixed interval of time afterwards (S2A). We recorded trunk muscle electromyographic (EMG) patterns to gauge the reticulospinal output to the spinal motoneurons during the S1A and S2A turns. There was a significant correlation between the size of the trunk EMG on the side of the initial contraction and the initial turn angle of the fish (S1A; Eaton et al. 1988). The covariation of EMG size and turn angle is explained by the action of a population of reticulospinal neurons (not just the Mauthner cell) that controls motoneuron recruitment and the consequent turn angle. Other experiments now support this explanation (Eaton et al. 1991). Thus, the improved understanding of the kinematics leads to a more refined picture of the underlying neurophysiology. The biomechanical model could not account for the subsequent turns, however, such as turns resulting in the S2A angle in Figure 1C. Even though the biomechanical model gave a correct picture for analyzing the propulsive forces underlying the C-start, it did not reveal how the directional cues of the stimulus were being converted to the motor commands controlling the trunk and the final escape trajectory. The *direction change model* (Figure 1D) of Mark Foreman solved this problem.

In the direction change model, each turn is measured relative to the position of the fish at the start of the turn being measured (Foreman 1991; Foreman & Eaton 1990). There are usually only two turns, labeled A1 and A2 in Figure 1D. They have a variable magnitude and interval between them and each turn is defined relative to its *prior* base of support. Thus, these kinematic measures are very different from those in the biomechanical model. For example, the measurements in Figure 1C and 1D are of the same response as in Figure 1A, but produce much different values. When one measures the response, A1 is 23° larger than S1A and A2 is counterclockwise, whereas S2A is clockwise. Most important, the direction change kinematic model accurately reflects the bilateral pattern of trunk muscle EMGs. Critical parameters are the size of the EMGs and their timing relative to each other. Thus, this model gives the desired reduction of the pattern of movement to the descending reticulospinal commands to the motoneurons. We have also shown that the turns during the C-start are determined by the stimulus direction (Eaton & Emberley 1991). This knowledge, coupled with the direction change model, makes it possible to reduce the behavioral stimulus-response relationship to a neural sensorimotor computation.

For behaviors such as the C-start, detailed kinematic analysis gives important insights into not only the neural organization of behavior but also its evolution. Permit me to speculate. The ancestral vertebrates, the ostracoderms, were limbless, fish-like animals that lived more than 440 million years ago (Romer 1976). Their anatomy suggests that they moved by side-to-side flexions of the trunk musculature and tail. Their aquatic descendants – lampreys, sharks, bony fishes, and amphibians – swim and escape by horizontal body flexions and also possess

Mauthner cells and reticulospinal systems for controlling trunk musculature. Thus, the reticulospinal system is a fundamental feature of the vertebrate nervous system. Moreover, Fetcho (1991) has recently illustrated the remarkable similarity among the neural circuits for swimming in lampreys and larval amphibians and the C-start of fishes. Thus, the fact that the first movements of many behavioral sequences are in the horizontal plane may correspond to the fact that the neural systems subserving *horizontal* movements are among the oldest and most fundamental of all locomotor pattern generators.

The evolution of terrestrial vertebrates resulted in limbs and trunk adaptations for resisting the force of gravity – for moving the animal in the *vertical* plane relative to the base of support. The neural circuits controlling these trunk and limb movements are therefore more recently evolved than systems controlling lateral flexions of the trunk. They are also probably more complex owing to the physically more difficult problem of maintaining balance in the field of gravity. Thus, the horizontal to vertical motion gradient in a behavior pattern may correspond not only to the evolutionary progression of horizontal to vertical locomotion but also to the recruitment of neural circuits from the simple to the complex.

Although detailed kinematic analyses can give insights into the neurobiological basis of behavior, there is another, less optimistic, conclusion. As recognized by Golani, it is not obvious what kinematic parameters are related to what neurobiological parameters. Even with relatively easy parameters to measure (two-dimensional movements and bilateral trunk EMGs) finding the answer took us years of frame-by-frame analysis. In contrast, 30 neck muscles are used in social displays that involve head movements in mammals. Most ethologists are probably unwilling to do a detailed three-dimensional kinematic analysis of such a movement (see accompanying commentary by Bekoff), and their agenda often does not include discovering the neurobiological basis of behavior. Thus, given the technical and conceptual difficulties and different research goals, it is not surprising that quantified kinematic studies are rarely done. Nonetheless, such studies can be valuable when applied to a carefully selected model behavior.

The mobility gradient from a comparative phylogenetic perspective

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The study of animal behavior has extended over the years into a variety of fields but the attractiveness of motor gestalts, a central concern of classical ethology, remains. I elaborate here on the pertinence of the motor gestalt described by Golani to the phylogeny of vertebrate locomotion, where a similar transition from lateral to forward and then to vertical movement is evident. The differential use of the appendages (fins or legs) that accompanies this transition is also described.

Three major forms of swimming, walking, or running characterize vertebrate locomotion: (1) locomotion based on lateral movements of the parts of the trunk; (2) locomotion in which the parts of the trunk do not move actively and the appendages produce the propulsive force (proximodistal transition); and (3) locomotion based on vertical movements of parts of the trunk. Following is a survey of the transition between these forms, as reflected in recent vertebrates.

Fishes. The ancestral form of swimming in fishes (and vertebrates) is lateral undulatory swimming where S-shaped lateral movements progress from the head caudally. This form of

swimming, which in recent fishes is represented by the Anguilliformes (e.g., eel, *Anguilla anguilla*), then diversified in two directions: (1) A cephalocaudal confinement of propulsive lateral movements. This is seen in the more progressive propulsive swimming of recent tunniform fishes (Lindsey 1978; Webb 1982). (2) A proximodistal transition of active movements from the trunk to the fins (Lindsey 1978; Webb 1982; Webb & Weihs 1986). This trend may be illustrated in the sun fish (*Mola mola*), whose trunk is short, rigid, and does not contribute actively to locomotion, which is generated by the back and anal fins. These two evolutionary trends occur separately in fishes of three general phylogentic "grades": (a) Paleozoic actinopterygians, (b) "lower" teleosts, and (c) "higher" teleosts (Web 1982; 1984). Body-related movements of the parts of the trunk in the vertical dimension have not been described in fishes, where the bilateral muscle segmentation is ideal for lateral movement.

Amphibians. Different combinations of usage of lateral movements and stepping are represented by the three orders of amphibians: (1) Limbless amphibians (Apoda) use only lateral movement in locomotion. (2) Recent salamanders (Urodela) swim with exclusive lateral movements. They represent the prototype tetrapod and serve as a model for primeval quadruped terrestrial locomotion (Edwards 1977) in which they use both lateral movements and stepping. Fundamental quadruped locomotion is thus partly based on lateral trunk movements. (3) Toads and frogs (Anura) have a relatively short and rigid trunk; they swim or leap by using their hind limbs. Golani refers to Coghill's description of the ontogeny of locomotion in the urodele amblystoma (*Amblystoma punctatum*). In this urodele, locomotion develops as a lateral movement that progresses in a cephalocaudal order. An increase in amplitude, speed of performance, and frequent alternations from left to right lateral bending result in S-shaped movements whereby the tadpole efficiently swims forward. According to Coghill (1929) forward swimming thus develops from "pure" lateral movements. Coghill also described how stepping is integrated with the S-shaped lateral movement to create the diagonal coupling between the limbs. The substitution of lateral movements for limb propulsion was described in the metamorphosis of the toad *Xenopus laevis* (Hughes & Prestige 1967). Lateral undulation diminishes in a cephalocaudal manner and is then replaced with hindlimb strokes, performed first in alternating and then in synchronized mode. Lateral trunk movements, which are a major component of locomotion in urodeles and apodes, therefore constitute the precursor of forward progression in amphibian ontogeny (see also Eilam & Golani 1988).

Reptiles. Recent reptiles exhibit the same trends seen in amphibians and fishes: Turtles (Testudinata) have a massive and rigid trunk and use their limbs for swimming or walking; snakes (Ophidia) are limbless and adopt different modes of locomotion, typically based on lateral movements of trunk segments (Edwards 1985; Gans 1974); lizards (Lacertilia) use a variety of combinations of lateral movements and stepping. The general forms of locomotion in reptiles thus resemble those of amphibians. Yet another mode of locomotion – the gallop – is seen in some crocodiles (Webb & Gans 1982). In this mode, the parts of the trunk facilitate forward locomotion by moving in the vertical domain (arching and unarching of the trunk). These vertical movements involve a specialized action of the backbone and adjacent muscles (Frey 1988). Galloping, however, is an exception in reptilian locomotion, one that is mostly based on lateral movements or propulsion of the appendages.

Terrestrial mammals. A major change in the anatomy of mammal-like reptiles was the rotation of limb posture (Romer 1922); in the new erect position all limb segments move only in the forward and vertical dimensions, rather than in three dimensions of the sprawling limb (Rewcastle 1981). With the new posture, mammals exhibit cursorial locomotion (Gambaryan 1974) in which the four legs produce the propulsive power without movements of the trunk. Many terrestrial mammals can move faster by incorporating the trunk segments to move in the dorsoventral (vertical) plane, as in the gallop.

In swimming, terrestrial mammals use mainly their legs. However, several species diverge from this general pattern. The otter shrew (*Potamogale velox*) and the muskrat (*Ondatra zibethica*) are the only mammals that have a laterally flattened tail, which they use as a paddle in swimming with lateral movements. More specialized swimmers, the semi-aquatic mammals like the beaver (*Castor canadensis*) and sea-otter (*Enhydra lutris*), swim with both synchronized leg paddling and movements of the trunk in the dorso-ventral vertical domain, as in the gallop.

Aquatic mammals. There are three forms of mammalian swimming: (a) lateral movements; (b) exclusive movement of appendages; and (c) vertical trunk movements. Seals (phocidae) have their hind limbs directed backward to a position that resembles the caudal fin of fishes. In swimming (and when alarmed on land) they progress with lateral undulatory movements of the hindquarters and hindlegs. The sea-lions (otariidae) swim by paddling with their forelimbs, whereas their hindlegs are directed forward and enable them to walk on land (rather than crawling like seals). Sea-cows and manatees (sirenia), like sea-lions, use their forelimbs in swimming. However, the hindlegs are absent in these creatures and their horizontal tail moves slowly in the dorso-ventral plane to facilitate swimming. The most specialized aquatic mammals – the whales (cetacea) – swim by moving their tails. Except for its plane, the form of this movement is similar to that of the vertical tail of fishes (Alexander 1975).

In his target article Golani suggests using the mobility gradient model as a "search image" in the examination of vertebrate behavior. Using the proposed model, this survey suggests parallel transformations across vertebrate phylogeny: from lower vertebrate locomotion, which depends on lateral trunk movements, to the more specialized forms of "pure" forward transport produced by the appendages or facilitated by dorso-ventral vertical movements. These parallels add a phylogenetic perspective to the behavior described in the target article.

Moving beyond words

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The special genius of ethology is its gift for teaching us to see animal behavior in new ways congenial with the scientific method. In Ilan Golani's work, ethology's fresh perceptions of behavior gain further momentum by incorporating unique insights about movement from students and performers of dance.

When I first studied Eshkol-Wachman (EW) notation a decade ago, I was in a novel academic setting where students learned not just by sitting and writing but by getting up from their chairs and moving. It was then that I first saw how bodies have their own ways of learning. Since then, an intense absorption in dance has coexisted happily in my personal and professional life with my earlier love for the study of animal behavior.

As a practicing ethologist, dancer, and recreational choreographer, I took up Golani's article with particular interest. Golani's approach to behavior, based on EW notation, is not unknown to ethologists at large but broad acceptance has been slow. Discounting simple inertia or resistance rooted in professional competitiveness, I can see three interesting reasons why Golani's work has been (quite wrongly, in my opinion) viewed as a curious methodological offshoot with little potential for important contribution to ethology, much less to science as a whole: (1) The method is too laborious and time-consuming to be practical;

(2) in a decade of availability it has not yielded novel behavioral descriptions of general biological interest; and (3) by setting aside questions of movement quality and meaning, it fails to address the very issues that make animal behavior so fascinating in the first place. I will argue that Golani's target article puts the first and second criticisms to rest very convincingly. The third criticism is admittedly a "straw man," but it has certain important implications that I will try to make clear by citing parallel developments in contemporary dance.

1. "EW is laborious." True, but not very true. Golani's bibliography reveals an impressive quantity and variety of EW-based studies of behavior, spanning several disciplines of the behavioral and brain sciences. Ethologists who have difficulty applying EW may not have learned the method well enough to use it rapidly and accurately. My undergraduate ethology students learn a subset of EW notation in three two-hour laboratory sessions and then use their knowledge to notate head positions and simple movements of perched bald eagles (*Haliaeetus leucocephalus*). But to achieve active, working knowledge of the entire notation, I estimate two years' regular study, including active studio work, might well be necessary. The truism "use it or lose it" certainly applies.

2. "EW descriptions are trivial, even as descriptions of the structure of ongoing behavior." Golani's target article, offering a wealth of testable predictions and provocative insights, effectively answers this criticism. I cannot imagine any objective, replicable approach, other than one based on a quantitative system of movement notation, that could have achieved the results Golani presents here. Nor is the effective use of the method somehow dependent on the unique talents of one particular scholar. Pellis (1989), for example, has completely (and, in my view, convincingly) overturned classic ethological interpretations of courtship in geese, using EW methodology. In my own specialty of animal play, both Golani's present suggestions and Pellis's (1989) earlier work represent real contributions that would not have been possible without EW methodology.

3. "The method asks us to deny the qualities and meaning of movement." I disagree in part with this criticism, in that I value description and find EW methods especially effective. Analogously, I had to learn basic dance technique before I could begin to interpret roles or express feelings and ideas in my work. It is painful; it takes time. I hope that the EW notation will be widely accepted, but I also feel it would be dangerous to stop with structure – a process that we might term the Balanchinization of ethology. Contemporary dance, and the recent behavioral science of gesture (e.g., Borchert & Zihlman 1990) have converged on a key insight: Meaning matters. The quality of movement is as important as its structure. Behavior, like dance, is most meaningful, both as science and as art, when it has a story to tell. I believe that a consequence of Golani's work will be that behavioral scientists will ultimately rediscover this insight as a valid and necessary response to an initial emphasis on structure. As dancer Gelsey Kirkland (Kirkland & Lawrence 1990) argues, neither science nor art alone can suffice now, but if our work and play come from the heart, they can change the world.

Connecting invertebrate behavior, neurophysiology and evolution with Eshkol-Wachman movement notation

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Eshkol-Wachman movement notation (EW) is a way of describing behavior that makes biological sense. Behavior is move-

ment, but the detailed analysis of movement is a neglected area of ethology (Barlow 1989). Most recent research is devoted to the functional consequences of behavior (mate choice, foraging, etc.; Dawkins 1989), but ill-defined conceptual frameworks lead to inconsistencies in recording behavior and to neurologically invalid theories (Jacobs et al. 1988) EW is an unambiguous language for describing behavior that takes into account the physical and biomechanical constraints imposed on movement.

EW should be equally valuable to neuroscientists trying to understand how physiology and anatomy produce coordinated movement. Neurophysiologists often treat movement as a *physiological variable* of the neuromuscular system; they need a way to measure movement so that neural events can be correlated with behavior. Indeed, aspects of the movement patterns detailed by Golani, including the mobility gradient, seem consistent with ideas about the organization of the spinal circuits that control contractions of synergistic muscles and the roles of descending inputs that orchestrate the large motor repertoire of vertebrates (Bizzi et al. 1991).

A major impediment to describing behavior in terms of the motor output of the nervous system arises from the dynamic nature of the linkages between them: The two are not isomorphic. There is no straightforward way to deal with the fact that the elastic components of biomechanical tissues act in complex ways, depending on frequency, acceleration, and phasing of movements; these must ultimately be taken into account to understand movement fully (Hasan & Stuart 1988; Van Leeuwen 1991). The potential strength of combining electromyograms (EMGs) with EW is that EMGs record the raw motor output whereas EW describes the combined effect of motor output plus all biomechanical factors influencing movements at a joint (including torques generated by movements at other joints). In addition, EW can describe subtle changes in the performance of a movement, thus revealing the effects of experimental manipulations. Currently, neurophysiologists must "custom-build" measures of movement (e.g., Kelly & Chapple 1990; Macmillan 1975; Paul 1981a). None match EW's elegance and successful application to at least fifteen species: three birds (e.g., Pellis 1983), eleven mammals (e.g., Golani et al. 1981), and *one* invertebrate (Faulkes et al. 1991).

Among the invertebrates, arthropods, with their jointed exoskeletons and complex patterns of movement, are particularly "EW friendly." Feathers and fur can be a significant hindrance to a notator (!) because they obscure joint positions (V. C. Pellis, personal communication). Arthropods' hinged joints do not allow rotations (Lochhead 1961), one of EW's three types of movement (Eshkol 1980). The behaviors of most invertebrates are tractable to analysis by the full spectrum of neurophysiological techniques. Consequently, a wealth of information is available on invertebrate nervous systems (Atwood & Sandeman 1982; Bullock & Horridge 1965) and the analyses of central pattern generation and proprioceptive feedback are relatively advanced (Getting 1989; Hasan & Stuart 1988; Sandeman & Atwood 1982). [See also Selverston: "Are Central Pattern Generators Understandable?" *BBS* 3(4) 1980.] Briefly, individual neurons and the circuits they form can be characterized by their morphology and physiology in enough detail to identify neurons that are homologous (common ancestry implied) across taxa. Neural substrates of behavior can then be compared, telling us *why* behaviors differ (mechanistically) and providing strong evidence that behaviors in different species can be homologous (Arbas et al. 1991; Paul 1991). In short, we can start to understand *how* behaviors evolved.

In fact, EW's potential contribution to evolutionary studies is suggested by Golani's exposition of behavioral "homologies" in vertebrates: He clearly wishes to conclude that the mobility gradient, like the vertebrate skeleton, is truly homologous throughout the vertebrates, thus explaining its ubiquity. Why, then, does he misleadingly use "homology" in the pre-Darwinian sense?

Tailflipping by decapod crustaceans is *the* paradigmatic case of a behavior explained in neural terms. Wiersma (1947) knew that the lateral giant (LG) and medial giant (MG) interneurons generate tailflips in crayfish, but he thought all tailflips were identical. Movement analyses revealed three different kinds of tailflips, each associated with different neural circuitry: (1) The LGs cause single tailflips that catapult the animal upward; (2) the MGs generate single tailflips that send the animal backward; and (3) nongiant fibers mediate swimming: voluntary, repetitive tailflipping (Krasne & Wine 1987; Larimer et al. 1971; Reichert et al. 1981; Schramek 1970). With this knowledge of tailflip kinematics, patterns of connectivity between the giant fibers and motoneurons were found that explain how the LGs and MGs produce different forms of the behavior (Krasne & Wine 1987; Mittenthal & Wine 1973). In addition, tailflips evoked by direct electrical stimulation of the LGs have trajectories different from those of "natural" tailflips, correctly suggesting that neurons besides the LGs are involved (Wine 1984). Some decapods have lost the giant neurons and the accompanying behaviors (Paul 1981b; Sillar & Heitler 1985; Wilson & Paul 1987). Other species have evolved new behaviors with the old circuitry (reviewed in Paul 1989), for example, a hermit crab's withdrawal into a shell is mediated by some of the same neurons used in a crayfish's tailflip. With this perspective, Paul (1991) sketched the evolutionary divergence of tailflipping behaviors and their neuronal substrates into "new" behaviors. Thus, the understanding of movement and neurophysiology illuminate each other and ultimately allow an evolutionary synthesis.

Finally, we should say something of EW's practical implementation, because some believe that EW is esoteric and hard to learn! Not so. One of us (Z. Faulkes) learned the basics of EW in about a week from Sergio Pellis, who in turn learned his basic skills from Ilan Golani by correspondence (S. M. Pellis, personal communication). On the technological side, the picture quality of standard videotape is fully adequate for EW, thanks to the introduction of CCD cameras, still-frame VCRs, and Hi8 or Super-VHS (although film's quality remains unbeatable). Physiological data (e.g., EMGs) can be recorded on audio tracks while behavior is being videotaped. In addition to video, computer systems for studying movement are becoming available. However, whereas such systems are undeniably useful for data *collection*, EW provides a conceptual framework for *analysis* that computers do not.

Alternative taxonomies in movement: Not only possible but critical

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Golani has provided a service in reminding us through elegant demonstrations that alternative taxonomies in behavior (and brain operations) are always possible. He is, for example, clearly right in pointing out that categorizations of movement by *function* are different from categorizations of movement by *form*. This distinction between classifications of behavior by form and by function is in itself deeply rooted in the ethological literature (Hinde 1970). One could equally categorize behavior by temporal patterns, movement force, or some other parameter. What is not clear is how any of these taxonomies can be mapped onto the brain. The questions raised by Golani are far from trivial ones.

Golani is right in suggesting that there may be more or less continuous distributions of variables across actions that are otherwise defined separately. It is therefore foolish to expect taxonomies constructed via different domains of emphasis to be

isomorphic reflections of each other. The polarities of continuous versus discontinuous variables, as well as the relative stability/instability of these variables, are obvious anchors for many taxonomic or categorical evaluations (cf. Fentress 1990; Harnad 1987). These evaluations can and do often deviate along other criteria (Edelman 1987; Fentress 1991).

The quest for regularities (or, in motor parlance, invariants) is one key to the solution of movement puzzles and for the more abstract issues that I have hinted at above. Many years ago, Lashley (1951) argued that mammalian brains are often remarkably adept at obtaining a common endpoint (goal) through variable means (the concept of "motor equivalence; cf. Bernstein 1967). The invariances, then, can be more obvious in movement property combinations rather than in the properties taken in isolation. This is an important lesson that still has not penetrated the neurosciences as fully as it should (Fentress 1991).

A key step in Golani's argument is that there may be gradients of movement that cross functional categories or "types" of movement. In this too he is surely right. I can move my head laterally via the same defined reference frame to communicate verbally, reach for food, observe a peer coming into the building, or kiss my wife. If the argument were left here, one might conclude that there was a vacuum in insight.

To his credit, Golani does not leave the argument here. Rather, he shows in a convincing manner that regularities can also be found across (a) sequences of expression, (b) ontogeny, (c) loss of expressive dimensions following pharmacological onslaughts, and (d) recovery of function. He also raises such interesting evolutionary issues as across which criteria we should expect homologies in behavior to fall. Movement form is indeed one of these criteria, but not necessarily the only one. It is highly conceivable, for example, that homologous neural circuits could generate patterns that differ in their surface manifestations. The work of A. Bekoff on developmental continuities in chick motor behavior makes a similar argument from an ontogenetic perspective (e.g., Bekoff 1986). As development proceeds, chick movements that differ dramatically in their external manifestations (such as form) may nonetheless be mediated by common circuits.

Golani's emphasis upon "gradients" in motor expression can provide an important corrective to strictly compartmentalized notions of motor control (cf. Fentress 1990). The most critical point is that activities that appear separate on the basis of some criteria often appear to have a common ground on the basis of others. Thus, Berridge et al. (1987) found that rat facial grooming sequences often enter into a particularly stereotyped phase once the animals express a highly rhythmic period of forepaw licking. The same rhythm is then carried over into facial wiping.

Such observations are useful, because they make us question the criteria we often use to say that motor behavior is "hierarchically organized." A given action can always be broken down into its subproperties, such as movement direction or timing. When we do this we are understandably tempted to view the properties as hierarchically "lower" expressions of control. However, when we find sequentially adjacent or even more widely distributed actions sharing common parameters, such as form and timing, we might well question whether it is the "actions" or the "parameters" that deserve top billing. As Edelman (1987) reminds us, behavior, as well as brain operations, are essentially polymorphous (multidimensional). The arrangement of these polymorphous properties into simple hierarchies may in itself be a misleading exercise.

A critical question arising from Golani's work concerns the extent to which his often admirable insights are direct derivatives of the Eshkol-Wachman (EW) movement notation system. To put the matter in somewhat different terms, I sometimes wonder whether or not it is the training to be a skilled observer of movement details that provides the insights. When many of us took our first look through a microscope, cells were hard to

see. We then attempted, with considerable initial struggle, to draw those cells. Then we could see them.

To pursue the argument, the fact that Golani is able to describe animal movements in terms of three dimensions (the fourth dimension, time, being given an unfortunate short shrift), is not at one level surprising; indeed, it becomes a truism. X, Y, and Z coordinates will by definition describe any three dimensional object. "Horizontal," "forward," and "vertical" are X, Y, and Z. One does not need a particular movement notation to make the point. The fact that animals may move their heads before their trunks in each of these dimensions is also of interest. Again, however, such observations could be made without any movement notation. So the question is, does the EW analysis generate these insights or merely support them? What I am asking is whether Golani's perspicacity in animal movement emerges (necessarily) from, or can simply be superimposed upon, the EW system. (Skilled anatomists have always impressed me; Golani is a skilled anatomist of movement – I will be happy with either answer.)

The details in Golani's paper generate some interesting questions. To cite from Havkin & Fentress (1985), I do not see why "falling" in wolf pups is assumed to ignore a vertical dimension (given gravity) or why the observation of the "top" wolf losing its grip is more interpretative than the observation that certain limb segment kinematic properties "result in" defined trajectories or even "contact pathways" between the forepaws and face in grooming mice (Golani & Fentress 1985). Movements in animals are, after all, the means by which tasks are accomplished. The issue of "accomplishment" is surely at least as important to evolution as "means." There are jobs to be done.

There are some deeper reservations I have in Golani's presentation. (1) At a descriptive level, he writes that "horizontal" movements precede other (forward, vertical) movements; but he seems to have forgotten his own admonition that horizontal must be described from an explicit reference frame. What would happen, for example, if the young animals were rotated 90 degrees around their body axis; would their "horizontal" movements now become "vertical," or would they stay "horizontal"? (2) It is not clear from Golani's account to what extent early horizontal movements reflect more than the fact that young animals are muscularly weak. What if they were supported, as in swimming? I suspect (indeed have observed) that they might move in both forward and vertical directions. (3) To what extent are Golani's generalizations in this target article confined to expressions of locomotor behavior? By chance I recently visited a patient (with probable basal ganglia disfunctions) in a Halifax hospital who confirmed that vertical dimensions were most difficult to deal with in actions that involved overt locomotion. But in reaching she has major problems moving her arm in a horizontal (earth defined) direction. Should I expect the earliest facial grooming strokes in mice to maximize horizontal trajectories? (4) To what extent can we expect to superimpose Golani's trajectories upon brain operations, in either people or other animal species? Here the jury is still out.

Because of my own interests, I resonate with Golani's references to the basal ganglia. It is now well established for rodents that basal ganglia (striatal) maturation occurs within a basically ventro-lateral-caudal to dorsal-medial-rostral gradient (e.g., Fentress et al. 1981; van der Kooy et al. 1987). It is still not clear, however, how these developmental gradients, defined at the neurocellular level, relate to patterns of movement expression. It is not even clear how various regions of the striatum contribute, selectively, to movements in horizontal, forward, or vertical planes. Should we expect patterns of striatal maturation to correspond with the patterns of movement Golani has outlined?

As I read him, Golani has suggested that we should look toward the possibility of mapping behavioral and brain functions through detailed analyses of the form of movement along complementary dimensions (e.g., ontogenetically). He offers one

path (EW notation) by which we might do so. We should accept his particular path as one among many possible others.

Golani has thus highlighted problems that we should investigate further. It follows that the solutions of these problems await further investigation. It is at this point that alternative taxonomies of behavior and its neural control are most critical. At present we do not have anything like a "periodic table" of behavior. From this perspective we remain in the dark about how we should either fractionate properties of behavior or evaluate the rules of relation among these fractionated properties.

Dynamical systems theory and the mobility gradient: Information, homology and self-similar structure

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Golani presents a fascinating means of perceiving and thereby understanding the sequential organization of vertebrate movement. He argues effectively that movement is best understood by seeking central themes rather than attempting exhaustive description. Such central themes may best be identified through a specialized notation for relating kinematic phenomena. In this commentary, I would like to try to link the mobility gradient to a consideration of the dynamical requirements of controlled movement. It is not surprising that a search for the "core elements" in the construction of a movement should be related to the physical constraints on movement that are the most pervasive throughout evolutionary time: (a) force-transmitting physical articulation with the environment (i.e., base of support), and (b) the force of gravity.

The control requirements for maintaining structural stability within a gravitational field place broad constraints on relationships between the base of support and the orientation of the trunk, given internal limitations on the rate at which muscular contraction forces can be generated. The central nervous system can be viewed as the source of patterns through which muscular forces are deployed to solve such motor problems (Bernstein 1967). This process can be viewed in terms of the rate at which information can be produced by the central nervous system in the specification of movement (Kugler & Turvey 1987). If the rate at which the central nervous system is able to generate information gradually increases during ontogeny, then the "mobility gradient" may be related to this gradual change in the "informational gradient."

Lateral, gravity-neutral movement is the least demanding in terms of the information required to specify the necessary patterns of muscular contraction. Such movement can be produced through the asymmetric activation of lateral muscles of the neck and trunk. On the other hand, forward progression of the trunk requires an elevation of the center of mass to propel the body forward. Thus, there is a need to coordinate transient elevation with forward propulsion – a somewhat more complex task than lateral movement. Finally, moving the trunk from a horizontal to a vertical orientation requires a narrowing of the anterior-posterior extent of the base of support and, at the same time, an elevation of the center of gravity by raising the anterior trunk. Clearly, the informational requirements to specify a stable, controlled process for this coordinated transformation

would be even greater than for forward progression. Thus, as the capacity to produce information in the form of coordinated patterns of muscular activation increases during the development of the nervous system on the ontogenetic time scale, the ability to move up the mobility gradient increases. Similarly, if one views the expansion of the central nervous system over phylogeny as enhancing the capacity to express as well as to extract information then this may be related to the development of the mobility gradient on this time scale (see last paragraph of sect. 3.11 of the target article).

Golani then postulates that "perhaps movement unfolds along self-similar geometrical manifolds across the three different time scales of moment-to-moment behavior, ontogeny, and phylogeny." There is some need to unpack this statement. The concept of self-similarity implies homologies that extend across scale. This possibility of a potential homology between processes embedded in one another in time assumes a lawful control of these processes that may transcend scale in the time domain. The possibility of such homologies is a central theme in the microgenetic theory of cognition (Brown 1988). Here the term "microgenetic" refers to what Golani terms the "moment-to-moment behavioral time scale." Furthermore, this concept of embedding a structure in time recalls concepts developed by the physicist David Bohm – that is, the presence of an "implicate" or "enfolded order" – in his approach to problems encountered in quantum mechanics (Bohm 1980; see also Peat 1988). In addition, this general concept of an embedding of homologous structure may be linked to emerging information about how genetic controls over developmental processes are elaborated over the course of speciation in the evolutionary time frame (Gould 1991). Thus, homeotic genes associated with the metameres in the development of the structure of the insect body appear to be homologous to mammalian homeotic genes associated with the rhombomeres of the developing hindbrain.

The concept of self-similarity is closely tied in a formal mathematical sense to that of renormalization theory, universality, fractal structure, and deterministic chaos (Schuster 1989). Does Golani, through his statement that movement unfolds over self-similar geometrical structures, mean to imply that the underlying system dynamics of the processes defined on these different time scales are chaotic and therefore characterized by "strange attractors" in phase space (Skarda & Freeman 1990) – that is, an attractor with fractal structure? How might one go about testing this prediction? [See also Skarda & Freeman: "How Brains Make Chaos in Order to Make Sense of the World" *BBS* 10(2) 1987.]

It is interesting to consider what is implied by the idea that the mobility gradient operates on the microgenetic time scale. Does this mean that there is a temporal ordering within the structure of a particular movement that follows the direction of the mobility gradient? How might this concept be extended to the control of the limbs?

Finally, I would like to comment briefly on the relation between the mobility gradient and the dichotomy of stimulus-bound versus "free" or "spontaneous" motor behavior. This is a complicated issue. I have hypothesized elsewhere that these two different types of behavior are organized through different premotor mechanisms in the central nervous system (Goldberg 1985; 1987). Golani relates the idea that functioning at a higher point on the mobility gradient allows an organism to respond with a larger number of options to a particular stimulus configuration and that such responses are manifest with variable latencies. Greater degrees of freedom are available when the organism functions at a higher point on the mobility gradient and, similarly, it has a more restricted repertoire when functioning at a lower point. This approach implies a continuum for action along which the capacity for movement varies. It therefore links increased degrees of freedom of movement with an expanded repertoire for the control of orientation of the trunk with respect to the supporting limbs. The supplementary motor

area of the primate brain, a major target for the cortical re-entrant projections from the basal ganglia, has been thought to be primarily responsible for the coordination of these types of axially based movements (Penfield & Welch 1951; Viallet et al. 1990). On the other hand, the same region has received recent attention with regard to its possible role in the elaboration of voluntary movement based on internal context (Eccles 1982; Goldberg 1987; Kornhuber 1984; Orgogozo & Larsen 1979). This dual role would seem to fit well with the concept that a greater freedom of movement may be observed in subjects who can achieve a more elaborate degree of axial control.

The concept of a mobility gradient and the related ideas of "warm up" and "shut down" may also help us understand impairments of movement produced by brain damage in humans. A reversion to synergy-bound movement seen clinically in the upper motor neuron syndrome may be better viewed in these terms as a "shut down" of movement along a gradient corresponding to a progressive restriction of the degrees of freedom available to the subject. The capacity of the damaged central nervous system to produce information in the specification of movement is degraded by damage. Furthermore, the idea that there is an ordered sequence through which the recovery of movement takes place in the brain-damaged subject could have important implications for the rehabilitation of such impairments of movement. Hypotheses derived from this theoretical framework can be tested not only in animal models of recovery (e.g., Golani et al. 1979) but also in patients recovering movement after, for example, a stroke. If "warm-up," viewed as a systematic sequential extension of the movement repertoire, can be applied to the clinical rehabilitation of impaired motor control, a rationale for physical training programs to restore movement may be usefully linked to these ideas.

In summary, Golani's "mobility gradient" may be related to limits in the rate at which information can be elaborated by the central nervous system in the course of specifying a motor act. The orderly process of acquiring new motor abilities may be related to increasing complexity of the patterns of muscle activation that must be produced in order to allow the organism to "warm up" along the mobility gradient. The idea that a similar systematic sequence may be observed on the three different time scales of microgenesis, ontogenesis, and phylogenesis along which organized movements unfold suggests that there may well be homologies in the way the gradient is defined on these different time scales. This would suggest that the process whereby movement unfolds may be characterized by the feature of self-similarity with respect to time, suggesting linkages to the related mathematical concepts of renormalization, universality, and deterministic chaos. The concepts put forward in the target article also suggest that regions of the central nervous system involved in the control of posture and axial stability may also be involved in determining the degree of stereotypy of behavior as well as the extent to which behavior is stimulus-bound. Factors related to the base of support as well as trunk orientation relation to the base of support are critical and form a foundation for motility. The potential clinical utility of this approach to the organization of voluntary movement in vertebrates, particularly with reference to the rehabilitation of the brain-damaged human subject with impaired motor control, is a related issue of significant interest.

Shapes of behaviour

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An ethologist who turns to movement notation as a tool in behavioural studies is probably looking for the same attributes

that led me to adapt Eshkol-Wachman movement notation (EW) for work in composing abstract visual images – namely, the capacity to serve as a record, for communication, for systematising; and above all, for formulating ideas in symbols that enable us to grasp structure through a scheme of manageable size. EW meets all the requirements and it may be useful to explain this in terms of my own field of shape-as-movement.

Any bounded area can be regarded as the path of the movement of a line – in descriptive geometry, a "generatrix." The line sweeps out a trace, the shape of which is determined by the way it moves. The usefulness of this idea depends upon the possibility of defining exactly how the line does move. This is precisely what is achieved when a movement is expressed in the symbols of EW.

EW is used mainly for the notation of human movement (Eshkol 1971; 1975; 1978; 1979; 1980; 1988; 1990; Eshkol & Seidel 1974; 1986; Eshkol et al. 1971; Harries 1989; Sapir 1987). Movements are treated as the paths produced by the limbs, which are seen (for the purpose of analysis) as chains of articulated rods or lines (see Figure 1) (Eshkol 1970; Eshkol & Shoshani 1979/1982; Eshkol & Wachman 1958; Harries & Richmond 1982; Yanai 1974).

Using EW, it is possible to define the movement of any line, and thus to describe shapes in terms of movements of articulated generating lines in relation to absolute or relative systems of reference encompassing two or three dimensions of space, plus time. The instructions of the notation are general in that they apply to any medium, but they are specific in that they work for each instrument (e.g., pencil and paper, computer graphics, or human performer).

Seen in the way proposed, a still picture is not only an immobile object but also one stage in a formative process and possibly the point of departure for subsequent emerging form. The continuity that links the static and dynamic, and the two- and three-dimensional, can be preserved only with the help of a powerful tool like EW. In three-dimensional space, if a single generating line moves about one of its ends, which remains at a given fixed position, the line may sweep out a curved surface or a plane. (In the case of a solid limb, rotation about its own axis is also significant.) In two-dimensional space, a circular shape results. A more complex shape is obtained if a second generator is articulated with the moving end of the first and simultaneously moves about their common "joint." Chains may be formed of any number of such generators, moving about the points of linkage, as explained in detail elsewhere (Harries 1969; 1975; 1983).

In every movement of articulated generating links, these are characterised in EW terms as "heavy" or "light" – i.e., carrying or carried by a neighbouring link. (A generator may simultaneously carry one neighbour and be carried by another.) When a generator moves, it carries with it all other links that are farther away from the origin, thereby changing their positions; the origin of the heaviest link corresponds to the base of support in the case of a living organism.

When independent movements of the light links occur as they are carried by a heavy link, the change of position of each link is the result of the simultaneous movement of the carried link together with the movements of the heavier links. The movement of each generator is written as though in relation to an immobile carrying link. But in fact the path of this movement will be modified because its heavy neighbour moves as well (see Figure 1). Simultaneous movements of generators, shown both as successions of positions and as the shapes that they sweep out, are shown in Figure 2. In (a) the carried link moves at twice the rate of the carrying link; in (b), at half the rate. The varied synchronisation of the movements of two or more articulated generators is the source of the apparently endless wealth of shape that can be obtained and composed using this system of symbolisation.
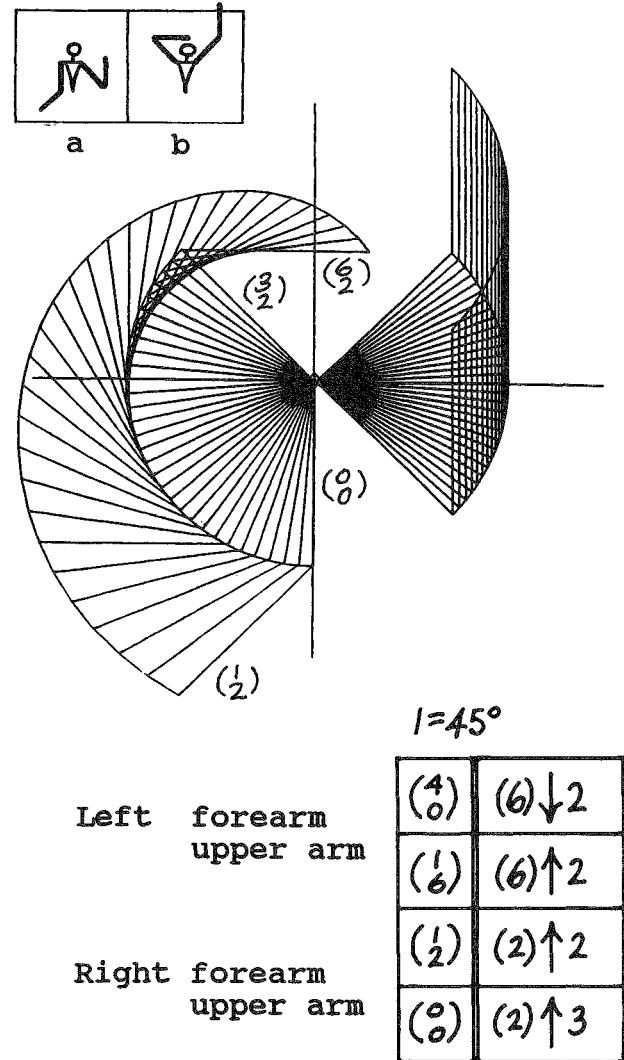

Figure 1 (Harries). A computer simulation of the movement of both arms in the frontal plane, from (a) to (b), the accompanying sketches. The right forearm, which begins at position (2,1), moves through 90 degrees (2 units of 45 degrees), but arrives at 6,2), a position separated from the starting position by 220 degrees. This is because of the simultaneous movement of the "heavier" upper arm through 135 degrees. (Graphics from Eshkol 1990.)

Work designed to be displayed in time is conveniently provided for in EW, where the measured flow of time is represented by the columns of the basic grid, upon which the synchronised patterning of movements of the generating links is written and easily perceived. These scores are implemented as abstract moving computer graphic images, transferred to videotape. The quantitative nature of EW makes it ideal for computer input. The software I have developed provides for the entry of data in an EW score on screen; when completed this is first interpreted as the visual process it represents and then displayed in movement (Harries 1981; 1986).

All the work of visual composition is written in the same notational system and does not require new parameters or new modes of symbolisation for different projects. The generality of the notation is more than sufficient and can equally well encompass the domain of three-dimensional shape. Furthermore, shapes and processes are defined with as much accuracy as can be matched in the given medium; this allows for both control and subtlety of variation.
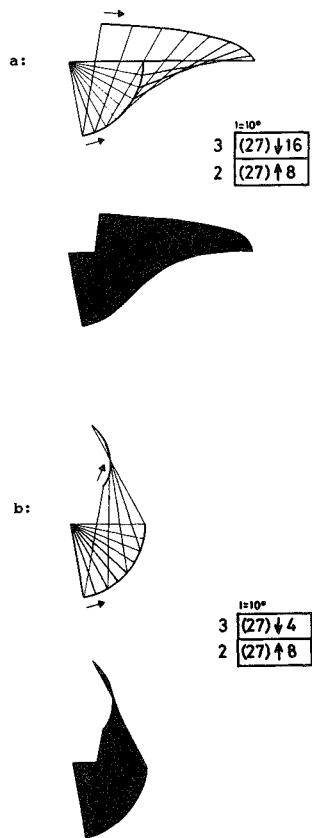
Figure 2 (Harries).   Shapes swept out by generating linkages. The notation of each shows, on the left, the relative lengths of the generating links; above the frame, the value of the unit of movement (one unit = 10 degrees); in parentheses, the plane in which the movements take place; following these, arrows indicate the direction (clockwise or counterclockwise) and numbers specify the amount of movement of each generator. In cases where the lengths of the generators change (like robot mechanisms rather than human limbs), this is integrated in the horizontal spaces. Colour and other non-EW information can be added when required, parallel with the movement score itself, in an additional space – in the same way that scores for human movement can incorporate information such as music, or the touching of extraneous objects. (Graphics from Harries 1983.)

The fact that Golani and I use the same notation system is significant, in that it places our work within the common universe of discourse of shapes of behaviour and makes it possible for me to obtain a definite picture of the phenomena he describes, despite the seemingly great distance separating our fields of interest.

Structure and function in the CNS

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Efforts to understand the organization and function of the central nervous system (CNS) through comparative studies have been based on the principle of homology. This principle states that similarities in structure due to a common ancestry are sufficiently conservative to allow their use in establishing phyletic relationships. Konrad Lorenz (1974), in his Nobel address, epitomizes its use: "A great part of my life's work has consisted in

tracing the phylogeny of behavior by disentangling the effects of homology and of parallel evolution. Full recognition of the fact that behavior patterns can be hereditary and species-specific to the point of being homologizable was impeded by resistance from certain schools of thought" (p. 231). One of these impediments was Gregory Bateson, who countered: "There is a certain elegance in the notion that evolutionary process must generate or differentiate two types of comparability: analogy, generated by the active process itself, and homology, generated by the failure of that process to change its own production. Clearly, this logical elegance would be spoiled by any other form of comparability which might demand recognition" (Bateson, unpublished manuscript). Bateson then goes on to enumerate the immense difficulties in making the distinction, especially among related organisms where it is the matter of the resemblance that is adaptive, not the structure itself. Alternatively, resemblances that appear to be adaptive responses to selection, analogies, may represent physical constraints that are only fortuitously adaptive – as is possibly the case for the similarity in wing patterns of edible butterflies and their inedible or toxic "models" (cf. Klopfer 1973).

The rejection of the homology-analogy dichotomy as a guide to disentangling phylogenies, especially of behavior, at once precludes extrapolation from one species to the next. The decorticate cat can then not be seen as having its reptilian brain revealed and the study of central function must proceed *de novo* with each species.

Hooper and Moulins (1989) show that individual neurons can switch from one functional network to another as a consequence of sensory-induced changes in membrane properties. In their system, the functional membership of a neuron in a central network is not even fixed ontogenetically, a view also shared by Easter and his collaborators (1985). Further examples are discussed by Falk (1990) and Alvarez-Buylla et al. (1990). The conclusion I draw is that whether we consider a nervous system as small as that of *Aplysia* or as complex as that of *Homo sapiens*, knowing a neuron's name and address doesn't assure knowledge of its function.

It is nonetheless the case that some behavior patterns are highly stereotyped, varying but little between individuals of a particular species and sex. It is also true that these patterns often seem to depend upon the integrity of particular neural structures, which are similarly constant in their appearance. How is this to be explained if we reject the notion that one-to-one structure-function relations are a primary, if not universal, rule of central organization?

Edelman's (1987) explanation of the ontogeny of "innate" perceptual schemata will serve as an example of one alternative approach. Consider the development of muscle cells from late-gastrula mesoderm. Their manner of growth, spatial alignment, and adhesions are all subject to invariant physical constraints, much as are the bees that construct a honeycomb. The distribution and organization of these complete structures cannot be random, though it may be chaotic. Physical forces will favor but not necessarily require certain design features (alignments, distribution, etc.) over others. Now, let us assume that whenever two or more adjacent cells contract simultaneously or in the same plane, their future tendency to act together will be enhanced. (Such a phenomenon was demonstrated by Nelson et al., 1989, to operate in an in vitro culture of nerve cells.) Where they act antagonistically, cell deterioration follows. Functional dyads that survive the first stage of selection are then able to forge larger assemblies, which are themselves "tested" and selected for their functional effectiveness. Given similar physical environments, the functional outcome will be similar; their physical basis may or may not be similar, since several (many) different structural configurations can still yield identical outcomes.

As I've stated before (Klopfer & Budnitz 1990), epigenetic

descriptions of the ontogeny of instincts are hardly new, though they seem to be enjoying a mild renaissance (Eilam & Golani 1988; Ho & Fox 1988; Plotkin 1988). These basic ideas, which have flowed from Waddington's (1966) study of development to Edelman's (1987) neural Darwinism, do offer an opportunity to expand our understanding of the mechanisms of behavior and they escape the limitations of models that depend on static relations between *a* structure and *a* function. The great merit of Golani's present work is that it provides a language (and a reinterpretation of homology) in which these issues can be explored without the preconceptions of earlier ethologists.

Animal motility: Gestalt or piecemeal assembly?

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To put it simply, Golani wants us to avoid prematurely defining complex behavior patterns by their functions and instead to describe them objectively in detail and thus detect their composite nature. In this he is not alone. As one example among many, I can quote from my own book (Leyhausen 1979) that Golani cites (but does not seem to have read): "It is the duty of the observer to describe, without abbreviation, categorization, comparison and the like, only what he actually sees happening, and *as if he were seeing the process for the first time*" (p. 10) and "These . . . are particularly instructive examples of why we should learn to stop naming movements after a function. . . . Especially when investigating the behavior of mammals, this can lead to confusion in many ways" (p. 297).

So far, then, there is complete agreement between Golani and myself. However, I take issue with some of his theoretical remarks, and with the extremes to which he is carried by his enthusiasm for the EW method.

When Golani claims (sect. 1.2) that language plays a major, even decisive, role in forming gestalt perception, it only shows that he is unfamiliar with the literature on gestalt perception and gestalt theory. The processes involved are prelinguistic and subconscious, and all higher animals are endowed with the capacity for them. How well we are then able to express verbally what we perceive is a different matter. But this is a question of semantics, not perception.

"Attention to the changes . . . reveals a morphological continuum that pervades a variety of seemingly unrelated behaviors" (sect. 1, para. 7). Yes – but does a continuum of bricks reveal a relationship between the brick stack and a Gothic cathedral? "The difference in status . . . is manifested in a difference in their range of movement in the vertical plane" (sect. 3.1, para. 2). This is not morphology but pure formalism. In short, I see Golani in danger of counting the notes and their durations but losing the melody. Moreover, such a formalistic procedure may, I fear, lead to just the kind of fallacy that Golani is struggling against: There is no guarantee that a movement sharing its plane and direction with another originates in the same way. Both may share a "common final pathway" but not a common origin.

This is illustrated by the way Golani treats "rolling over" (sect. 3.4.2). First, the term does not bear any functional significance but is merely descriptive of what happens. If Golani had read my detailed description, he would also have noted that the movement is *not* identical to the defensive tumble he cites from Havkin and Fentress (1985). "Rolling" starts with rubbing the chin and cheek along the ground and then gradually rolling over onto the back and the opposite side. "Tumbling" goes over the shoulder, with the head being kept off the ground unless it is pressed down by the adversary. Thus, what is important is not

that "the terms used to represent the movement obscure the fact that it takes place in the vertical dimension," but that the preoccupation with spatial formalism prevents Golani from seeing that the significant element in rolling over is torsion along the longitudinal axis, whereas in tumbling such torsion is absent.

Likewise, when Golani attempts to reduce to a common basis of horizontal rotation the "circling" movement as produced in pharmacological experiments (or by the kitten chasing its own tail) and the "search automatism" of a pup for its mother's teats, he misses the essential fact that circling persists in one direction only whereas the all-important feature of the searching movement is not the sideways swing of the head as such but its rhythmic change of direction.

I certainly share Golani's aim to describe movements more objectively. The EW notation may help one do so. But its danger is that it could lead into a formalism that takes similar elements in a notational system as a revelation of intrinsic behavioral organization. And what we are really after is how movements are organized or programmed. The EW notation could tell us nothing about this. "Common" language could, as long as we remember that language, when properly mastered, is a precision tool of the highest grade. That our educational systems no longer teach children how to hone it to perfection may yet prove the greatest loss science has suffered over the last century.

Somewhere in time – temporal factors in vertebrate movement analysis

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The Eshkol-Wachman (EW) method of movement analysis is a considerable improvement on previous measures of sequential behaviors. However, an important feature has been left out of this analysis, perhaps in part because Golani considers language to be the primary organizational "gestalt" in determining an informational system of description. A gestalt, however, implies that things are very close to each other in time or space in order to be perceived as a unit, with a sentence or a melody as examples. This does not include patterns in behavior that are not closely related in time, yet these may be of great importance. Golani has mentioned the possible importance of similar behaviors performed in "other seemingly unrelated contexts." This suggests that there may be expressions of behavior that occur at times when their function is not obvious, but it does not seriously consider the possible direct relationships between these recurrences separated in time.

This might be simply a matter of choice in subject matter, but in examining the serial order of behavior under amphetamine or apomorphine, Golani appears to misinterpret the earlier theoretical analysis by Lyon and Robbins (1975). The implication that those authors considered it "impossible" to explain why certain responses dominated the drugged animal's behavior at any given point in time is not correct, because the major point of that article was to indicate that the behaviors chosen depended on the time they required for completion. If a behavior cannot be completed, it will not serve its usual function. This indicates the importance of the time period in behavioral performance. Examples of incomplete behaviors under stimulant drug treatment in animals have been found in sexual behavior (Hard & Larsson 1970), aggressive behavior (Schmidt 1983), and maternal behavior (Wegener 1986).

Thus, the Lyon-Robbins analysis points out that time plays a most important function in the choice of behavioral responses.

Behaviors are seen as subdivided into functional acts, each taking a certain amount of time. As the time for each act is gradually removed by stimulant drug effect, behaviors will change and even seem to disappear. In fact, they may simply be occurring more rapidly. Eventually, a rapid behavior becomes nonfunctional. The EW method is quite exact in its description of particular joint movements reaching measurable angular points, but having an exact description of behavior does not remove the problem of deciding when the behavior is complete (i.e., functional in its normal manner). To do this, it will also be necessary to have a completely automatic system for recording and scoring movements in order to avoid judgmental error on the part of a human observer. This is not a minor point; rescoring of video tapes after a few months, even by the same individual, will rapidly provide examples.

The importance of the time variable in measuring behavior cannot be overestimated. For example, in analyzing the effects of amphetamine and apomorphine on behavior, Golani and others (Geyer et al. 1987) have suggested that these two drugs produce behaviors with a major qualitative difference between them. Apomorphine acts much more quickly upon dopaminergic systems than amphetamine does, however; the initial stimulation of incipient vertical movements, for example, may be missed under apomorphine because it occurs so rapidly that it may be overlooked. It is not surprising that Paulus and Geyer (1991) found it necessary to introduce a combined temporal and spatial scaling algorithm to assess such problems. This is only one example of the type of problem that occurs when behavior is telescoped in time.

Such problems cannot be addressed properly by the EW system alone. Yet, if used in combination with a time analysis method, the EW system could be extremely powerful. One such time-related system uses temporal configurations in the analysis of behavior (THEME), as developed by Magnusson (1988; 1989). This method, which has already been used in experiments with both animal and human behavior (Lyon & Magnusson 1982; Montagner et al. 1990), is capable of finding relationship between behaviors even when they do *not* occur in sequence. For example, in a two-choice task in which human subjects could press one of two buttons for a randomized reward sequence, the latencies for each button choice and its reinforcing function were recorded by a computer (Lyon & Lyon 1990). Using the THEME method, response events occurring with a fixed temporal relationship to each other, *regardless of whether they were sequential*, formed temporal configurations that, individually, were highly significant patterns of behavior ($p <$ 0.0001). It is of interest that the number of these temporal configurations and their variety were both increased in schizophrenic patients compared to normal control subjects. These unusual findings are consistent with predictions of increased switching and stereotypy in behavior (see Robbins et al. 1990). Many of these event relationships would not be found with EW analysis no matter how exactly the movements were measured. The analysis of such temporal configurations does not yet form a language, nor do we yet know the function of some of them, but this simply indicates the power of the Magnusson THEME method in opening new areas of explanation. In general, the EW method will not realize its full value until it is able to free itself entirely from the language-suggestive assumptions taken from ethology. As Golani surely agrees, these assumptions have long hampered efforts to be objective about behavior, particularly as behavior assumes yet unknown forms and configurations.

In conclusion, the EW method should be combined with some form of temporal analysis and such a system should be based entirely on an automatic, nonhuman-observer type of movement description.

Joint torque precedes the kinematic end result

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The two central theses of Golani's target article are probably unassailable. Ordinary language is indeed the frequent bane of scientific clarity: The Wittgenstein quotation (sect. 4.1, para. 2) should be seen more often. Movement configurations in particular are awkward to render semantically. Second, the existence of a mobility gradient in vertebrates makes a lot of phylogenetic and ontogenetic sense. I doubt, however, that the EW notational system does an adequate job of movement classification. When motor dynamics are stripped from the body leaving a skin of static kinematic snap-shots. the way is clear for ambiguity and dubious homologies. Granted that Golani's argument for simplification (sect. 4.2) is well taken, the fundamental output of a motor is still torque, whether it is applied to a horse's hip or a racing car axle. The call to attend to the base of support and relative trunk orientation from which distal movements arise was certainly heading in the right direction, but it did not go quite far enough. As a result, some possibly erroneous comparisons were made.

In normal forward progression, the nonforward torques generated at the hips must be counterbalanced at the shoulders. Otherwise, circling or zig-zag lurching will occur in the lateral direction. In other words, forward progression is made up of balanced couples of the same elements used for lateral progression. A higher order of organization and regularity is imposed on the lateral elements in order to generate a resultant force in the forward direction. Forward stretching, although it was used in Figure 10 to illustrate forward progression in general, is really very different. Because of the bilateral symmetry expressed at the pelvic and shoulder girdles, considerable torque is generated in the sagittal plane. Surely this is an early stage of "vertical" movement. With the idea of the mobility gradient I agree completely, but I am not completely satisfied with the detailed account of it.

The reticular core of the CNS from the brainstem through to the intermediate zone of the spinal cord would be the most likely substrate for the mobility gradient. Basic forward locomotion in most vertebrates requires only the spinal cord (Grillner & Wallén 1985). To my knowledge, however, no spinal animal has been observed to gallop (vertical oscillation of the vertebral column), although this can occur in high decerebrate preparations (intact midbrain) with sufficient stimulation of the mesencephalic locomotory center (Shik & Orlovsky 1976). Thus, vertical progression may require a still higher order of organization imposing bilateral symmetry on spinal step pattern generators. In this view, the three modes of progression are a nested series of neuronal networks.

Although the analogy may be spurious, horizontal and vertical saccade generating networks are well separated in the brainstem (Sparks & Mays 1990). Horizontal eye movement circuitry is localized in the paramedian pontine reticular formation in the vicinity of the abducens nuclei, whereas the equivalent area for vertical movement is situated more rostrally in the midbrain (interstitial nucleus of Cajal, etc.). Since eye movements generally lead head or limb movements and are correlated to them (Biguer et al. 1982), this segregation could have general significance in the control of modes of progression.

I am not convinced that systemic drug application is of much value in analyzing the mobility gradient. What is essentially an anatomo-physiological issue is unlikely to be aided by compounding it with pharmacological problems. Receptors, after all, are not neatly segregated within functional networks. Moreover, the functional divisions of the basal ganglia maintain the

order already established elsewhere in the motor system. Neglected as it may be, the reticular core of the brain, not the more fashionable basal ganglia, should be duly recognized as the primary basis of the mobility gradient.

It should be noted that the mode of progression has less to do with bilateral symmetry or gravity (sect. 3.11, para. 5) than with the mechanical constraints of the substrate or body. Caterpillars that have to traverse narrow petioles and are more primitive than fish necessarily use vertical bending of the longitudinal axis. An aqueous medium allows bending in any direction but the body structure has to be suitably adapted to use the horizontal or sagittal plane efficiently. Most fish are flattened sagittally to allow for lateral undulations but skates and rays are flattened horizontally for dwelling on the seabed. They accordingly exploit vertical undulations. One wonders whether the development of the primordial red nucleus in the midbrain of elasmobranchs (Schnitzlein & Faucette 1969) is not related to the potential for this new mode of progression. It is strikingly close to the center for vertical eye movements.

Ultimately, any symbolic representation of reality can lead us astray by its own inherent conventions, but in terms of Golani's carpet weaving metaphor (sect. 3.6.1, para. 3), joint torque is more closely related to the "procedure" of generating movement than is the "pictorial end result" of trunk orientation angle. A notational scheme representing net torques between supporting limbs and the vertebral column would, I believe, be the best means of classifying modes of progression.

Time-based objective coding and human nonverbal behavior

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Golani's target article outlines a methodological approach and uses it to derive theoretical hypotheses concerning vertebrate behavior. Research on human nonverbal displays shows that many of his methods are relevant to the study of Homo sapiens. In human applications of time-based objective coding, however, it is necessary to qualify some of the hypotheses Golani derives from his research on other mammals. At least five of the principal methodological concepts in Golani's target article are important for understanding human social interactions:

Objective coding of nonverbal behavior. In place of holistic categories described in natural language, Golani suggests a need to define objectively the dimensions of bodily movement and to record behavior in terms of the combination of movements along these dimensions. The "Bernese" system for coding human bodily postures on 51 dimensions demonstrates that such a method is both feasible and fruitful in describing and analyzing human behavior (Frey et al. 1981; 1983; Hirsbrunner et al. 1981). Even where holistic categories are to be identified, their definition can best be achieved with reference to a set of objective dimensions (Ekman & Oster 1979; Masters 1989, Ch. 2; Masters et al. 1986; van Hooff 1969).

Time based recording of dynamic sequences. Too often behavioral categories and coding systems are static (e.g., Ekman et al. 1972). Although such approaches are often useful, in nature behavior is dynamic. To capture and analyze temporal features of which we are often not conscious, time-based recording is essential. Descriptive coding of human behavior sequences in the temporal dimension often reveals features that have escaped previous investigators, whether concerning levels and trends in a specific postural dimension like the upward sagittal movement of the head (e.g., Frey & Bente 1989: Figures 2a–b), dyadic interactions that could not be deduced from individual behavior

(e.g., Fisch et al. 1983), or rhythmic patterns in behavior (e.g., Bente et al. 1989; Frey & Bente 1989: Figures 3 & 5). Similarly, studies of emotion often fail to measure episodic responses in real time, even though this is the only way to relate the physiological substrate to cognitively experienced feelings (McHugo et al. 1985; McHugo et al. 1991).

Interpreting bodily movements as social cues. Some analysts of human nonverbal behavior focus too exclusively on the *expressive* element of nonverbal displays (cf. Izard 1978). Although facial or bodily movement is a valuable indicator of an individual's motivational state, such cues often originate in patterns of social interaction that cannot be reduced to properties of the isolated individual. In some cases, the response of one partner to a social interaction depends on the structure of the situation and the expectation of the dyad (e.g., Fisch et al. 1983). To take a striking example of context dependence, a given videotape of a known political leader has different evocative properties depending on that leader's status at the time the excerpt is seen (Masters & Carlotti 1988; Sullivan & Masters, in press).

Assessing behavioral aspects of drug action. It is often useful to study the effects of specific drugs on the dynamics of nonverbal display behavior in humans. For example, subclinical doses of a widely prescribed medication like Haloperidol have characteristic effects on body movement that do not relate primarily to single parts of the body but rather to higher levels of the integration of body movement (Frey et al. 1987).

Analyzing use of the behavioral repertoire as a sign of social dominance. Although many ethologists have associated specific displays with dominant or inferior status (van Hooff 1969; Masters et al. 1986; 1987), social status may be signalled by the variety of the behavioral repertoire that an individual uses. Preliminary data from a study of the nonverbal display behavior of American, French, and German leaders (Bente & Frey 1990; Frey & Bente 1989; Masters et al. 1991) show that those with high status, like presidents, prime ministers, or cabinet officers, tend to use more of the postural repertoire than lower status leaders. Such individual differences in behavioral performance can be very important in communicative situations, translating into political effectiveness and electoral success (Lanzetta et al. 1985; Sullivan & Masters 1988).

As the foregoing indicates, Golani's methods deserve attention by human ethologists and psychologists as well as by students of animal behavior more generally. Indeed, the need to look at the dimensions underlying human nonverbal behavior is enhanced by the tendency of cultures to attribute cue-value to a specific constellation of body movements, making it likely that the informed observer will try to explain unusual displays by means of holistic categories (e.g., Wylie 1977).

Despite the importance of these methodological proposals, caution is needed with regard to Golani's theoretical hypothesis. A specific dimension of nonverbal behavior, such as the "mobility gradient," is ritualized in different ways from one culture to another. What matters is often the contrast between displays, governed by Darwin's "principle of antithesis" (Darwin 1872), rather than cues defined abstractly. Movements that in other species follow rather rigid sequences may differ in organization or pattern depending on culture or even on individual performance style. Although we do not yet know much about national differences in the way the nonverbal repertoire is used, preliminary data indicate that such differences exist – and that they are highly significant in social behavior (Warnecke 1991).

Without the type of time-based objective coding suggested by Golani, some of these features of cultural behavior will be impossible to analyze. Humans vary in their ritualization and use of the postural repertoires of our primate heritage. Aggressive cues exhibited by French leaders elicit positive emotions for French viewers, whereas similar displays performed by American leaders produce negative emotions for American viewers (Masters & Sullivan 1989).

Whereas some cultures use the horizontal shaking of the head to signal an affirmative answer and most Western cultures ritualize the motion to mean the negative, care is needed in extrapolating the meaning of the underlying dimensions of human body movement. When two national leaders like Reagan and Quaddafi exhibit characteristic differences in the dynamics of the upward sagittal movement (Frey & Bente 1989, Figures 2a–b), it is not clear whether the effect is due to differences in cultural expectation, individual performance, or relative dominance. As Golani himself would doubtless agree, the methods described in his target article need to be embedded in a broader framework in order to explain fully the complexity of human nonverbal communication.

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Human observation and human action

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Golani's analysis of animal behavior needs to be considered in terms of recent developments in the understanding of human motor organization. His recommendation of the Eshkol-Wachman (EW) movement notation as an alternative to observational coding schemes can be strongly seconded on the basis of studies of human behavior perception.

The problem of action analysis is much like that of analyzing the acoustic signal underlying speech. The difficulty is to find an analytic system capable of recording behavior with sufficient completeness, while not wasting effort to record the large number of possibly irrelevant dimensions. EW is such a system because it is productive or generative, not merely descriptive. If one accepts the linguistic dictum that a system that can comprehend a language can also speak it, then the system seems to contain, however indirectly, the important bases of action structure.

The EW system is quite objective. The kinds of stick-figure representations it uses have proved sufficient for a wide range of biomechanical analyses. And, as Golani and his colleagues have demonstrated, it is highly flexible, adaptable to many different species.

Human actions consist of the composition and cycling of what have been called "coordinative structures": configurations of body components organized according to the task at hand (Hollerbach 1981; Kelso & Clark 1982). Salzman and Kelso (1987) call these "special purpose devices" that, in humans at least, may be flexibly composed according to the task environment. If two people are playing catch, for example, each may alternate between a "throwing" configuration and a "catching" configuration. The transition between the two will be marked by a reorganization of body components.

Schoner & Kelso (1988) have shown that such structures interact with environmental constraints so as to produce self-organizing, stable dynamical systems. The structure and identity of the action is thus present only in the dynamic interaction of the organism and its environment. One interpretation of Golani's mobility gradient is that he is detailing sets of coordinative structures that determine the set of interactive products – the range of actions – in particular animal species. One consequence of this view is a considerably different approach to the problem of action regulation. The importance of locating the trunk of the animal in relation to the base of support in

Golani's analyses follows from this basic fact of action organization.

As my students and I have adapted the EW system for action perception research, tracings of body position are made at successive half-second or one-second intervals from images frozen on a video monitor. Coders then overlay successive tracings and make same-different judgments for the angle of each coding feature relative to its pivot joint. The result is a vector of 17 zeroes and ones, each indicating the status of the limb over the successive time interval. Vectors may be summed, yielding an overall index of position change, or analyzed for the structural interdependence of particular sets of body features over time. It is important to recognize that the notation system, even in this simplified form, can discriminate between 131,072 (i.e., 2^{17}) different positions of the human body. The best categorical coding schemes for human behavior can discriminate about 30 different classes of action. Thus the number of patterns that can be analyzed for and detected by this system offers an enormous advantage over categorical schemes. Factor analyses of the vectors of position change coded in this manner have consistently yielded 4–6 clear-cut factors in human behavior. Factor composition varies according to sequence content, each corresponding to a recognizable coordinative structure (Newtson et al. 1977; 1987). No generalized "human movement structure" exists.

Dynamic analyses are also greatly facilitated by this approach. Such analyses require dynamic variables, that is, variables that are continuously present, even if zero. Analyses of the summed index of position change have produced clear-cut results in human behavior, as well. Measurements show clear spikes of high-magnitude position change at transitions between coordinative structures. Human observers discriminate action unit boundaries in the behavior stream at precisely these reorganizational spikes (Newtson et al. 1977; 1987). If actions are understood as dynamical systems, the powerful formalisms of that approach can be applied directly to behavior analysis (Newtson 1992). Human behavior, for example, has been found to have a fractal dimensionality of 1.82. The degree of change registered by these analytic procedures thus depends upon the temporal density or precision of measurement. Optimal precision for detecting action patterning may thus be far less than for movement regulation in relation to microlevel neurological mechanisms.

In addition, when viewed as a succession of dynamical systems, action sequences may be understood to display, as an objective property, a flow of information arising from the expansion and contraction of the phase spaces of their component movement systems. Golani's notion of the expansion and contraction of behavior along a mobility gradient could be understood this way. Examining position change gradients in human behavior over time has shown that these fluctuations are cyclic; behavior contains waves of information flow with stable, identifiable spectral components. Such waves are coupled in human interaction at stable phase relations and are intimately involved in the organization and regulation of social interaction.

Finally, the limitations of verbal descriptions of behavior that Golani notes may be seen to follow from the fact that behavior is not a categorical, discrete phenomenon. It has been shown that the sample of action unit boundaries that human observers discriminate contains the objective information sufficient to reconstruct the wave properties of the observed behavior (Newtson et al. 1987). Classification of actions at the cognitive level is an additional mental act; the basic process of action perception is rather more like that detailed by Skarda and Freeman (1987) for smells (cf. Newtson 1990).

The yin and yang of behavioral analysis

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As pointed out in the target article, the apparent complexity of a structural analysis of behavioral organization has steered researchers away, shifting the focus to the analysis of behavior in terms of its consequences. Such endpoint analysis can be useful, but it can also lead the researcher into false hypotheses about evolution or neural control. For example, Johnsgard (1965) identified circling of the female by the male as an important behavioral element in the courtship of the Cape Barren goose (*Cereopsis novaehollandiae*). The presence or absence of circling by the male was then used to make inferences about the phylogeny of courtship. Analysis of Cape Barren goose courtship sequences using the Eshkol-Wachman movement notation (EW) revealed that circling by the male was a product of the combined movements of both female and male, and hence not an isolated behavioral feature of courting males (Pellis 1982). This differs from the case of species where the male walks around a stationary female (Pellis 1989). The functional label of "circling" draws our attention to the circular path of the moving male and can be misleading if viewed independently of the angular relationship with the female. EW forces us to view the structure of the behavior simultaneously juxtaposed against its functional consequences. This, in my view, is the main methodological strength of using this system.

This differs from the philosophical stance taken in the target article where structural and functional analyses are held as complementary but separate endeavors. Using EW, Golani presents a geometric analysis of the relationship of the trunk to the base of support in a variety of social and nonsocial behaviors. These analyses reveal a mobility gradient that appears to be an underlying organizational principle of vertebrate movement. The abstraction here is that the geometric analysis assumes the underlying form of behavior to be due to intrinsic properties of organization. Such an assumption can be as misleading as the implicit assumption of functionalist labelling. Some of Golani's own examples reveal the difficulties.

In Figure 9, it is shown that the inferior honey badger can only pivot on its hindlegs whereas the superior can pivot on either fore- or hindlegs. This is regarded as evidence for the constriction of movement of the inferior compared to the more expanded range of movement for the superior animal. However, the inferior bites the superior on the cheek, whereas superior bites the inferior on the rump. Therefore, even though the movements of the animals were recorded in what appeared to be a similar context (i.e., when they opposed each others' hindquarters with their snouts), the stimulus situations faced by each partner are not the same. If the functional context in which the behaviors occur are not the same, then it is not possible to attribute the differences between animals to differences in the intrinsic structure of the behavior (Pellis & Pellis 1991).

Another problem can be seen in the example of motor expansion of movement in an open space by brain-damaged rats. The "warm-up" phenomenon was first uncovered in the gradual onset of locomotion in adult rats following electrolytic lesions of the lateral hypothalamus (Golani et al. 1979). During recovery, the rat first moves its head and body laterally, then forward, and finally, vertically. However, a rat that cannot as yet scan forward or upward in an "exploratory fashion" can do so when it performs a "stretch-yawn," — the forelegs step forward as the head, neck, and torso are stretched forward and the head and neck are raised upward. Therefore, movements (both forward and vertical) that do not occur during exploratory locomotion are present in stretch-yawns. The motor expansion present in the "warm-up" phenomenon only applies to the locomotory exploration evident after a period of immobility. The warm-up phenomenon, as explicated in the target article, pertains to movements in a specific context: exploratory locomotion (Golani et al. 1979), a term with clear functional connotations. So even though the target article makes detailed structural analysis of behavior its main focus, this is only possible because behavior is "chunked" into functionally organized groupings, such as locomotor and comfort behaviors.

Although structuralism and functionalism are sometimes cast as contrasts, as has been done in the target article, I believe this to be a mistake. As pointed out by Dwyer (1984), the choice of perspective relates to the types of constraints operating on the object of inquiry: "Where none or few of the constraints on form are intrinsic, functionalist analysis, which holds object separate from environment, may contribute much to an understanding of form. Where some or many of the constraints on form are intrinsic, a structural analysis may contribute much to an understanding of form" (p. 746). At the beginning of an analysis of a complex behavior, the problem is to disentangle intrinsic from extrinsic constraints (e.g., Whishaw & Pellis 1990; Whishaw et al. 1991). If most of the constraints are intrinsic, then the kind of structural analyses conducted by Golani are appropriate. Indeed, many of his examples reveal patterns of behavioral organization hitherto missed by conventional approaches. Nonetheless, the predominant role of intrinsic constraints needs to be empirically determined, not assumed a priori. EW, with its multiple frames of reference, allows the same behavior to be scored in relation to either the animal's own body, gravity, or a partner and it is ideally suited for identifying intrinsic and extrinsic constraints. The structure and function of behavior are best viewed within the complementarity of the Taoist concept of yin and yang, where each contains an element of the other, and neither exists in the absence of the other. Our aim should be to develop methodologies that can make the relationship between the structure and the function of behavior explicit and amenable to objective analysis. In this endeavor, EW can be an important tool – I would also add that this very methodology reveals the unity of structure and function.

Testing for controlled variables

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I was surprised to see my work cited in this ethological article on the description of movements in animals; it was even more surprising to see my version of control theory used correctly and with relevant and accurate insight in a field far from my own.

Golani, starting in the Epilogue, voices exactly the recommendation that was taking form in my mind as I read through the preceding material. In attempts to systematize observations of animal behavior, ethologists and animal behaviorists have quite naturally focused on those aspects of behavior that seemed salient to them. They have attempted to find regularities in the motor actions of animals – with some, but limited, success.

Golani has seen correctly that control theory offers a different basis for systematization. In ordinary language, he is suggesting that a purpose of the behavioral acts may prove to be more invariant than the means employed by animals to achieve the purpose. In the language of control theory, a purpose is simply an internally specified reference state that is visible in behavior as a repeatable accomplishment brought about by variable acts. Such "repeatable accomplishments" are, as Golani recognizes, controlled variables. A theoretical model is needed to show how a system must be organized to exert dynamically stable control over external variables, but the observable manifestations of control are not theoretical.

Controlled variables can be roughly identified simply on the basis that they show less random variation than other variables affected by behavioral movements and acts. There is, however, a more objective and specific way of testing variables to see whether they are under control. Applying disturbing influences (not so large as to prevent successful behavior) directly to the proposed controlled variable should, if the variable is actually under control, elicit alterations of the detailed behavioral acts of exactly the kind, direction, and magnitude required to oppose the effects of the disturbance.

If it is hypothesized, for example, that lateral foot placement is involved in controlling lateral body position (i.e., that body position is a controlled variable and variations in foot placement are among the means of controlling it), then by applying mild sideward forces to the body one can test this hypothesis. If it is correct, the feet should move in such a direction as to result in a quantitatively equal and opposite lateral force (perhaps because of gravity acting on the body mass above the displaced support), with the body remaining relatively undisturbed. The only precaution is that any applied forces must remain within the animal's normal capacity to resist them – they should be just large enough (and be applied and removed slowly enough) to allow successful opposition by the animal if it is going to occur.

Note that without the concept of control in the background, the movement of the feet during the application of the lateral force would appear to be simply a response to a stimulus, and the actual controlled variable would remain unsuspected. Slight variations in leverages or initial positions might create variations in the effectiveness of the "responses," so it would seem that the responses were variable. In terms of their effect on the controlled variable, however, they would not be variable at all.

This is a straightforward test based on the definition of control; it can be applied by the experimenter or the experimenter can record the occurrence of natural disturbances and look for expected effects from them that are counteracted by limb forces, changes in posture, and so on. The expected effects that are diminished or prevented by the behavioral acts are the controlled variables – or are at least closely related to the variables actually under control. This method may thus be amenable to use in the field as well as the laboratory.

Golani cites Hinde (1966) as saying that "variations in posture and relative positions of the interacting animals . . . may lead to a hopelessly confusing mass of detail, and divert attention from the essentials of the problem." If "relationship" is indeed an intrinsic part of two-animal behavior, it would probably be fruitful to consider various aspects of the relationships as controlled variables relative to one or both animals. A mass of detailed movements can be understood if they prove to be required to oppose observable disturbances of an identifiable controlled variable.

From psychopharmacology to neuropsychopharmacology: Adapting behavioral terminology to neural events

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Since the early 1960s the behavioral changes induced by dopamine agonists in animals have become a "growth industry" in the literature on dopamine function. Legions of investigators have studied the ways in which rats, the subjects of choice for this line of research, respond to drugs that alter dopamine transmission. The reason for this effort arises from the presumed importance of dopamine in a variety of neurological and psychi-

atric conditions. In fact, the behavioral response to dopamine agonists in rats often serves as a model of paranoid psychosis and thus as a screen for testing new antipsychotic drugs. It is also used to shed light on dopaminergic function in the central nervous system. Precise behavioral characterizations are therefore crucial, yet precision is often lacking in the terminology typically used to describe the behavioral effects of dopamine agonists. Consider the behavioral response of rats to amphetamine, described briefly in Golani's target article. This drug elicits dose- and time-dependent changes in a wide range of movements, many of which become increasingly repetitive and invariant (i.e., stereotyped). In the literature, however, the amphetamine-induced behavioral response is often reported as an increase in locomotion or stereotypy, where stereotypy is treated not as a description of behavior but as a behavior itself. Moreover, locomotion and stereotypy are often viewed as two incompatible responses, even though amphetamine-induced locomotion itself is stereotyped. The problem involves more than semantics because a lack of precision in behavioral characterization hampers efforts to assess underlying neural mechanisms.

For many years, drug-induced changes in neural function were studied independently of behavior. Animals were anesthetized or decapitated, and measurements were obtained from brains that were probed with electrodes or processed for biochemical analysis. Such studies were very useful in explaining how drugs altered specific neural circuits but very limited in explaining drug-induced behavioral effects. The neural substrates of these effects were largely inferred from lesion studies. Recent technological advances, however, now make it possible to relate ongoing neuronal events directly to behavior. Microdialysis, in vivo voltammetry, and single-unit electrophysiology, for example, allow precise neurochemical and neurophysiological changes to be monitored in awake, behaving animals (Rebec 1991). Thus, as psychopharmacologists begin to use the tools of neurobiology (and become neuropsychopharmacologists in the process), they must also develop correspondingly precise descriptions of behavior.

A useful feature of Golani's mobility gradient is that it focuses on relatively simple elements of behavior that can be related directly to neuronal events. The rules that Golani applies to behavioral organization and to movement of specific body parts can help guide the search for the neurophysiological variables that control dopamine-mediated behavior. In fact, this point was stressed in a previous discussion of Golani's use of the Eshkol-Wachman movement notation to characterize the behavioral response to dopamine agonists (Rebec & Bashore 1984). In the target article that forms the basis for this commentary, Golani not only describes the Eshkol-Wachman analysis but he also speculates on its potential application for the study of dopaminergic functions in the striatum. The neural substrates of the drug-induced behavioral responses that Golani describes, however, are considerably more complex than his account suggests.

In the striatum of the rat, which receives a rich supply of dopaminergic input, a clear majority of neurons (70%–90%) appears to change firing rate in temporal association with movement (Gardiner et al. 1988; Haracz et al. 1989; in press; West et al. 1987; 1990). The neuronal response typically consists of bursts of activity coinciding with characteristic movements (e.g., head turning and forward locomotion), although some cells respond with a tonic activation that begins several seconds before movement onset and continues for some time after movement cessation. Perhaps not surprisingly, neurons excited during movement also tend to increase their firing rate following amphetamine injection (Haracz et al. 1989; West et al. 1987), and the time-course of the change in neuronal activity roughly parallels the drug-induced behavioral response (Haracz et al., in press; Rebec et al. 1991). These results cannot be explained simply as a secondary effect of a drug-induced behavioral change because efforts to control for the effects of behavioral feedback

clearly suggest a direct action of amphetamine in the striatum (Haracz et al., in press; Rebec, in press; West et al. 1987). In contrast, striatal neurons that fail to change their firing rate during movement are typically suppressed by amphetamine (Haracz et al. 1989), as are some slow-firing striatal output neurons (Ryan et al. 1989). Indeed, the level of basal activity in some striatal cells seems crucial in determining the direction of their response to amphetamine (Rebec, in press; Ryan et al. 1989). Also noteworthy is evidence that high doses of amphetamine, which elicit highly focused stereotyped respond-ing, sometimes reverse the direction of the neuronal response to low doses of the drug, which increase nonfocused behavioral activity (Gardiner et al. 1988).

Collectively, these results emphasize the complexity of the striatum and thus the danger of emphasizing a single underlying process to explain the mechanism of action of amphetamine. Although dopamine undoubtedly contributes to the neuronal effects of this drug in the striatum, dopaminergic mechanisms alone cannot account for amphetamine-induced changes in striatal activity. Not only does amphetamine elicit both in-creases and decreases in striatal firing rates, but haloperidol, a dopamine antagonist, reverses the increases and actually poten-tiates the decreases (Haracz et al., in press; Rebec et al. 1991). Moreover, cortical afferents, which are widely believed to release glutamate, appear to play an important role in the activation of motor-related cells following amphetamine admin-istration (Tschanz et al., in press). Rather than acting indepen-dently on striatal neurons, therefore, dopamine may modulate other neurotransmitter systems (e.g., Chiodo & Berger 1986); thus the action of amphetamine as a dopamine agonist may depend on the level of activity in these other systems (Haracz et al., in press). This hypothesis may also explain the seemingly large number of neuronal inhibitions produced by amphet-amine in the striatum of anesthetized animals (e.g., Rebec 1987). By reducing cortical activation, anesthesia may effec-tively remove a major source of striatal activity, in the process unmasking an inhibitory action of dopamine. It is interesting to note in this regard that a motor-related striatal neuron, which is normally excited by amphetamine, responds to this drug with an inhibition following pretreatment with chloral hydrate anesthe-sia (Rebec et al. 1991). Thus, although Golani concedes the involvement of nondopaminergic systems in the amphetamine behavioral response, he treats them largely as modulators of dopaminergic function. In fact, dopamine may play the true modulatory role; assessing the ways in which this role influences behavior requires further analysis of striatal function in the freely moving preparation.

In summary, Golani highlights a behavioral characterization scheme of fundamental importance for neuropsychopharmacol-ogy. The challenge is to apply this scheme to the acquisition of corresponding neuronal data and to use this combination in the search for the mechanisms by which the striatum and all of its neurochemical systems guide the behavioral response to amphetamine and other dopamine agonists.

Describing behavior: A new label for an old wine?

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The analysis of behavior patterns as discrete, unitary events has a long history, and distinguished scientists have contributed to

its theories and methods. Darwin's concept of "innate gestures" (1872), Heinroth's "Triebhandlung" (1911), Huxley's "ritualized displays" (1914), Lorenz's "Instinkthandlung" (1937), and Tin-bergen's "fixed pattern" (1951) were benchmarks on the way to our understanding of patterned behavior. Golani's "perception of movement through symbolic language" adds a new tool to our repertoire of analytical skills. I see three points in his target article that need further elaboration and clarification: first, the criteria for the selection of the "label" he wants us to attach to a particular behavior pattern; second, the alternatives to "infor-mal verbal description" for describing such a behavior pattern; and third, placing that behavior pattern on the hypothetical "mobility gradient."

From my experience, a good label for a behavior pattern is one that I can remember easily, reminds me of a characteristic formal feature of the behavior, avoids functional connotations, and is not likely to be confused with another label. I prefer a formal feature, because it is obvious that it is only one of many, and I specifically avoid functional connotations in a label be-cause they distract from other functions. For example, I fully agree with Golani (sect. 3.2) that "hip thrust" and "neck-bite" are useful labels, but I cannot see why he deplores the fact that they do not include a functional interpretation and do not direct attention to "the free end of a linkage of moving segments." Why would we gain anything on the level of labelling, and how could one add to the label something to insure that "both labels direct attention to the free end of a linkage of moving segments" without being terribly awkward? There are several other fea-tures of "hip thrusts" and "neck-bites" that both have in common and others that distinguish the two (the position of ears, tails, angle of joints of extremities, etc.). If it is a matter of scientific analysis, I cannot see any a priori criteria to select one feature over another. I can only point to Lorenz's advice to build a broad "inductive basis" (Lorenz 1959; a collection of descriptive ele-ments) and to establish empirically which features occur in different situations, species, functions, and so forth. If it is a matter of finding a label, any word that fits the criteria given at the beginning of this paragraph will do.

I disagree with Golani's statements concerning the role of "informal verbal description" among the possibilities for de-scribing a behavior pattern in general, and especially with respect to his presentation of Lorenz's (1959) use of gestalt perception, namely, that he "did not consider . . . the role that language . . . plays." Lorenz did not cite Whorf in his paper, but he did cite a remark by Metzger: "There are some people who are incurably prevented, by theoretical considerations of cognition, from using their senses for the purpose of scientific understanding." Theoretical considerations of cognition include language. Furthermore, I remember that Lorenz, being fluent in several languages, was from his own experience very much aware of the channeling effect of a word's meaning on one's thinking.

"Ordinary language" has not been the sole form of description in ethology for some time. Looking from different vantage points and describing by new means have become standard procedure. Lorenz himself extensively analyzed on the editing table the egg-rolling behavior of the greylag goose and the courtship displays of ducks from footage he had filmed himself, resulting in numerous tracings on which he based the figures in his papers. This method was already very popular in the fifties and became especially fruitful when it was extended to the analysis of sonagrams (e.g., Finley et al. 1983; Schleidt 1974; 1982). I also wish to mention that the Eshkol-Wachman move-ment notational system is not the first and only alternative to "ordinary language" in ethology (e.g., Schleidt & Crawley 1980; Schleidt et al. 1948).

Finally, to me the concept of Golani's "mobility gradient," from immobility to increasing complexity and unpredictability, implies that we can compare the exact locations of particular

behavior patterns on this continuum. Where do I find "hip thrust" and "neck-bite"?

Sensorimotor reference frames and physiological attractors

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Golani's is, in my opinion, an extremely interesting paper, essentially because of its novel methodological approach. The Eshkol-Wachman notational system (EW) has an obvious justification: A universal equilibrium constraint requires that the vertical of the barycenter of the body at rest meet its supporting base (polygon of sustentation), but in motion this constraint is in general not satisfied. Each time a leg leaves (or reaches) the ground, the base of support undergoes a "catastrophic" area reduction (or expansion); this does not affect the global continuity of movement, however. The (EW) system is well adapted to the case of vertebrate Tetrapoda, but what about flying or swimming animals? I think the basic frame to consider in the problem of modeling animal motion is not a frame attached to the animal body, but a spatial frame (R) drawn from fixed external data. Any animal "knows" that it can move, but it is more important for it to know, at any instant, where it is with respect to its local environment.

Such an external frame (R) given by exterior sense data may be called a "reference frame" (from the French word référentiel introduced by the Swiss epistemologist Ferdinand Gonseth (Gonseth 1970). This localization problem is solved – in a mobile frame associated with the body – by a method akin to the classical "moving frame" method of differential geometry (the instantaneous matrix terms in the right member of the differential system are given by the variation of perceptual and kinesthetic sense data).

This notion of reference frame can sometimes be localized, and there may (in exceptional cases) be conflict between incompatible reference frames. All this means that the EW model has to be generalized if one wishes to consider the case of flying or swimming animals.

The main idea of the target article is of course the "mobility gradient." Let us try to express this mathematically: Let W be the space of all possible kinetic states of the animal body. It is a Euclidean space of finite dimension N, N being the total number of degrees of freedom attached to the skeletal joints. In W there are particular loci of high frequency occurrence. Most of them are highly canalized and are the supports of global motor fields (global sequences of movement such as walking in the case of man). We call these attractors. Now we consider a sequence of highly probable physiological events such as the change: rest-movement (more generally: ground state-excited state). This sequence can be considered in our dynamical model space W as a "natural" sequence of bifurcations that arises when the blocked degrees of freedom of a sequence are successively released. (Algebraically, this means passing from a degenerate singular situation to a less degenerate one, a process known as "unfolding a singularity.") The process may also be reversed, as in warm-up and shut-down sequences, in Golani's terminology (sect. 3.6.1). His description of such a warm-up sequence brings to mind an analogy with the well known "march to chaos" described in the Ruelle-Takens theory of weak turbulence (Newhouse et al. 1978), where chaos is homologous to the "hypermobile" end of Golani's sequence (sect. 3.8). This model has the great merit of drawing attention to the problem of describing the ontogeny of motion in embryos, a subject about which very little is known despite its obvious interest. As the embryo's body is formed by the successive branchings of a clone of cells (associated perhaps

with cellular differentiation), one can by analogy expect animal physiology to be shaped by a sequence of temporal ramifications of a tree of "functions." (It should not be thought that a physiological function cannot exist in this set of ramifying trees until its corresponding organs are organically formed in the embryo: The "totipotent" character of blastula cells seems to show that the full tree of physiological functions already exists at that stage, albeit on a "virtual, purely metabolic, support" that is realized as a chain of organs only much later.) Just as a homeobox in a gene may create a local translation of a segment of a metameric animal in the cephalic direction, so the impact of a neurotropic drug may enhance or inhibit a natural "warm-up" sequence at one or many points of the physiological branch of the tree (cf. in this respect Waddington's old epigenetic landscape model [1939]).

Golani's ideas are likely to be confronted with some contradictory experimental facts, but because of the great degree to which they expand the horizon of biology, this should not lead us to reject them. In the search for a "natural sequence of bifurcations" one meets with a difficulty in that this concept is not well defined mathematically outside the (too restrictive) theory of gradients. So for each particular case, the scientist must indulge in the same kind of guesswork as that resorted to by physicists like Bohr, Schrödinger, and Heisenberg, when they were confronted with atomic spectra in the period 1920–1925. Moreover, we should be aware that the importance of the internal geometrical structure of an attractor might be minor in comparison with its biological importance. The perfect periodical character of a rhythm, the paradigm of normality for the cardiac and respiratory functions, becomes highly pathological for neuronal activities in the case of epileptic seizures, or for the locked perseveration cycles induced by neurotropic drugs. Hence, to understand the statement that the meaning of a physiological attractor is its shape we have to add to its internal shape the position of the attractor in the global space W of activities (a space of very high dimensionality, hence practically unknown). Fortunately, in the study of animal motion, the shape is immediately observable. Note that in his theorizing, Golani (without making it explicit) draws heavily on facts that are essentially mathematical, arising, as they do, from mechanical constraints. Yet no equations are written or solved, only plain ordinary language is used. This does not render Golani's account less convincing, although the use of mathematics is only qualitative here. I hope this work will serve as an example. In its methodological aspect, the importance of Golani's article can hardly be overrated.

I end with a final remark. It has often been stated that "hominization" of primates occurred through a *neoteny* process, a return to an ontogenetically primitive state. This fits astonishingly well with Golani's statement that the rear part of the support base (the hind legs) precedes the forelegs in his sequence. It seems that bipedality in man occurred through a restriction of the hind legs to their basic supporting function, the front legs enjoying full freedom of development and of hand and finger activity.

Birdsong: Variations that follow rules

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Ilan Golani's target article makes an excellent contribution to both the theory of vertebrate movement and the list of methods that allow us to analyze movement in depth. His mobility gradient concept will help recognize behavioral details that may

not be considered otherwise. In particular, the gradient provides an outstanding model for neuroethological research.

It is clear that Golani's mobility gradient of movement covers only a certain sector of vertebrate behavior. We want to emphasize this because we anticipate disagreement from ethologists who work basically on the sort of movement that Golani has described as "complex" and "unpredictable." Our suggestion on this matter is: Extend the search for rules and make the complex behaviors predictable. We have two pertinent points to make here.

First, in dealing with unpredictable occurrences of particular behaviors, we have had good experiences using the "differentiating analysis of systems" (DAS; Todt & Hultsch 1980; Todt & Wolffgramm 1975; Todt et al. 1991). The core idea of this approach is that after assessing the basic rules, one systematically investigates *deviations* from them by examining factors covarying with the occurrence of the "exceptions" instead of eliminating them on statistical grounds (Todt 1986). Second, the Eshkol-Wachman notation is quite advanced in the space domain of movement. We feel that it may profit, however, from a more differentiated representation of the time domain (Posner 1978). An appropriate instrument is a multichannel approach in combination with time series analysis (Todt 1975; 1988; Todt & Fiebelkorn 1979). An example of a phenomenon that has been studied successfully through coordinated use of both methods is the singing behavior of birds (Hultsch 1980; Thimm 1980; Wolffgramm 1980). [See also Baker & Cunningham: "The Biology of Bird-Song Dialects" *BBS* 8(1) 1985 and Johnston "Developmental Explanation and the Ontogeny of Birdsong" *BBS* 11(4) 1988.]

Currently, birdsong is regarded as a model par excellence for behavioral processes that are extremely complex in terms of different process units produced within a relatively short span of time, but which are nevertheless clearly organized in terms of unit combination, temporal segmentation, and hierarchical levels (Hinde 1958; Hultsch & Todt 1982; 1989; Kroodsma & Miller 1982). Findings from birdsong studies prompt a comparison with the results from the movement analyses documented by Ilan Golani. Let us briefly address two topics.

Repertoires and performance rules. Repertoire sizes (measure: different song types, or different types of song elements) vary strikingly among species and skilled songsters such as nightingales (*Luscinia megarhynchos*) compose their singing out of more than 200 song types. Nevertheless, their song performances are not unpredictable but reflect a fascinating system of rules (Hultsch 1991).

Typically, a song takes 4 s and comprises 5 to 15 element types. In all songbird species, element types have their specific sequential position within a song. Since many songs are initiated concurrently by the same type of element while differing in the element types occurring in their middle or terminal parts, the within-song organization follows a "one-to-many" decisional hierarchy (Todt 1968). In other words, there is a "gradient of alternative choices" at this level of singing. Interestingly enough, such a gradient can also be found on a higher level of song organization, namely, at the very beginning of a bout of song. Typically, a bout of songs (which in nightingales may last more than two hours and comprise more than one thousand consecutive songs) begins with a repetition of a specific type of song, whereas high performance versatility is typical later on. To complete the picture: Parallel to the "gradient of alternative choices" a "gradient of increasing vocal intensity" (in terms of performance amplitude, density, and rhythm) can be evidenced on both levels of song organization (Hultsch 1980). And both gradients appear surprisingly similar in character to the mobility gradient described by Golani.

Rules of ontogeny. A comparison of locomotor development with motor development in birdsong is confounded by both the latter's tremendous plasticity and the fact that birdsong on-

togeny involves the production of motor patterns acquired through perceptual learning. As to the former, and from a phenomenological point of view, vocal performances during early stages of vocal ontogeny are of bewildering complexity and get progressively crystallized (i.e., stereotyped) as the bird matures. Hence the ontogenetic realization of increasing behavioral complexity along with the mobility gradient in locomotion seems at first sight to be turned upside down in bird song development.

We would not elaborate on this issue, however, if there were no analogies. "Warm up" in moment to moment behavior could have been involved in what Marler and Peters (1982) described as a "regression" to ontogenetically earlier stages of performance quality during the late plastic song of song sparrows (*Zonotrichia melodia*) and swamp sparrows (*Zonotrichia georgiana*). Hultsch (1989) has shown that a similar phenomenon occurs in the vocal development of young nightingales (*Luscinia megarhynchos*): In a given performance, subjects switch back and forth between longer phases of so-called UPA-vocalizations (unidentified patterns) and IPA-vocalizations (identified patterns, that is, pattern types or their precursors that later constitute the crystallized vocal repertoire). The analysis of pattern performance during phases of IPA-vocalization revealed a number of interesting features bearing on the concept of "warm up."

Finally, concerning Golani's last section (4.2), we would like to emphasize that the problem of "detail versus economy in description" did not play a major role in birdsong analyses. Here, the current state of the art rather includes a detailed investigation of single acoustical parameters and their variation in time (i.e., in parallel with the behavioral process). Such variations are described either by specific parameter gradients (e.g., those trends or oscillations reflecting short-term changes in an internal variable; Hultsch 1980; Todt 1986; Wolffgramm 1980), or by a specific target value (Sollwert), which has to be attained before the process can get continued by another specific behavior (Todt 1988). Specific gradients as well as target values may play a role in the domain of communication as well. Female robinchats (*Cossypha heuglini*), for example, do clearly respond to density variations in their mate's vocalizations, and a particular response (onset of a duet contribution) does occur when the male's singing approximates a distinct rhythm (here: 0.8s; Todt & Hultsch 1980). Referring to findings like these, we would make a strong plea for an intensified examination of behavioral processes that are complex in organization and dynamically variable.

What are voluntary movements made of?

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Neuroscience tradition suggests that the cortex produces the chords of voluntary movements by playing upon subcortical keys. The work of Golani and his coworkers is a significant advance over the modal action patterns of ethologists in providing a description of the notes that those subcortical keys produce. Furthermore, whereas the action pattern analysis stressed individual actions and emphasized species differences, the mobility gradient reveals commonalities among animals and shows that actions can be described as portions of a more fundamental gradient. I would like to suggest that including the contributions of other forebrain areas in addition to the basal ganglia could expand the usefulness of the mobility gradient and enrich our understanding of behavior.

My own work on foraging (Whishaw 1988; Whishaw & Gorny 1991; Whishaw et al. 1990; 1991) has been very much influenced

by both the method and the findings of Golani and his coworkers. I will briefly describe some of this work to show the utility of the mobility gradient and also to mention some extensions of the analysis.

To study foraging, a rat is first placed in a covered "refuge" and then allowed to leave it to travel different distances down an alley in which food pellets of various size are located. Generally, it eats the small food pellets where they are found and carries the larger food pellets to the refuge to eat them. After eating a food pellet, it can leave the refuge to look for another food pellet.

Much of the behavior of the rat in this situation can be described as an expression of portions of the mobility gradient. For example, once a rat has finished eating a piece of food in its home cage it makes small lateral head movements that become successively larger in amplitude and eventually result in the snout traversing the area around its body. The forelimbs and then the hindlimbs are secondarily recruited to expand the area that the snout covers. When the rat reaches the wall of the cage, vertical movements of increasing amplitude appear intermixed with the lateral head movements. At some point the animal arrives at the exit and here it becomes immobile, with its head just protruding through the doorway. If the distance it must go to food is short, it again uses an obvious warm-up sequence of lateral, forward, and vertical head movements followed by slow stepping movements, which bring it to the food. Once it obtains the food, it grasps and swallows pieces of food that can be eaten quickly. If the food takes longer to eat, it moves laterally away from the food and the distance it moves is proportional to the time it will take to eat the food. If it will take a long time to eat the food, the turn will be expanded to a run back to the refuge.

These sequences of behavior can be seen as expansion and contraction along the mobility gradient. That is, weight is transferred to the hindlimbs when the rat sits back to eat, and weight is transferred to the forelimbs as the rat finishes eating and starts to forage again. The movements also seem to follow mobility gradient rules. For example, after eating a food pellet the scanning movements are lateral (movements must be lateral, then forward, then up), they involve first the head and then the trunk (a part of the body does not move until a part anterior to it has moved), and they cover a larger and larger area (there is a gradual increase in amplitude in successive movements). In addition, the duration of this scanning fragment of warmup is related directly to the time just spent immobile and eating.

Whereas Golani has emphasized the central role of postural support in his target article, we feel that complete behavioral descriptions must include other sensory systems, environmental context, and even cognitive processes. Only by analyzing behavior within other frames of reference can a complete description be obtained. For example, when the rat stops at the exit before leaving, it is obviously transferring control of its movements from the olfactory tactile cues of the floor and walls of its cage to the visual and auditory cues of the external environment. When it has to travel a long distance, the initial cautious movements of warm-up are attenuated in favor of brisk forward locomotion, a response that obviously depends upon the rat's cognitive appreciation of the distance to food and the adaptive significance of getting there and back as quickly as possible. In a sense, when the rat runs to the food and then runs back with it, it moves free of constraints in Golani's terms or beyond direct sensory control in Gallistel's (1990) terms. Similarly, its cognitive appreciation of the time that will be required to eat a piece of food will determine whether it will shut down into an eating posture or escalate a warm-up to run to its refuge.

Superficially, restating foraging activity in mobility gradient terms may appear to be a recounting of the obvious in the face of numerous disconfirming exceptions. But the strength of the approach lies in its demand for a better description of behavior and its provision of a theoretical framework. It requires that all of the movements, their durations, and interrelations be

carefully described. It requires that the sensory system that is primarily in use be identified and that the past experience and cognitive abilities of the animal be monitored. It allows the behavior to be evaluated with respect to rules of spatial dimension, body sequence, amplitude, and sensory hierarchy. This is a significant advance over the usual question of "how many food pellets did the rat carry home?" The descriptive analysis can in turn be related to evolutionary questions and brain function. It is germane that the forebrain is always active during movements encompassed within the mobility gradient and even reflects details of the movements but it can be inactive during other movements (Vanderwolf et al. 1973). [See also Vanderwolf & Robinson: "Reticulo-Cortical Activity and Behavior" *BBS* 4(3) 1981.] This relationship between the mobility gradient and forebrain activity suggests that the forebrain can both monitor and direct expansion and contraction along the mobility gradient, as I have suggested above. Thus, even though one could find much to quibble with in Golani's analysis, his approach clearly leads to a rich description of behavior and may eventually lead to some insights into how the forebrain plays upon subcortical keys to produce voluntary behavior.

Author's Response

The natural geometry of a behavioral homology

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In my target article, linguistic considerations and empirical findings were intermingled. In this Response they are discussed in two separate sections. I thank all commentators for examining my proposal with such vigor from the vantage point of their respective disciplines. There were many constructive suggestions from which I profited and will continue to profit in the future. If some of my counterarguments appear oversharp I trust that this will be taken as a measure of the importance I attach to the present interaction.

1. The language

1.1. The need for a specialized language

In the target article I wrote that classical ethologists took for granted the use of everyday language in the description of movement. I also implied that Lorenz considered the relationship between perception and language a one-way street. **Leyhausen** represents these views faithfully: Gestalt perception is prelinguistic and subconscious; all higher animals are endowed with this capacity; ordinary language, when properly commanded, is a precision tool of the highest grade. **Schleidt** believes that I misrepresented Lorenz's views on the subject. He quotes Lorenz as saying that "some people are incurably prevented, by theoretical considerations of cognition, from using their

senses." Theoretical considerations of cognition include language, writes Schleidt. But Lorenz never used this citation in relation to language and perception. He used it to advocate "direct observation, devoid of hypothesis" (Lorenz 1971, vol. 2, p. 256; see also pp. 1, 281; 1981, p. 40) or to attack premature quantification (1971, vol. 2, p. 256). He offered two solutions to "the sad sight of completely serious investigators stooping to vocal and balletic mimicry of animal behavior in order to understand each other at all": (i) "a useful and uniform nomenclature," and (ii) "there is . . . only one way out of these difficulties [of ambiguity] – the photographic medium [and], where possible, the ciné-film" (1971, vol. 1, pp. 285, 286). Thus, direct exposure to the behavior or to a film of the behavior, which is again the behavior, must accompany the verbal account if mutual understanding is required. What Lorenz did not see was that for a rational and articulated science, mutual understanding must be achieved without ceaselessly recurring direct exposure to the behavior. This can only be achieved through the use of a specialized language.

1.2. EW movement notation is more than an objective coding system

On the one hand, for **Thom,** the methodological importance of the target article can hardly be overrated, and its ideas extend the horizon of biology. In contrast, for **Schleidt,** the proposed methodology is just another tool, certainly not the first or only alternative to the use of ordinary language in ethology. **Schleidt and Masters** point out that objective coding systems have already been used in the description of human and animal movement. To evaluate these statements I will differentiate more clearly what I consider a valid movement notation, compared to a coding system. To be able to use the "Bernese" data matrix (Frey et al. 1983) mentioned by Masters one must memorize the number of the coded "dimensions" for each part of the body (e.g., 3 for the head, 9 for the hands, 7 for the feet), the identity of these "dimensions" (e.g., sagittal, depth, x/y orientation, turn, closure, folding, lateral, touch), the type of scale (ordinal or nominal) and the number of units used for each part (e.g., 5 units for head, 14 for the vertical dimension of the upper arms, 8 for the depth dimension of the hands, and 52 for their touch dimension), and the type of movement (e.g., tilt, rotation, shift, sway, turn, opening/closing, folding). This system is applicable to a sitting human; it is not clear how Frey et al. would handle the description of any other action but sitting. Would it entail further *ad hoc* extension of the coding system?

To use the coding system proposed by **Schleidt** et al. (1984) one must memorize 53 signs which are really abbreviations of ordinary language expressions (e.g., BoP for body posture, A for airborne, FX for flexed, UP for unipedal, U for up). The orientation of the parts of the body is described in relation to the axes of a 26-sided solid, centered at the animal's center of gravity. There are separate rules for describing the orientation of immediate attachments to the trunk and for more distal parts. The neck, for example, is coded by an imaginary vector that originates at the animal's center of gravity and ends at the neck's distal end. (The orientation of a neck that is parallel

to the ground will be coded as forward up if the animal's trunk is oriented forward up). Head and digits are coded in reference to their proximal joints. Orientation is always described proximodistally. Thus, the mechanical interdependence between the parts of the body is ignored (by not taking into account the base of support), the direction of the longitudinal axis of a limb is replaced by a direction of an imaginary vector, and the unit of measurement is fixed.

In contrast to these coding systems, to notate any body configuration of any organism which consists of linkages of rigid segments, one must be familiar with the syntax of EW, which uses Arabic numerals as the basic elements and a few "qualifiers" consisting of brackets and parentheses. The orientation of a part of the body is always described in relation to a spherical frame of reference following one and the same rule. Any stipulated unit of measurement can be used depending on the research requirements and observational capacity, but the main difference between these coding systems and EW emerges as soon as the organism begins to move. In Schleidt's system a body part moves out of his coordinate system every time it leaves a position. Also, his description of movement is based on the erroneous assumption that when a single segment moves from one position to the next it follows the shortest path. He thus codes movement by specifying the series of extreme positions reached by the animal in a so-called climax state. When a rigid segment moves within a sphere from one position to the next, however, it can follow several paths with varying curvatures (Eshkol 1979; Eshkol & Shoshani 1982; see Fig. 1 in **Harries;** this point is also elaborated in Golani 1986). In the Bernese system this problem is partly overcome by a redundant specification, at fixed time intervals, of the positions traversed by the limb. In EW the curvature of the path is represented by a single symbol denoting the angle between the axis of movement and the axis of the limb (Eshkol & Wachman 1958).

In summary, when I wrote about a movement notation I meant a system based on geometrical primitives that correspond to reality; there is an intrinsic relation between its constituent parts and it implies the internalization of a general system of reference in relation to which one creates a mental image of the moving organism. As elaborated by **Fagen,** a notation places a demand for empathy on the user, who must, so to speak, put himself in the place of the moving organism. Finally, by its nature, a kinematic notational system is potentially public because it is based on geometric universals. All of this contrasts with a coding system which is arbitrary, idiosyncratic (therefore entailing constant memorization), readily forgettable, and by definition inaccessible to those who do not share its underlying rules of application. Bearing in mind the fact that EW was available long before these coding systems were devised, I join **Bekoff** in asking "why few . . . have used EW?" Could one reason be the demand on the mind's eye made by EW?

1.3. Descriptions in terms of kinematics, torques and EMGs are complementary, not alternative

MacKay suggests that a notation representing torques between supporting limbs and the vertebral column, and

not trunk orientation, would be the best means of classifying modes of progression. He is unsatisfied with the account of forward progression in the target article, which ignores the fact that in normal progression nonforward torques generated at the hips must be counterbalanced at the shoulders. Forward progression is therefore made up of balanced couples of the same elements used for lateral movement. A higher order of organization is imposed on the lateral elements in order to generate a resultant force in the forward direction. **Barlow** similarly wonders to what extent the universality of the mobility gradient is just a matter of biomechanics. For **Byers,** a sequence of muscle contractions is a better way to define units of behavior than a series of postures. He and **Fentress** quote Ann Bekoff (1986; 1989; Bekoff et al. 1987) who has shown, using EMGs, that chickens use the same motor program in hatching and walking. Byers doubts EW would detect that the same motor program is being played out in both instances. My stance, in accord with Powers (1973), is that of course any of these modalities – torques, muscles, or kinematics – could provide a "key" for the classification of behavior by demonstrating an invariance, and of course *none* could be assumed a priori to provide the key. I can move my body in a variety of ways to achieve the same torque or I can use a variety of torques and muscles to achieve the same form, or the same muscles to obtain different patterns of movement. As elegantly demonstrated by **Eaton,** the description in these modalities is complementary, rather than an alternative (as suggested by Fentress). The point made in the target article is that the level of description of whole-animal movement in terms of movements of body parts is as legitimate for analysis as the other levels and yet it has been studied the least. Byers's argument about muscular contractions being the best way to define units of behavior has often been used by ethologists as an excuse for staying at the level of description by consequence: "Behavior may be described . . . in terms of muscular contractions or in terms of consequences" (Hinde 1970, p. 16).

The point made by **MacKay** about forward progression representing a higher level of organization of lateral movements is also made in Eilam and Golani (1988): The whole morphogenetic continuum of lateral and forward[1] movement is generated, for example, in amphibian tadpoles and infant rats out of one building block – lateral movements. MacKay's torque description adds a useful complementary perspective. The shape of locomotion must of course abide by torque considerations, but how would MacKay explain the fact that when an infant rat is held in the air it performs precisely the same body-related lateral movements and stepping patterns it performs on the ground? During the pivoting stage, for example, lateral trunk movements are accompanied on the ground and in the air by sideways foreleg stepping in the ipsilateral direction and by backward stepping of the inside hindleg. Similarly, when an infant rat is placed on a vertical wire mesh, thus confronted with totally different forces, it freezes and then performs the warm-up sequence using the same trunk movements and stepping observed on a horizontal surface (Eilam & Golani, personal observations). This also tells us, in response to the question posed by **Fentress,** that the invariance is manifested in body-related, not absolute, space. And how

would torque considerations explain the different types of pivoting observed in inferior and superior animals? On the other hand, since torque is produced by movement, torque considerations can often be derived from the observation of movement. **Byers's** doubts concerning EW's capacity to reveal underlying invariant muscular contractions are, however, well founded. EW cannot reveal such invariants because it is designed to describe the spatial orientations and the relations and changes of relation between the parts of the body; this and no more. Nevertheless, the fallacy in classifying muscles in terms of flexors and extensors has been deduced by using EW (Ganor & Golani 1980).

In response to **Barlow's** and **MacKay's** queries about the primacy of a biomechanical explanation, **Eaton** demonstrates that, sometimes at least, a kinematic model and not a biomechanical one may give the desired reduction of the pattern of movement to a neural sensorimotor computation. **Faulkes & Paul** point out that EW describes the combined effect of motor output *plus* all biomechanical factors influencing movements at a joint (including torques generated by movements at other joints). Finally **Thom** and **Goldberg** point out that the requirements for maintaining structural stability within the gravitational field constrain but do not explain the shape of the global continuity of movement. In conclusion, given that the *form* of whole-animal movement is a legitimate field of study occasionally manifesting invariant features (see the section on coordinative structures in **Newtson**), the next question is whether we should look for a "best" way (à la **Bekoff**) to describe it.

1.4. A structural analysis is preferable

"He has persuaded me of its utility, but is it the only way, all things considered? I doubt it," writes **Barlow.** Behavioral events are to be selected by the astute investigator according to the question being asked. This might mean functional consequences or modal action patterns. A similar plea for plurality is made by **Bekoff. Byers** would never use EW to find out whether, for example, house mice showed sex- or individual-specific play partner preferences. Finally, **Fentress** suggests that the EW path should be accepted as one among many possible others.

The commentators cited above will surely agree on the following points: (1) Every description can be useful. Many of the seemingly anecdotal descriptions of animal movement made by Lorenz, for example, yielded profound insights about the organization of movement. (2) Every description is partial, therefore complementary descriptions are essential. (3) If the question being asked is taken for granted and the validity of a simple measure used to examine this question is taken for granted, then one should by all means use that simple measure. (4) If, however, in trying to answer a question one is also interested in examining the validity of the very question being asked, and if one is also willing to cultivate a certain uneasiness about the appropriateness of the measures being taken, then a thorough structural analysis of the behavior may be more productive than taking "simple" measures. For example, **Byers's** instance of where EW analysis would be utterly inappropriate – assigning a choice of mate – is presented by **Barlow** as "an often

ambiguous determination in behavioral experiments," and therefore appropriate for EW analysis. The main value of a thorough analysis, however, is in a redefinition of questions. For example, in studying interactional behavior in canids within the classical ethological framework, I came to realize that in order to isolate so-called ritualized behavior patterns specifically evolved for communication I should sift out locomotor components from the behavior, because the apparently specialized postures are performed while the partners locomote around each other. But after sifting out locomotion through EW analysis, hardly anything was left: Postures that were described, for example, as ritualized signals of submission (Lorenz 1943) or superiority (Schenkel 1967) were shown to be, first and foremost, manifestations of locomotion of a free or stimulus-bound animal in the proximity of the complex environment of a moving (free or stimulus-bound) rival (Golani 1976; Golani & Moran 1983; Yaniv & Golani 1987). In particular, because the maintenance of a fixed opposition between the snout of the stimulus-bound animal and the forequarters of the free animal often acquires priority, a "joint" is formed between the two partners. Through this joint, which is often maintained at a distance, the free animal can twist the bound animal, forcing it to run, rear, or even flip on its back. The "bizarre" postures whose form has been attributed to evolutionary forces are first and foremost shaped by the maintenance of a specific relationship of opposition (compare Fig. 9, fr. 1334–1403). Most important, (i) communication *emerged*, and therefore was demonstrated instead of being assumed from the outset; and (ii) whereas in the classical model "social communication is embodied in its own terms, defying reduction to physiological terms" (Beer 1980, p. 19), in the new model relationships are formulated in terms of a sensorimotor algorithm (which was anticipated in **Powers**'s last paragraph). This also shows why **Bekoff** is wrong in expecting EW to fail to be useful for understanding animal communication. This leads me to the question of structure and proximate function.

1.5. Proximate function should be demonstrated, not assumed

Several commentators are concerned that excessive preoccupation with form may lead to sterile descriptions which ignore the meaningful context in which behavior takes place. **Bekoff** is uncertain whether the common formal features I describe mean anything to the animals that "have to read each other's signals." By describing EW as "acontextual" he presumably means that the formal description is stripped of the meaningful context in which behavior occurs. For **Masters**, patterns of human social interaction are social cues, signals of status subject to cultural expectations. To make EW useful for the study of human nonverbal behavior, they should be embedded in a broader (meaningful) context. **Fagen** disagrees in part with the criticism that EW asks us to deny the meaning of movement, yet he feels that it would be dangerous to stop with structure because meaning matters. **Fentress** reminds us that movements are means by which tasks are accomplished: "There are jobs to be done." Finally, **Pellis** criticizes me for considering structural and functional analyses as complementary but separate endeavors.

To clarify my position I should first state that I am an ardent believer in von Uexkull's (1934) dictum that every behavior is performed in a meaningful context and is therefore an answer to a question; the sum total of questions and answers constitutes the animal's operational world – its *Umwelt*. The only question is whether these meanings or proximate functions should be taken for granted or shown to be an emergent property of movement. With EW, proximate functions can be revealed and proved systematically: EW is based on a general *spatial* coordinate system (an "absolute system") which yields several derivative systems. In the target article I referred to only two such derivative systems, a "body-related" coordinate system and "opposition" (which is also body-related), because they highlighted the invariants relevant to the mobility gradient. By describing the same behavior in relation to each of the coordinate systems, one can reveal the invariants of movement. As lucidly explained by **Powers**, these invariants are often nothing but repeatable accomplishments, presumably reflecting internally specified reference states – "purposes" in ordinary language. These "jobs" are revealed by EW analysis, not taken for granted. They provide part of the contextual meaning which concerns **Fagen**, **Masters**, and **Bekoff**. Another part is an *emergent* property, derived indirectly from the interaction between these relatively independent invariants or between them and the world (e.g., another animal; Steels 1991). One example of an emergent function is the "joint" formed between the partners. It makes them move as one "superorganism" (Golani 1976) due to the priority given to maintaining a steady opposition by one or both. Others are "superiority" and "inferiority," which emerge as byproducts of the number of degrees of freedom each of the partners displays, their degree of stimulus-boundness, and the types of movements they perform. The sum total of all the internally specified and emergent functions defines a part of the organism's world of meaning – its *Umwelt*. EW can help in revealing parts of this world.

Pellis is concerned that I assume rather than prove intrinsic constraints. His concern is based on Fig. 9, in which "it is shown that the inferior . . . can only pivot on its hindlegs whereas the superior can pivot on either fore- or hindlegs." He rightly points out that opposition differs in this figure for each of the partners. Clearly, to show a difference in the freedom of movement of the two partners it is necessary to compare the respective repertoires of the partners by examining their response(s) when confronted by the *same* stimulus situation. But this is done in the second and third paragraphs of section 3.3., which **Pellis** missed: Role reversal provides an opportunity to compare the responses of each of the animals to the same stimulus situations. In each of the situations, the inferior responded with only one type of movement, located on the gradient closer to immobility, whereas the superior responded unpredictably. For example, upon being bitten in her hindquarters the female immediately pivots on her hindquarters toward the male, whereas the male responds to similar biting, immediately or after a while, with one of four possible options (Yaniv & Golani 1987).

Pellis also asserts that by the a priori chunking of motor recovery after brain damage into functional groupings such as comfort behavior and exploration, terms with

clear functional connotations, we performed functional analysis without realizing it. Stretch-yawns, and, I may add, grooming, which include large amplitude forward or vertical movements, were excluded a priori, he writes, leaving for analysis only the components which conform with the mobility gradient regularity. In reality, EW analysis was performed on the *whole* behavior, revealing a continuous structure, interconnected by common rules of transformation and interrupted sporadically by isolated large-amplitude forward and vertical movements. These instances of deviation from the rule were then examined and found always to involve yawning or grooming. As such, they stood out as isolated structures which showed no relatedness whatsoever to the surrounding organized matrix. The label attached to this organized matrix – whether it was called locomotor activity or, for ease of communication with others, exploratory behavior – is not that important once the behavior has been thoroughly mapped. This is also my answer to **Schleidt's**, **Bekoff's**, and **Leyhausen's** concern with functional versus neutral criteria for labeling.

Pellis states the obvious by writing that behavior is shaped by both intrinsic and extrinsic constraints and that analysis should disentangle the two. He is also right in pointing out that with its coordinate systems EW is ideally suited for this purpose. But then he cites Dwyer as advocating functional analysis in instances where invariance of form is presumably shaped by external constraints. In Dwyer (1984), external constraints are selective pressures; invariants are thus shaped by external constraints. In contrast, in the case of moment-to-moment behavior, the haphazard effect of external constraints on shape should be ruled out. As emphasized in Powers (1973), regardless of the coordinate system being used by an organism, all invariants always reveal intrinsic constraints. If Pellis implies that some invariants are shaped by external constraints then he is committing an error similar to the one made by Lorenz (1970), who equated "core" structure with intrinsic constraints (instinct), and "taxis" with learning. In summary, I did *not* assume intrinsic constraints as suggested by Pellis, but demonstrated them by showing a fixed sequence of movements that resists disordering in a variety of situations and external constraints (see also **Beck**). I thus agree with **Pellis** that structure and proximate function are two aspects of the same movement material, but I repeat my claim that suspension of judgment about proximate function is a prerequisite to demonstrate the existence of such function.

1.6. A universal language for the description of movement is not only necessary but also possible

While recognizing some of the merits in using EW, **Barlow, Leyhausen, Schleidt, Byers, Fentress,** and **Bekoff** express doubts about the claim for universality. These are expressed most directly by Bekoff: "I get the feeling that Golani views EW as being somewhat universal and perhaps even timeless." To unpack this statement we should first agree that if the kinematics of whole-animal movement are to be described at all, then the most universal language available for such a description is the language of geometry. There is no better expression of the universality of such a description than the one offered by D'Arcy Thompson (1942, vol. 2, p. 1026):

We begin by describing the shape of an object in the simple words of common speech: We end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity. Thus, for instance, the form of the earth, of a raindrop or a rainbow, the shape of a hanging chain, or the path of a stone thrown up into the air, may all be described, however inadequately, in common words; but when we have learned to comprehend and to define the sphere, the catenary, or the parabola, we have made a wonderful and perhaps a manifold advance. The mathematical definition of a "form" has a quality of precision that was quite lacking in our earlier stage of mere description; it is expressed in few words or in still briefer symbols, and these words or symbols are so pregnant with meaning that thought itself is economised; we are brought by means of it in touch with Galileo's aphorism (as old as Plato, as old as Pythagoras, as old perhaps as the wisdom of the Egyptians), that "the Book of Nature is written in characters of Geometry."

Thom has therefore done a service to the proposal made in the target article by recognizing that the mobility gradient model "(without making it explicit) draws heavily on facts that are essentially mathematical . . . Yet no equations are written or solved, only plain ordinary language is used. This does not render Golani's account less convincing, although the use of mathematics is only qualitative here." Thom recognizes that a prerequisite for the development of a computational approach to the study of whole-animal movement is the formulation of qualitative algorithms that describe it.

Given that a geometrical description of behavior is universal, the next question concerns the basic requirements for an appropriate geometrical description. Surely, because (1) a vertebrate's body (and the body of arthropods, see **Faulkes & Paul**) consists of a linkage of rigid segments, it would be appropriate to (2) describe the orientation and changes of orientation of each of these segments in time. It would also be appropriate to (3) describe the movements of a single segment in reference to a sphere centered at the joint (see **Harries**). As recognized by **Eaton, MacKay, Faulkes & Paul, Goldberg,** and **Thom**, and elaborated in **Harries**, (4) it is essential that the sphere be centered at the joint closer to the base of support. Only in this way can the geometry be described "as it arises from mechanical constraints" (Thom). (5) The coordinates attached to the individual spheres centered at the joints should be spatial (Thom: given by exterior sense data), not body-related. The latter can be derived secondarily in relation to an absolute reference posture of the body.

The close correspondence between the underlying primitives of a descriptive framework and skeletal, biomechanical, and perceptual reality increases the prospect that it will yield descriptions that are not only geometrical but also natural. Because EW is based on the above listed primitives, any challenge to its universality should be accompanied by specific suggestions to replace, modify, or add new primitives. In not being able to get hold of Gonseth (1970), I cannot presently answer **Thom's** suggestion to use a referential for the description of flying and swimming animals. (The general spatial coordinate system of EW [the "absolute" frame which was not pre-

sented in the target article] is perhaps akin to the *referential* suggested by Thom.) **Todt & Hultsch** and **Lyon** are wrong in suggesting that the representation of time is not sufficient in EW. What they probably mean is that I didn't represent my analysis in relation to time (which I indeed did not, see 2.5). In the EW score itself, however, the timing of the initiation and termination of the movements of each segment is fully represented in relation to the columns of the basic grid of the manuscript page. Any value can be assigned to a time unit, so movement durations, degree of synchrony, speed, and acceleration (by the insertion of so-called mute positions into the score [Eshkol 1990]) can be calculated and analyzed. The score is therefore ideally suited for any method of time analysis (as well as for the addition of horizontal spaces that would concurrently specify, for example, EMGs, sonagrams, forces, or color). In summary, though most commentators, notably those who offer suggestions for improvements, applaud the generality of EW, the few who question its generality do so without offering an appropriate alternative. (In response to **Bekoff**'s request, a systematic comparison of EW and Labanotation is provided in Eshkol & Shoshani [1979; 1982].)

Fentress's suggestion that alternative taxonomies of movement are critical is somewhat ambiguous. If by this he means complementary taxonomies based on neural, EMG, torque, and kinematic invariants, then we agree. If he addresses only the level of kinematic form and suggests that every kinematic description is partial and therefore complementary descriptions are necessary, then we agree. We also agree on the need to analyze the same notated material in a variety of ways, including the time dimension. We disagree, however, if by this he means that we should not aspire to a universal language for the description of movement. As to **Bekoff**'s and **Barlow**'s plea for plurality – should a science not aspire to a universal language? Why is it that the universal technologies used to record data on, for example, the neural, muscular, and biomechanical levels, are taken for granted, whereas an attempt to establish a universal description at the kinematic level of whole-animal movement encounters resistance? How is it that in the history of neuroscience there is as yet no established universal language for the description of movement? What is the future of ethology, nonverbal communication, neurology, and behavioral pharmacology without a universal language? Could the answer to **Bekoff**'s question about the resistance to EW be that the acquisition of such language requires a jump in consciousness so as to allow a mental articulation of complex space-body images, often related to an intimate awareness of one's very own body?

2. The model

2.1. A new method for identifying behavioral homologies

For **Klopfer** the great merit of the proposal made in the target article is that it provides a language and a reinterpretation of homology in which the issues of structure and function in the CNS can be explored without the preconceptions of earlier ethologists. In contrast, for **Barlow** my interest in homologies is an example of a stated concern whose utility I appear not to understand.

He adds that the mobility gradient, a purported homology, is the height of sterility for evolutionary studies. A similar contrast is found in other commentaries. On the one hand, **MacKay, Eilam, Eaton,** and **Goldberg** provide a comparative phylogenetic perspective that supports the notion of a homology at the morphological, neural, and information processing capacity levels. On the other hand, **Byers** finds that my article did not deal substantively with the question of how to identify a behavioral homology.

To answer **Byers** and **Barlow** it is necessary to examine the pre-Darwinian anatomical definition of a homology: "Homology holds between two structures when they occupy corresponding positions in a structural design common to whatever forms carry them, irrespective of the function they serve" (St. Hilaire's principle of *Connections* rephrased by Owen 1848 in Beer 1980, p. 36). For example, the third metacarpal bone of a human and a horse are homologous (and therefore carry the same name) because they occupy corresponding positions in the skeletal anatomy of the forelimb. The behavioral equivalent of this principle is a correspondence in the positions occupied by two movements in the sequence of movements in which they occur. As explained by Beer, this position differs markedly, however, for similar behavior patterns between even the closely related species of ducks studied by Lorenz (1941). In the absence of a consistent analogy to the principle of connections, ethologists had to turn to a criterion of similarity between behavior patterns. But, as vividly argued by Beer, this criterion is vague and begs the question. **Leyhausen,** for example, claims that rolling over in cats has nothing to do with tumbling head-on in canids because rolling also includes a torsion of the trunk which tumbling does not; and **Bekoff** suggests that even a play bow is not a play bow in the same animal in different contexts. In other words, what is the morphological criterion relevant to establishing a homology? In failing to provide a satisfactory criterion, comparative ethology, which was brought into being by the notion of behavioral homology, had to abandon the rigorous study of homologies and retreat into subjectivity "as in the judgments of works of art" (Beer 1980, p. 47).

As elaborated by **Klopfer**, this situation is amended in my proposal by showing that the principle of connections applies to component-variables, not to (composite) behavior patterns. If the mobility gradient is valid then there is a "stubborn" sequence of trunk movement types, both in space and along the body, which resists disordering in a variety of situations, species and time scales. Because this sequence is a common denominator of all the examined behaviors, it suggests itself as the skeleton of these behaviors, thereby lending priority to trunk movements in relation to the base of support, compared to other kinematic features in establishing similarity. The answer to **Barlow**'s, **Byers**'s, **Bekoff**'s, and **Leyhausen**'s queries is, therefore, that in the examined behaviors, identity of trunk movement type *and* identity of position in the prescribed fixed sequence (the principle of connections) suggest themselves as the relevant criteria for establishing homology. Any attempt to refute the model should therefore be based on counterexamples consisting of types of trunk movements that violate the prescribed sequential order.

2.2. Counterexamples

2.2.1. Cats. To use rolling over in cats as a counterexample that would refute the model, Leyhausen should have shown that it violates the prescribed sequence. Yet, as reported in Leyhausen (1979), pp. 244–45), rolling over occurs in precisely the contexts in which large vertical movements on a forequarter-base-of-support are anticipated by the model: estrus and play. Furthermore, an upward orientation of the trunk from shoulders to hips is evident in the female's mating posture illustrated in Leyhausen's book (p. 246). Leyhausen further cites a description of the female lynx's mating posture which consists of crouching in front with fairly extended hindlegs. Young female domestic cats often do the same, and Leyhausen suggests that this posture might correspond to an earlier phylogenetic stage. On pages 212–13 he provides illustrations of encounters between foxes, hyenas, and bears. In all of these, the forequarters of the superior are lowered. As prescribed by the model, all postures reported by Leyhausen to include "a droop of the thorax" are assumed at the culmination of a build-up process, be it in social status, heat, or mobility, yet for Leyhausen all these postures are unrelated because in each, trunk orientation is accompanied by characteristic but different morphological features.

"There is no guarantee that a movement sharing its plane and direction with another originates in the same way" writes **Leyhausen**. He claims that by reducing unidirectional pivoting and the "search automatism" of a pup to a common basis of horizontal movement I miss the all-important fact that the first persists in one direction whereas the second, being a search automatism, consists of a rhythmic change of direction. **Fentress** comes to my help by pointing out that I did not leave the argument there, and based it convincingly on sequential regularities (the principle of connections). Indeed, the most compelling demonstration of the gradual transformation of side-to-side head movements into almost unidirectional pivoting is accomplished by high-speed projection of a film of, for example, an amphetamine-induced shutdown sequence: As sporadic head movements to one side at a time gradually increase in frequency, they become rhythmic and side-to-side; their amplitude then gradually increases to incorporate also the chest and then the pelvis in movement along the same plane. As soon as the pelvis movement increases to a full circle or more, rhythmicity and bidirectionality wane and the rat often pivots in one direction for relatively long time intervals (Adani 1990). A similar transformation from sporadic head movements to bidirectional rhythmic, and back to whole-body sporadic and often unidirectional movement can be observed in infantile moment-to-moment and ontogenetic warmup. In more than one situation and preparation there is a continuity in the transformation of the amplitude of movement of the parts of the body involved, of directionality, and of the rate of performance. These continuities force themselves on us so as to reduce these movements into one spatial component-variable on which the variables of recruited body parts, directionality, and rate are superimposed.

2.2.2. Ungulates. An apparent refutation of the model in the form of a clear-cut counterexample is presented by **Byers:** Whereas the model predicts that in the transition from recumbency to standing the forelegs are extended first and the hindlegs next, ungulates, and deer in particular, violate the rule by extending their hindlegs first. In finding the appropriate counterexample, Byers has demonstrated how *easy* it is to refute the model, yet he complains that the model is not presented as a refutable hypothesis. Byers invites *BBS* readers to join him in a good laugh by (erroneously) imagining a deer first stretching its forelegs as its haunches remain in the initial recumbent position ("you don't need EW to see this in the mind's eye," he suggests).

As illustrated in Figure 1B, drawn from a videotape, extending the forelegs is precisely the first thing a deer does in moving from recumbency to standing. Only after rearing fully on its carpal joints in precisely the same way as the dog illustrated in Figure 6-2 of the target article does the deer extend its hindlegs. The difference between the two is that whereas in dogs the carpi and toes are directed forward during recumbency, in deer they are directed backwards and placed under the forelegs. Also, in dogs the upper- and lower forelegs (humerus and ulna-
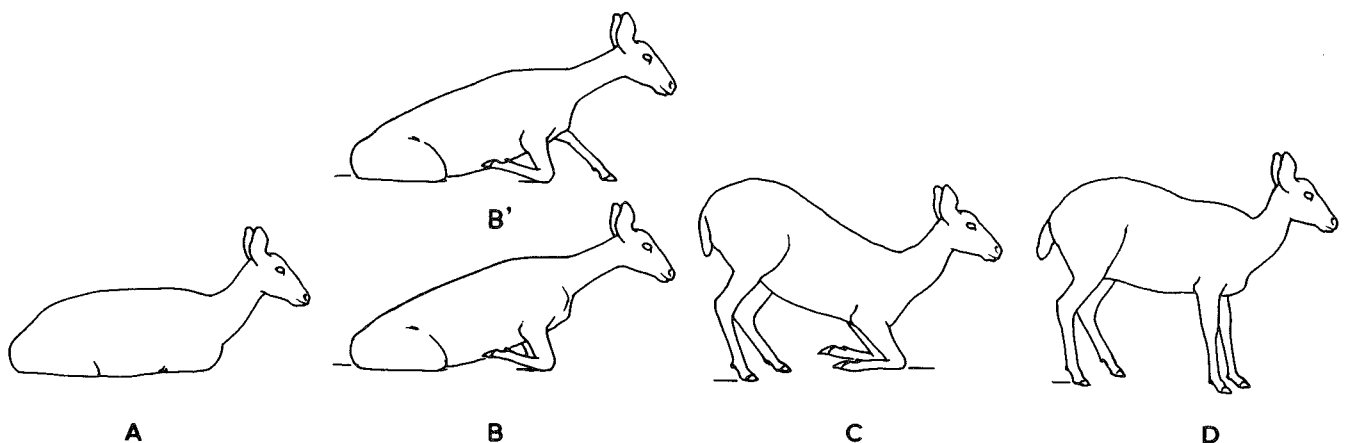

Figure 1.   Successive stages in the transition from recumbency to standing in a female hog deer (*Rusa porcinus*). Drawings were made from a videotape. A: recumbency, B: extension of the forelegs on the carpal joints, C: extension of the hindlegs, D: rearing on tips of toes of forelegs, B': an occasional intermediate stage between B and C, in which a foreleg is stretched forward even before extension of hindlegs.

radius) are long and the carpi and toes relatively short, in deer the humerus and ulna-radius are relatively short, and the carpi relatively long. Hence the transient excessive rearing of the hindquarters observed in deer (Fig. 1C). Deer also conclude the process by rearing on the tips of their toes (Fig. 1D), a stage missing in rats and dogs, who remain standing on their forepaws. Figure 1B' presents an occasionally observed variant of this process in which the deer stretches one "long front leg in front of itself" before even starting to extend its hindlegs, in precisely the manner humorously imagined by **Byers**.

The lesson is that: (i) Sometimes it doesn't pay to imagine behavior without using an appropriate descriptive discipline. (ii) It is not sufficient to assert that skeletal plans demand different sequences of postures; such assertions should be accompanied by attention to anatomical differences. And (iii) details can sometimes reverse one's conclusions about universal regularities. All the other counterexamples mentioned by **Byers** in passing should be examined using similar rigor.

2.2.3. Fishes. In contrast to **Barlow**'s claim, during S-starts fishes do propel themselves directly forward with the head and trunk, maintaining a fixed orientation in relation to the environment. During such starts the undulations of the trunk in body-related space cancel each other out to produce the fixed orientation in the absolute frame (see **Eilam**; Wassersug 1989, p. 76; see also previous section on torques, muscles, and kinematics). Barlow also points out that submissive plankton feeders on coral reefs flee downward after an encounter with a territory holder – a fact which apparently violates the head-up posture predicted by the model. This example is irrelevant because the shoulders-up posture of the submissive animal is predicted for quadrupeds and fishes alike only in the *proximity* of the dominant animal. As pointed out by Barlow himself, this is indeed the position assumed by submissive fish during head-on encounters. The inactivation of the fins at the rear end of the fish during the assumption of this posture, reported by Barlow, is presumably homologous to the inactivation of the hindlegs of, for example, the inferior wolf in the proximity of the superior. Barlow's force vector explanation is *complementary* to a description based on the mobility gradient model – of course the posture must abide by physical law. It should not be used, however, to explain away the geometrical regularity.

2.2.4. Behavior with apomorphine and amphetamine. The effects of manipulation of the features of the testing environment on the robustness of behavioral shutdown in drug-treated rats are examined by **Beck**. All observations except one support or fail to refute the model. Furthermore, in one case the model prompted reanalysis of the data, which confirmed the prediction. The only apparent threat to the model stems from the observation that when tested on a small table, amphetamine (AMPH) rats performed vertical and other movements throughout the session. Beck rightly points out that with AMPH, rats show considerable flexibility in response to environmental manipulations whereas with apomorphine (APO) they do not (see also Robbins et al. 1990). Indeed, with high doses only AMPH rats show regularities in the horizontal absolute frame and in locale space (Eilam 1988; Eilam &

Golani 1989; 1990). Beck concludes that the model of a reflexive output of a hard-wired circuit is appropriate for APO, not for AMPH. This provides me with the opportunity to clarify the hard wiring concept.

2.2.5. Only constraints, not actual content, are hard wired in the mobility gradient. Hard wiring pertains only to the constraints imposed on the sequence, not to its content. The model merely predicts that *if* types of movement appear or disappear, they will do so in the prescribed order. For example, the APO rats E1 and E2 in Figure 13 of the target article performed both lateral and forward movements throughout the session. This formulation of the mobility gradient is consistent with the view that the basal ganglia participate in *enabling* particular movements (including direction as a major determinant) and thus in controlling their sequencing rather than in directly causing them to occur (Chevalier & Deniau 1990; Neafsey et al. 1978). This is also the answer to **Schleidt**'s question about the *exact* location of, for example, hip thrust and neck bite on the gradient. The model merely predicts that rotation on forelegs will never precede rotation on hindlegs in the same animal and that in an interaction an animal performing the first also has access to the second, but not vice versa.

2.2.6. The Lyon-Robbins hypothesis. According to the Lyon-Robbins hypothesis, the criterion for the performance of specific behaviors under AMPH is the time required for their completion. The incomplete performance of sexual, aggressive, and maternal behavior is cited by **Lyon** as support for the hypothesis. But all these examples refer to AMPH's effect on long sequences of movement; the hypothesis fails to explain why vertical movements whose duration is similar to that of horizontal movements are eliminated first, forward next, and so forth. This is explained only in reference, for example, to the ontogenetic order. Incidentally, Lyon's call for automatic recording of movement is welcome only as a followup for studies based on direct perception guided by the use of an articulated language.

2.2.7. Infant rats. His examples of infant rats performing vertical movements in utero or in early infancy in response to saliva or milk odors do not refute the model, as **Beck** recognizes. An infant performing a constricted portion of the warm-up sequence on the testing platform may be seen to display the entire repertoire unpredictably upon being placed back into its nest (Eilam & Golani 1988). This merely highlights the fact that initial immobility is a prerequisite for warm-up. Such immobility may be imposed by the contrast between the nest and the testing environment or by the proximity of a rival. This also answers **Fentress**'s concern that early infantile restriction to horizontal movements merely reflects muscular weakness. The dependence of reduced mobility on the immediate stimulus situation is akin to the *kinesia paradoxa* reported in human Parkinsonism (Sacks 1982).

2.2.8. A restricted number of displays. To refute my claim that ethograms generate an endless number of behavior patterns **Barlow** cites Moynihan (1970), who showed that each species possesses "remarkably few displays." But Moynihan provides a list of 1,241 behavior patterns collected in 64 species – how does this refute my claim?

2.3. A natural geometry based on spatial component-variables

Fentress comments that since "horizontal," "forward," and "vertical" are nothing but X, Y, and Z coordinates, the fact that I am able to describe animal movement in three dimensions becomes a truism. In this he ignores the fundamental question of what the natural frames of reference used by the brain are. A description in Cartesian space, derived from the projection of complex movements on three arbitrary orthogonal axes, tells us nothing about the natural organization of movement. In contrast, the fact that in infant rats there are relatively pure horizontal and vertical movements and almost no movements within planes which are tilted in relation to the body-related horizontal plane does tell us something fundamental about the natural geometry of brain function (Eilam & Golani 1988).

The search for natural coordinate systems is also central to the tensorial approach to the geometry of brain function (Pellionisz & Llinas 1979; 1980). Prime examples of such systems are the frame of nonorthogonal axes used in gaze control by the six extraocular muscles, and the frame of nonorthogonal axes of the semicircular canals. Whereas it is extremely difficult to establish the frames and the invariants used by the brain in the transformation of perception to action, behavior is fortunately all out there for us to examine – provided that we are equipped with appropriate geometrical tools, such as those offered by EW. This is appreciated by **Powers**, who notes that "a theoretical model is needed to show how a system must be organized to exert . . . control . . . but the observable manifestations of control are not theoretical," and by **Thom**, who writes:

> To understand the statement that the meaning of a physiological attractor is its shape we have to add to its internal shape the position of the attractor in the global space W of activities (a space of very high dimensionality, hence practically unknown). Fortunately, in the study of animal motion, the shape is immediately observable.

2.4. A new tool in the study of behavioral adaptations

In the first paragraph of my target article I said that of the two issues which concerned comparative ethology – homology and adaptation – I will handle the first. Nowhere did I imply that the study of adaptation is unnecessary. **Allen**'s call "EW is not enough" is therefore stating the obvious: What, I should ask, *is* enough? There is no reason why the historical enterprise of Darwinism should be in conflict with the generative principles specified in the target article (Goodwin 1988).

Barlow considers the mobility gradient to be the height of sterility for evolutionary studies because it ignores variations. First, as illustrated by the comparison of amphetamine- and apomorphine-induced behavior, and as emphasized by both **Wishaw** and **Todt & Hultsch**, the main merit of EW is that it forces one to recognize meaningful variations that may otherwise remain unnoticed. Second, Barlow seems to have forgotten that in the study of behavior we do not even know what a morphogenetic unit is (Gould & Lewontin 1979). Whereas anatomists know that a kidney is a kidney (cf. **Goldberg**'s citation of Gould 1991) and can therefore

proceed to examine its adaptive variations across species, in the study of behavior we must first establish that a play bow is a play bow in the same canid in different contexts (**Bekoff**) and that tumbling head on in canids is rolling over in cats (**Leyhausen**). For example, only after having established that warm-up in rats is homologous to warm-up in spiny mice (*Acomys cahirinus*) (based on the reductionistic language of geometry) can we proceed to examine adaptive variations in these respectively altricial and precocial species (Eilam, work in progress). In the ensuing framework, the question will not be What is the adaptive significance of this or that atomized piece of behavior? but rather How is each of the component-variables transformed across species? What are the variations in the coupling between component variables (as in the comparison of behaviors with APO and AMPH)? and What are the effects of all these on the shape and adaptive significance of the *entire* species-specific behavioral spectrum?

2.4.1. A rational definition of homologies. Why do I, in wishing to conclude that the mobility gradient is truly homologous, misleadingly use "homology" in the pre-Darwinian sense? wonder **Faulkes & Paul**. My answer is that a definition based on common descent precludes conclusions about descent from judgments of behavioral homology. "We need a definition . . . that does not include reference to phylogenetic relationship, and this ethology failed to find" (Beer 1980, p. 46). There are other serious considerations, however, and for these I am grateful to **Klopfer**: Similarities in behavior can stem from similar physical intrinsic constraints, similar physical environments encountered in ontogeny, ontogenetic constraints (Edelman 1987), similar or different neural substrates (see also **Fentress**), *and* historical continuity. To *prove* similarity by common descent it is necessary to rule out the other shaping forces, which is immensely difficult. A rational definition of homologies based on the demonstration of invariants and on the principle of connections avoids these difficulties (see also Goodwin 1988).

2.5. Self-similarity, the march to chaos, and the mobility gradient

The suggestion that self-similar morphogenetic structures unfold in moment-to-moment behavior, ontogeny, and phylogeny is supported by the phylogenetic perspective provided by **Eilam**. Three trends – a transition from horizontal to vertical movements, a cephalocaudal increase (as well as a subsequent cephalocaudal reduction of movement in the horizontal plane), and a proximodistal transition of active movements from trunk to appendages – are evident in the diversification of ancestral forms of locomotion to derived ones. These trends are also evident in, for example, the ontogenetic time scale. The cephalocaudal confinement of propulsive lateral movements corresponds to the fixation of the head in the absolute frame in amphibian ontogeny; the shift of propulsive movements to the tail (as in tunniform locomotion) corresponds to the late appearance of a forequarter base of support in ontogeny; the derived appearance of vertical antagonistic trunk movements in whales corresponds to the late appearance of the gallop in rodent ontogeny (see **MacKay**); and the proximodistal shift of active propulsive move-

ments to the appendages is evident in both amphibian and rodent ontogeny. **Eaton** points out that the neural systems subserving horizontal movements are among the oldest (thus explaining the phylogenetic order) and simplest (thus explaining ontogenetic order), and **Goldberg** postulates a gradient of information processing capacity that would partly explain self-similarity.

Because of its abstract nature, EW could reveal the generative rules that breed complexity out of simplicity. It is no coincidence that the only ethologists coming up with examples of comparable generative rules are **Todt &** **Hultsch,** who are equipped with a rigorous tool for the recording of vocal motor output – the sonagram. **Barlow** and **Fentress** insightfully ask for examples of transitions from stereotyped to variable behavior in systems that are independent of the constraints of quadruped morphology; Todt & Hultsch supply them. A "gradient of alternative choices," implying increasing versatility in content and a concurrent buildup in vocal amplitude, density, and rhythm, "surprisingly similar to the mobility gradient," has been documented in nightingales at both the level of individual songs and bouts of songs. A "regression" to ontogenetically earlier stages of performance quality has been reported in sparrows and young nightingales. The correspondence is even more provocative given that song production, like the mobility gradient, is of striatal origin, being mediated by a nucleus located in the bird's archistriatum (Nottebohm 1991). Note the correspondence between Todt & Hultsch's decisional "one-to-many" hierarchy (their "gradient of alternative choices" between element types and song types), the increase in the number of degrees of freedom along the mobility gradient, and **Thom**'s "natural" sequence of bifurcations, which arises when the blocked degrees of freedom of a sequence are successively released. **Thom** and **Goldberg** further recognize the analogy between these processes and "the march to chaos," where chaos corresponds to the hypermobile end of the sequence. Todt & Hultsch point out that the well-known transition of birdsong from complexity to stereotypy on the *ontogenetic* time scale is the opposite of the mobility gradient. Because it depends on perceptual learning, however, it should not correspond to the mobility gradient, but to the establishment of stereotyped routes in the animal's locale space in the course of repeated exposures to the same environment (von Uexkull's [1934] "familiar path").

Todt & Hultsch suggest extending the search for rules to the stage of "unpredictable" movement and **Barlow** correctly points out that the mobility gradient is overt and therefore refutable only in its less mobile portions. Although I plan to examine Todt & Hultsch's powerful methods of sequence analysis, I should remind both of them that even in the less mobile portions, the model merely predicts what is *not* going to happen next. Indeed, the very essence of the model is that once a blocked degree of freedom is released the actual performance of the released movement type becomes unpredictable in time and sequential order. I am therefore thankful to **Goldberg** for drawing my attention to Bohm's (1980) notion of the implicate order. The mobility gradient could perhaps be envisaged as a simplified process of "enfoldment and unfoldment" limited to the three spatial component-variables and to the body dimension. Starting from immobility, the three component-variables are se-

quentially superimposed on each other. Although they intermingle with each other, the movement types belonging to a specific component-variable nevertheless act as a relatively independent ensemble. These movement types become progressively separated from each other in the process of enfoldment, by variable sequences of movement types belonging to other component-variables and by variable intervals of time (a point not realized by **Lyon**). Yet they nevertheless abide by a common, component-specific rule. Whereas in warm-up the component-variables become enfolded into each other and their order is "implicated," apomorphine and amphetamine bring together their constituent movement types so that they are reconstituted sequentially, in the reversed order, to their relatively pure forms. Because the time onset for movement within each spatial component varies, as the component specific rate of buildup perhaps also does, time may not be directly relevant to the description of the implicate order, nor would the methods of sequence analysis used to examine the more familiar instances in which the order is "explicated" (Bohm 1980, p. 154).

2.6. The examination of behavioral detail is a prerequisite for the establishment of generalities

For **Schleidt** "a fundamental assumption we must confess is our belief that units of behavior, in the form of behavior patterns are *a priori* present and are not a construct of the human mind" (Schleidt & Crawley 1980). For **Barlow** (and **Bekoff**), modal action patterns are recognizable patterned units of motor output used to test specific hypotheses. One term originally attached by Lorenz to these patterned units was the *erbkoordination* – an innate coordination. This term had the advantage of highlighting the (qualitative) aspect of motor coordination. The English term "fixed action pattern," which replaced it since the 1949 ethological conference (Lorenz 1970), sidestepped the issue of coordination and highlighted the less fundamental, quantitative question of "how fixed is fixed" (Schleidt 1974; Barlow 1977; Bekoff 1977). Since that time the very existence of discrete packages of motor output was taken for granted by quantitative ethologists who thus became the "atomists" criticized by Lorenz (1971, p. 256). Because in the majority of cases this entity could not be shown to have a physiological reality, the concept practically separated ethologists – who should have remained the custodians of the morphology of movement – from students of motor control. Perhaps because of the absence of a viable concept of motor coordination, ethologists shifted their attention either to the interface between behavior and ecology or to the neuroethology of partial systems where one could sidestep the problem of whole-animal movement description.

It is no wonder that in being committed to the convenient assumption of one-behavior-at-a-time, reading my descriptions is for **Barlow** like reading a newspaper with a microscope; **Bekoff** cannot decide whether my descriptions are too coarse (commentary) or too detailed ("the temptation for 'overkill' [in terms of detail] must be resisted"; Bekoff 1979, p. 77); and for **Byers** it is too detailed for many questions and too coarse for identifying units of behavior. Like **Schleidt** and **Bekoff** I cannot see any a priori criteria for selecting one behavioral detail

over another. I therefore see no other way than to start with a mass of detail. EW analysis singles out the details that are relevant; they are established as such because together they yield an overall pattern. It is the sequencing rules of the mobility gradient that thus establish the types of trunk movements and the stepping associated with them as the elementary building blocks of this gradient. This is also the answer to Byers's question "How should I go about defining behavioral units?" In summary, the only danger with detail is that one may get lost in it. By showing how to get there and come back reliably I have shown that "messing" with detail is not only feasible but also fruitful.[2]

2.7. The natural geometry of behavior is indispensable for the assessment of brain/behavior relations

Because the brain can be regarded as a geometrical object (Pellionisz & Llinas 1979) and because the mobility gradient rules specify the geometrical demands on the brain, I suggested that these rules should be indispensable in the study of the neurobiological basis of the examined behaviors. Whereas for **Fentress** the jury was still out on this suggestion, **Eaton** and **Cools** have tested and supported it in species as remote as a fish and a rat. In Eaton's study the description of the fish's C-start is provided in kinematic terms which were derived independently of EW yet are equivalent to it. Only this description provided a smooth reduction of the movement to the EMG and to the electrophysiology of a population of descending reticulospinal neurons, including the Mauthner cell, whose commands to the motoneurons were monitored. By also taking into account the stimulus direction, Eaton and colleagues established a neural sensorimotor computation of the process.

Cools produced portions of the mobility gradient by local bilateral injection of drugs to the rat's olfactory tubercle, the ventral striatum, and the dorsal striatum. By either blocking or stimulating dopaminergic receptors in each of these nuclei he was able to shift the root of the movement – the joint(s) caudal to which there is no movement – along the body dimension. Cools postulates a neural mechanism that should explain warmup and shutdown in moment-to-moment behavior and in ontogeny. He also points out that the six anticipated features of hypermobility listed in section 3.8 of the target article provide an "excellent summary" of the behavioral effects seen in rats with reduced GABA-ergic activity within the deeper layers of the superior colliculus, a striatal output station. Note that whereas based on my previous familiarity with play behavior I cannot refute **Barlow's** suggestion that the six features have been established *post hoc*, here these features characterize a behavior I have never seen.

Although **Rebec** considers the behavioral scheme I present to be of fundamental importance to neuropsychopharmacology, he points out the danger of emphasizing a single underlying process to explain the mechanism of action of amphetamine. He cites recent evidence that rather than other neurotransmitter systems being modulators of dopaminergic function, as implied in my presentation, it is dopamine that may play the true modulatory role. **Cools** adds the colliculoreticulospinal and/or colliculospinal system to the systems that form

part of the hard-wired coordination of the mobility gradient. **Whishaw**, who revealed a surprising association between this gradient and feeding behavior, suggests that because the forebrain (1) is always active during movements encompassed in this gradient, (2) reflects details of the movements, and (3) can be inactive during other movements, it could both monitor and direct expansion and constriction of mobility. **Goldberg** reports that the primate's supplementary motor cortex has been separately reported to be engaged in the coordination of axially based movements and in the elaboration of voluntary (free, nonstimulus-bound) movements based on internal context. He points out that this dual role fits well with the intrinsic relationship highlighted in my model between the freedom of trunk movement and the organism's ability to change its base of support. In our own work with Parkinsonian patients we have noted that when asked to perform tasks which required extensive changes in their base of support, such as crawling, walking on all fours, or barrel rolling, they became practically pinned down to the ground (Eshkol & Golani, unpublished results).

I should like to end this section by recalling that not unlike the rules formulated in linguistics, the abstract rules of the mobility gradient have a validity of their own, independent of the particular brain operations that mediate them (Teitelbaum & Pellis, in press) and independent of theoretical models which account for the underlying organization.

3. Conclusion

In writing the target article I had two purposes that I believe are now fulfilled: The first was to highlight a blind spot in the behavioral sciences with regard to the need for a universal symbolic language for the description of whole-animal movement. The state of this art is now documented in the commentaries. The second purpose was to demonstrate how, by using an appropriate language, a simple set of common generative rules can be shown to produce the transition from stereotyped to what appears to be free behavior.

As I see it, the main value of this proposal is not in the particulars of the model, but in providing an integrative method for establishing behavioral continuities. In using this integrative method, attention will be attracted to new meaningful details that will either fit the model or modify it, or even suggest a better one.

NOTE
1. Unlike horizontal and vertical movements, forward "movement" refers to a composite product which should have termed forward transport.
2. A detailed investigation of single acoustical parameters and their variation in parallel with the behavioral process also proved fruitful in **Todt & Hultsch's** analyses of birdsong.

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Letters *a* and *r* appearing before authors' initials refer to target article and response respectively.

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