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Applied Animal Behaviour Science 65 (1999) 191–220

APPLIED ANIMAL BEHAVIOUR SCIENCE

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The D.G.M. Wood-Gush Memorial Lecture

Phenotyping stereotypic behaviour: collective variables, range of variation and predictability

I. Golani [*], N. Kafkafi, D. Drai

Department of Zoology, Tel Aviv University, Tel Aviv, Israel

Abstract

Stereotypy is the narrowing down of an animal's behavioural repertoire. Starting from normal behaviour there is a continuum between rich and free behaviour on the one hand, and dull and predictable stereotypies on the other. To study the continuum all that one needs are ''knobs'' (like drugs or stress) that shift the behaviour from one end to the other, and a method for documenting the behavioural shift. The degree of narrowing down of the animal's repertoire is measurable in terms of the number of ''collective variables'' available to the animal, the range of values each collective variable can take, and the predictability of sequences of movements. We substantiate this thesis by presenting examples taken from the normal and drug-induced behaviour of the rat.

Keywords: Drug-induced stereotypies; Behaviour pattern; Coordination dynamics; Dynamic Systems; Motor control; Mobility gradient

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1. Introduction

1.1. The problem — 1st round

A sense of uneasiness pervades the current literature on animal stereotypic behaviour: a field of science begins with some objective definition of the building blocks of its subject matter, yet stereotypy is an ill-defined concept. Anyone can identify a stereotypy upon observing it, yet the morphological properties of stereotypies are vague, their borders are blurred, the diversity of kinds of stereotypies is very large, and the claim that stereotypies have no obvious goal or function is often based on a subjective impression. Stereotypies are defined as unvarying, but so are many normal behaviours; they are

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[*] Corresponding author.

PII: S0168-1591(99)00085-4

defined as repetitive, but so is every oscillatory normal behaviour; and the goals or functions of normal unconditioned behaviours are also seldom obvious (Mason, 1993).

1.2. The solution — 1st round

To overcome these problems we suggest a framework for an objective definition of animal stereotypic behaviour. Such definition should be based on intrinsic structural properties of the behaviour (as opposed to ad hoc definitions). Therefore, we build our framework around the concepts of invariance [1] and stability, which have demonstrable objective properties. We first look at variables that disclose kinematic invariants and stabilities. The variables that disclose such stabilities are considered to be good ‘‘collective variables’’, and the stabilities they disclose define behaviour patterns. Next, we find or create situations in which there is a gradual transition (a gradient) from normal behaviour to stereotypic behaviour, or vice versa. We finally characterize the animal’s repertoire of movements at a particular position along that gradient, by listing (i) the collective variables it includes, (ii) the types of patterns included within each variable, and (iii) by describing the degree of predictability within and across patterns.

Before presenting our solution in a formal way, we will first re-formulate the problem, then illustrate the concept of collective variables and the behaviour patterns included in the concept, and then list and define the collective variables featured in the present review.

1.3. The problem — 2nd round

The uneasiness formulated by Mason points to a major problem in the study of motor behaviour.

(i) Since vertebrates consist of a linkage of rigid segments, each joint adds at least 1 micro degree of freedom (micro KDF) to the animal’s kinematics. It is extremely difficult and sometimes even impossible to know from the outset which of all these micro KDFs is, and which is not relevant to the objective definition of a behaviour pattern.

(ii) Had the coordination among all these micro KDF been fixed, then all of them could have been wrapped up in a single, synchronous behaviour pattern. In this way the many potentially available micro KDF would have been reduced to a single collective variable. Even the most rigid stereotypies, however, show some variation in the coordination among the various micro KDFs. Had it been the case that, say, side-to-side head movements (e.g., Meyer-Holzapfel, 1968) were always executed with the same coordination between the micro KDFs, then it would have been sufficient to record, for example, head angle in order to know what the neck, the chest, the pelvis, the forelegs and the hind legs were doing. In reality, however, the execution of the same stereotypic pattern does not imply that the same timing between movements, or even the same

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[1] The property of invariance has been included in the definition of sterotypy by, for example, Ödberg (1978) and Würbel (1997).

movements of the same parts of the body will be performed (and in this way reduce the actual number of degrees of freedom). This may be true even for ‘‘simple’’ stereotypies (e.g., Cronin and Wiepkema, 1984; Szechtman et al., 1985; Adani et al., 1991; Kafkafi et al., 1996). This problem which exists at the time scale of synchronous coordination of the micro KDFs belonging to a single motor pattern becomes more severe when the phenomenon consists of a sequence of patterns.

1.4. A solution — 2nd round: using good collective variables

(i) Since we do not know from the outset which of all the micro KDFs is and is not relevant to the objective definition of a behaviour pattern, measuring all the relations between the segments is not a matter of becoming too detailed, but an indispensable preparatory stage in the search for the relevant ones.

(ii) We need a framework within which both the variable and the stable aspects would be an intrinsic property of the structure of behaviour. To establish such framework, we look for good collective variables of movement.

1.4.1. What are good collective variables of movement?

The problem of the heterogeneity of coordination patterns could be overcome by finding kinematic invariants that are generated by the relations among several micro KDFs. During gallop, for example, the changing angular relations between the parts of a leg generate a relatively invariant step cycle, which in turn generates, together with the step cycles of the other three legs, a specific stable value of *relative phase*. This value identifies in an objective and reliable way the gallop pattern. A continuous change in the animal’s speed involves a shift from one such stable value to other sets of stable values, yielding, e.g., gallop, canter, trot and diagonal walk (Collins and Stewart, 1993). Relative phase is a good collective variable because it identifies several stable gait patterns. Put differently, it could be said that it is a good collective variable because it: highlights several stable values that wrap up all the micro KDFs of the four legs into few functional patterns (invariants); shows how all the micro KDFs are enslaved to maintain few invariants; or, compresses all the micro KDFs of the legs into a single degree of freedom (relative phase). A good collective variable must thus be shown to be informative, in the sense that a specification of, say, a momentary phase of the gallop cycle would serve as an estimator of the values of the micro KDFs that generate this momentary phase.

Another example of a good collective variable is taken from honey badger (*Mellivora capensis*) ritualized fighting interactions (Yaniv and Golani, 1987). Here, the collective variable is the relationship of opposition between the partners. This variable specifies the surfaces of the parts of the bodies of each of the two partners that touch or almost touch each other. During ritualized fighting, two specific values of opposition are stable. In one, opposition is maintained between the snout of the inferior and the cheek of the superior for relatively long time intervals. The inferior maintains its position by tracking the superior’s moving head. The tracking has a priority over the other movements, so that an apparent ‘‘joint’’ is formed between the snout of the inferior and the cheek of the superior. Through this joint, the superior ''forces'' the inferior, without actually pushing it, to rear, roll, run and tumble. The inferior's movements (and to some extent also those of the superior) are enslaved so as to maintain the specific snout-to-cheek opposition. In Dynamic Systems (Kugler et al., 1980; Abraham and Show, 1992; Kelso, 1995) terminology, the cheek of the superior forms a point attractor for the trajectories of opposition on the superior's body surface. The relationship of opposition is a good collective variable because it compresses the micro KDFs of the partners during ritualized fighting into two stable patterns and the transient trajectories between them (the second pattern of opposition is maintained between the hindquarters of the inferior and the snout of the superior).

A specification of momentary phase in a gait pattern is sufficient for establishing the respective phases of all the movements of all the segments of the legs. A specification of an opposition pattern is much less informative, since the partners exercise a variety of strategies to maintain the pattern (the kinematics of the micro KDFs are less predictable).

Both relative phase and opposition relate exclusively to synchronic organization, i.e., they wrap up only simultaneously recorded micro KDFs.

1.4.2. What are good collective variables of rat locomotor behaviour?

The methods we use for uncovering good collective variables are described elsewhere (N. Kafkafi and I. Golani, submitted). Here we merely list and describe the variables that have already been established.

1.4.2.1. The mobility gradient collective variables. Our micro KDFs describe the relations and changes of relation between the parts of the body of a quadruped in time. Our aim is to compress this large set of time series into a few collective variables.

Pronounced immobility in infant rats is a good starting point because it is followed by a gradual and slow build-up in movement. The first movements to appear are horizontal (lateral) movements (Fig. 1). During this type of movement the moving part of the trunk moves on its next, immobile neighboring segment. Because the parts of the body are recruited in a cephalo-caudal order and because of the mechanical interdependence between them, a movement of the head on the immobile chest involves only an angular displacement of the head. A movement of the chest on the immobile pelvis involves a displacement of both the chest and the head. A movement of the pelvis involves a displacement of the pelvis, the chest and head. A specification of the most caudal segment that moved implies therefore that the segments anterior to it were displaced as well. Therefore, this is a good measure of the portion of the body that participated in a movement.

Forward movement is added to the infant's repertoire later on in the sequence, following the same regularities observed in the horizontal dimension, and vertical movement is added last, also abiding by the same regularities (Golani et al., 1981; Eilam and Golani, 1988) (Fig. 1).

The first movement of a part of the trunk within a specific dimension announces the repeated performance of this type of movement from that time and on. Therefore, a specification of the timing (since initial immobility) of the first movement of a segment within a spatial dimension provides a measure of the build-up accomplished so far

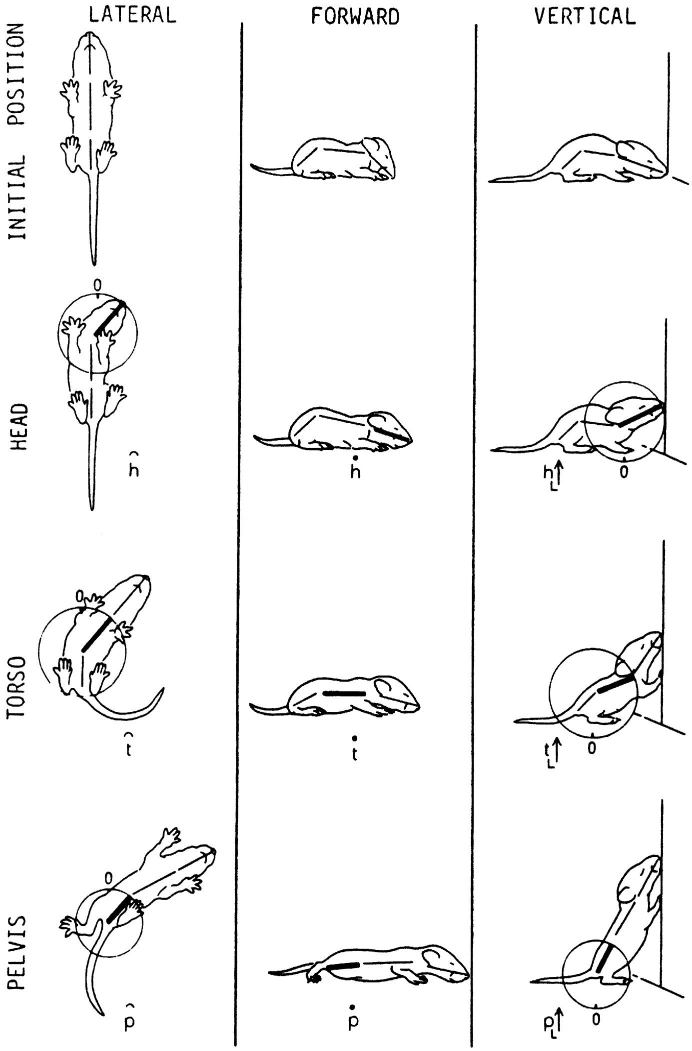
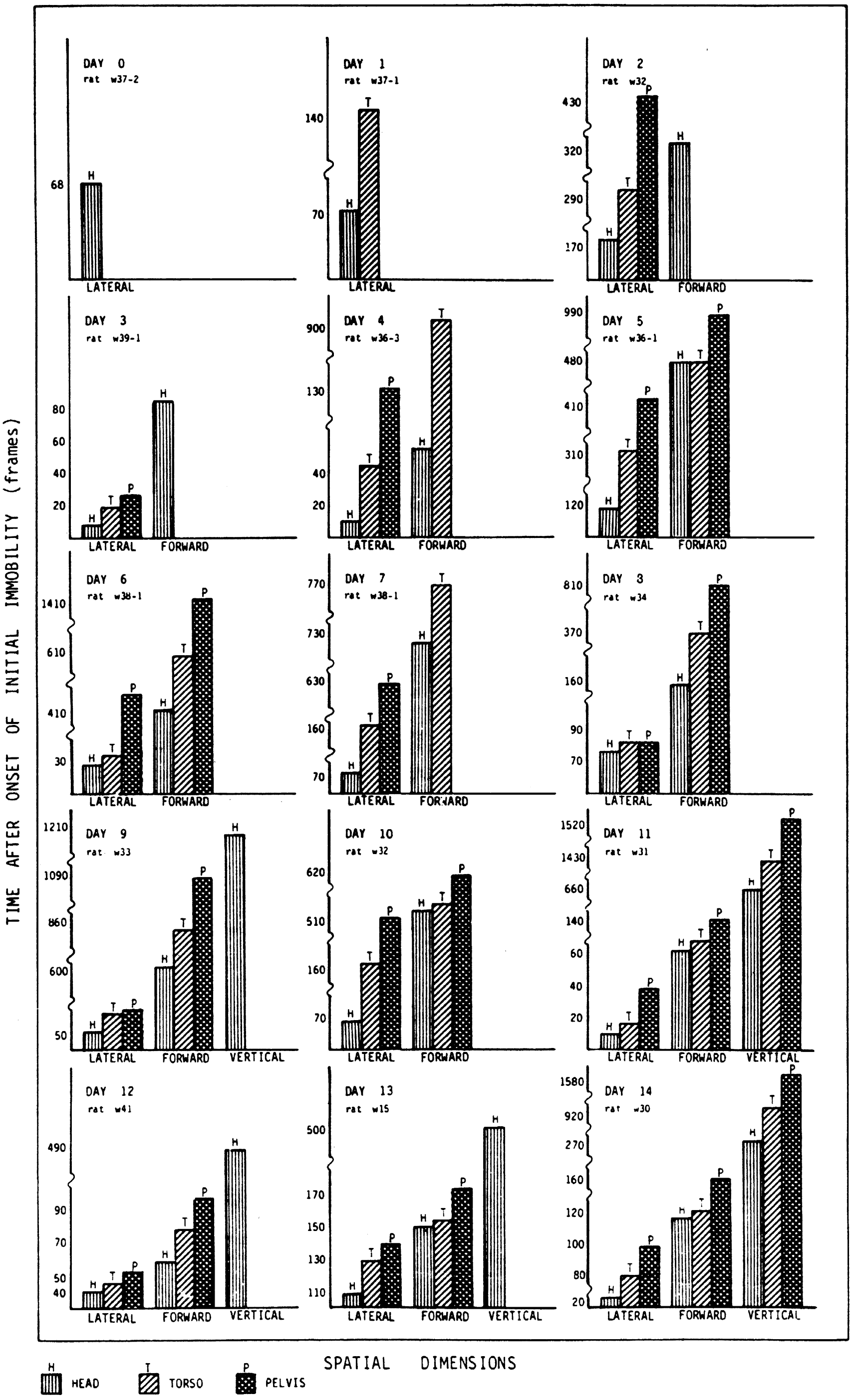


Fig. 1. The infant rat's trunk as a linkage of articulated axes: examples of the effect of movement of a caudal part of the trunk on the parts anterior to it. Columns represent the three mobility gradient collective variables. Horizontal lines represent the most caudal part of the trunk that moved. The axis of the most caudal part that moved is represented by a thick bar line.

within that dimension (Fig. 2). The dimension-specific cephalo-caudal regularity provides a partial justification for the definition of the following collective variables.

(a) Horizontal (lateral) movement: Lateral angular displacement of the head in the absolute frame, together with a specification of the most caudal part of the body that participated in lateral movement wraps up lateral head scans, lateral forequarter scans, sideways stepping of the forelegs, backward stepping of the inside hind leg and pivoting in place.


TIME AFTER ONSET OF INITIAL IMMOBILITY (frames)
SPATIAL DIMENSIONS
DAY 0
rat w37-2
DAY 1
rat w37-1
DAY 2
rat w32
DAY 3
rat w39-1
DAY 4
rat w36-3
DAY 5
rat w36-1
DAY 6
rat w38-1
DAY 7
rat w38-1
DAY 8
rat w34
DAY 9
rat w33
DAY 10
rat w32
DAY 11
rat w31
DAY 12
rat w41
DAY 13
rat w15
DAY 14
rat w30
LATERAL
FORWARD
VERTICAL
H
T
P
HEAD
TORSO
PELVIS

(b) Forward movement: The amount of transport of the tip of the quadruped's snout along the direction of the longitudinal axis of the head, together with a specification of the most caudal part of the body that participated in forward movement wraps up forward neck stretching, forward torso stretching, forward shift of weight without stepping and forward stepping of each of the four legs.

(c) Vertical movement: The amount of raising of the tip of the quadruped's snout, together with a specification of the most caudal part of the body that participated in vertical movement wraps-up head raising, forequarter raising without release of foreleg contact with the ground and rearing on hind legs.

Note, that these collective variables relate to both synchronic organization (i.e., they wrap up simultaneously recorded micro KDFs), and diachronic (sequential) organization (i.e., they also condense into a single symbol the build-up accomplished that far).

1.4.2.2. Collective variables of the rat's path. On a two-dimensional surface, forward progression and horizontal movement (turning) generate the animal's path in the environment. Because of technical reasons, these two variables are not available to us. We do have access, however, to a single time series of coordinates that describe the animal's location in reference to an arbitrary axis of origin. In studies of the open-field behaviour of rats performed in our laboratory, this time series is first compressed, based on intrinsic statistical properties of the raw data, into an alternating sequence of segments of progression and segments of ‘‘staying-in place behaviour’’ (termed in this review ‘‘stops’’; D. Drai et al., submitted). To become a good collective variable, this time series should be described in reference to an axis of origin that is meaningful to the animal. A natural point of reference for the required transformation would be the animal's most preferred place — its home base — a most stable pattern of exploratory behaviour. It is defined as the place to which the rat pays the highest number of visits, and in which it spends the highest cumulative time (Eilam and Golani, 1989). In the next computational step, the animal's overall path throughout the session is partitioned into ‘‘excursions’’ — sequences of progression and stops that start and end at the rat's home base. This yields a collective variable termed

(d) The number of stops per excursion. This collective variable is established by showing that in normal rats, excursions including one stop are as frequent as excursions including two stops . . . as excursions including n stops, where n is an upper limit, after which there are no excursions with a higher number of stops. In statistical terms, this means that the number of stops per excursion has a uniform distribution, or — that the probability of returning to the home base increases after each stop (Golani et al., 1993).

The appropriate collective variable generating the animal's path in the environment should be a vector describing the animal's momentary velocity, again in reference to the home base. A candidate for a good collective variable would thus be as follows.

(e) The collective variable of the rat's trajectory in locale space. This variable consists of the rat's location measured in reference to the home base, and of its velocity

Fig. 2. The timing of the first appearance of movement of each of the three parts of the trunk within each of the three collective variables. One example was selected at random for each developmental day.

vector measured in reference to the home base. Although it is defined in pure kinematic terms, this collective variable reveals several patterns that already imply (tacitly) spatial memory, rat-defined places, and familiarity. The rat's behaviour consists of excursions from the home base and back to it; the outbound portion of excursions is slow and intermittent, and the inbound portion is fast and continuous (attractive excursion); with time and repeated exposure the rat establishes new places in the arena; the length of excursions increases, and the attractive excursion is partitioned into a proximal portion which becomes repulsive in relation to the home base, and a distal portion which is attractive in relation to the home base (Tchernichovski and Golani, 1995; Tchernichovski and Benjamini, 1998; Tchernichovski et al., 1996, 1998).

2. The thesis of the present review

We propose the following.

(1) Stereotypy can be expressed as a function of the number of collective variables available to the animal at a particular time, a function of the range of values these collective variables can take, and a function of the predictability of the sequencing of elements within and across collective variables. It is *not* a kind of behaviour.

(2) Stereotypy (or its inverse, freedom) is a property of a behaviour seen within a continuum. Therefore, it is necessary to generate this continuum by finding a parameter — a ''knob'' which by being ''turned'', can generate the continuum from relatively free to increasingly more stereotyped behaviour and back.

More formally, ''a behaviour is stereotyped when there exists a set of collective variables that characterizes the behaviour, and a manipulable variable we will call a parameter (drug effect, stress level, etc.), such that setting the value of the parameter to higher values results in:

(i) Reducing the number of collective variables available to the animal,
(ii) Constraining the range occupied within collective variables, and
(iii) Increasing the predictability in sequences of movements within and across collective variables.

In the case of other parameters (age, stage of recovery), setting the value of the parameter to higher values results in the opposite effects.''

In Section 3, we present examples of rat stereotypic behaviour that support this thesis. We illustrate, first how the rat's repertoire of collective variables changes, then how the range of values these variables can take changes, and finally, how the predictability of sequences of movements and of patterns changes.

3. Examples that illustrate our thesis

3.1. Changes in the rat's repertoire of collective variables

3.1.1. Increasing the number of collective variables

When placed outside its nest in a novel environment, an infant rat becomes immobile and then starts to move. In an infant, of say 15 days, the three mobility gradient collective variables are added to its repertoire one by one, each setting in separately in a cephalo-caudal order. Early in ontogeny, however, this ‘‘warm-up’’ process culminates somewhere along the way, without reaching a full-blown build-up. In a novel environment, the infant’s behaviour in the first few days appears rather stereotyped: only one collective variable — the horizontal one — is available to it. During days 3–7, as the forward collective variable is gradually added to the repertoire, two collective variables are available to the infant. At that time, the behaviour already appears less stereotyped, since the horizontal and forward movements intermingle (and are, as often, also

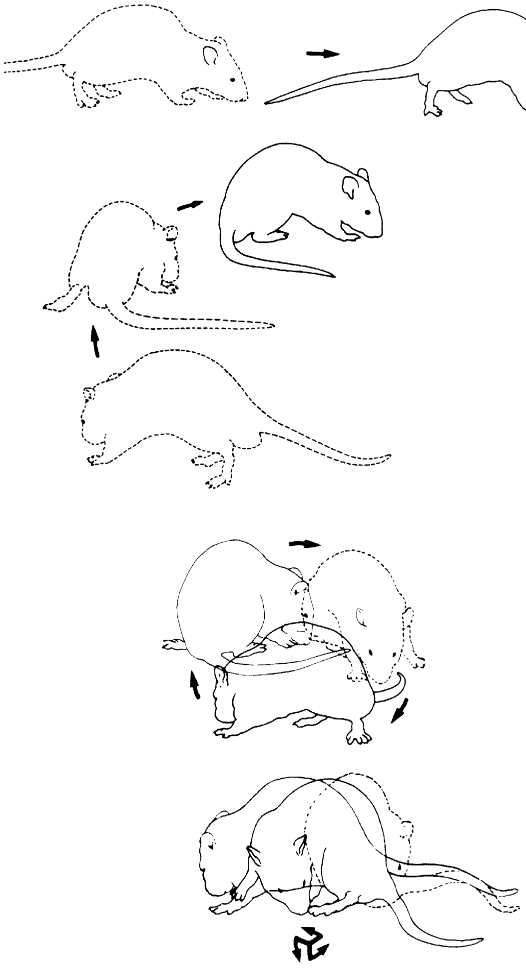


Fig. 3. A schematic illustration of the shut-down of collective variables under APO. Four stages are illustrated from top to bottom, starting with the first stage. In the first stage, the rat’s snout is in loose contact with the ground all the time, i.e., the rat’s repertoire does not include the vertical collective variable, while in the fourth stage, the rat’s repertoire does not include the forward collective variable. In the second and third stages, the range of forward movement is gradually reduced.

superimposed on each other). Finally, the infant's behaviour appears rather unpredictable (free) as vertical movements are added to its repertoire.

In this study we characterized the infant's level of stereotypy by the number of collective variables available to it at each stage (Eilam and Golani, 1989; Figs. 1 and 2). The degree of stereotypy following severe bilateral lateral hypothalamic damage has been similarly assessed, by listing the same collective variables in the recovering rat's repertoire (Golani et al., 1979).

3.1.2. Reducing the number of collective variables

The mobility gradient collective variables. With the nonselective dopaminergic drugs, the knob is turned in the opposite direction. Under both 1.25 mg/kg s.c. apomorphine (APO) and 5 mg/kg s.c. amphetamine (AMPH), there is a progressive reduction in the number of collective variables available to the animal. The vertical collective variable is eliminated from the behaviour first, and the forward next, leaving the animal to exercise only the lateral collective variable. This ''shut-down'' process allows us to partly assess the level of stereotypy by specifying the number of collective variables available to the animal at each moment in time, per stage, or per dose (Fig. 3; Szechtman et al., 1985; Eilam, 1987).

In warm-up, the emergence of a new collective variable is accompanied by a temporary excessive performance of movements within that collective variable. For

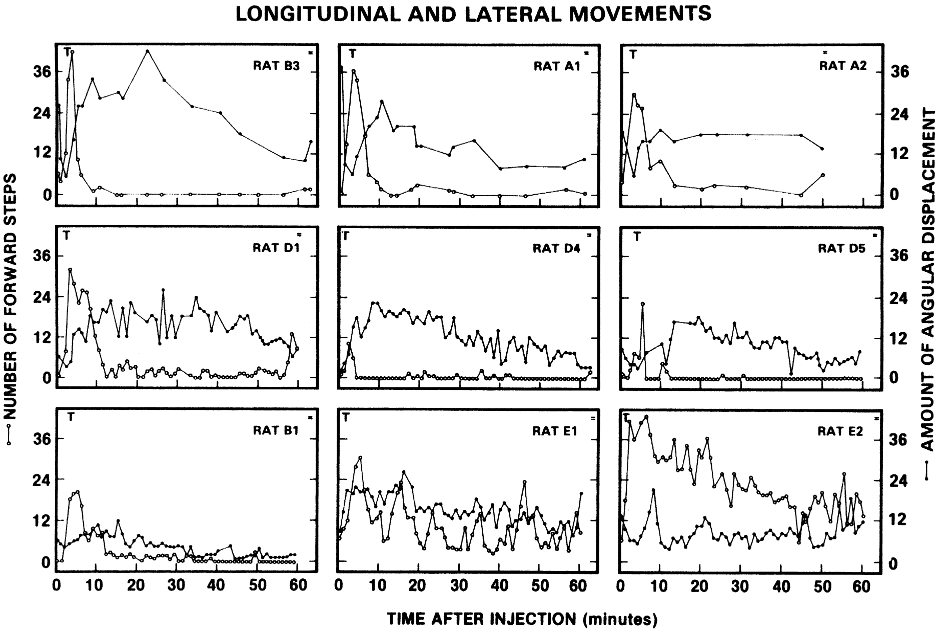


Fig. 4. Time course of forward (longitudinal) progression (number of forward steps; designated by open circles) and of lateral angular displacement of the rat's head (1 = 45°; solid circles) in individual rats, per 15 s of activity, injected with 1.25 mg/kg APO. The sign ''T'' indicates the timing of complete elimination of vertical movement.

example, the developmental day in which side-to-side head movements first appear is marked by an outburst of side-to-side head movements. The developmental day in which rearing first appears is marked by repetitive rearing, etc. (Golani et al., 1981; Eilam and Golani, 1988). During shut-down, there is a temporary enhancement of a collective variable before its elimination. For example, excessive rearing precedes the elimination of vertical movement, excessive forward locomotion precedes the elimination of forward movement, etc. The paucity of collective variables together with the excessive repetition of the same movements creates the impression of an aimless stereotypy (Fig. 4; Golani et al., 1979, 1997; Szechtman et al., 1985; Adani et al., 1991).

The collective variable of the animal's path. A total and abrupt elimination of this variable is seen right at the start of the session in hooded and Wistar rats treated with 1.25 mg/kg APO (but not in tame wild house rats *Rattus rattus*; D. Eilam and I. Golani, unpublished data). The laboratory rat keeps moving incessantly in the environment, but there appears to be no relation between where it is and what it does, nor is there any topographical regularity in the path traced by it (Szechtman et al., 1985). Tame wild rats treated with AMPH similarly drift haphazardly on the platform toward the end of a 1-h session (Eilam and Golani, 1994).

3.1.3. Keeping the number of collective variables stable

The mobility gradient collective variables. At a dose of 0.5 mg/kg, the D2/D3 receptor agonist quinpirole (QUIN) induces levels of hyperactivity that are not lower

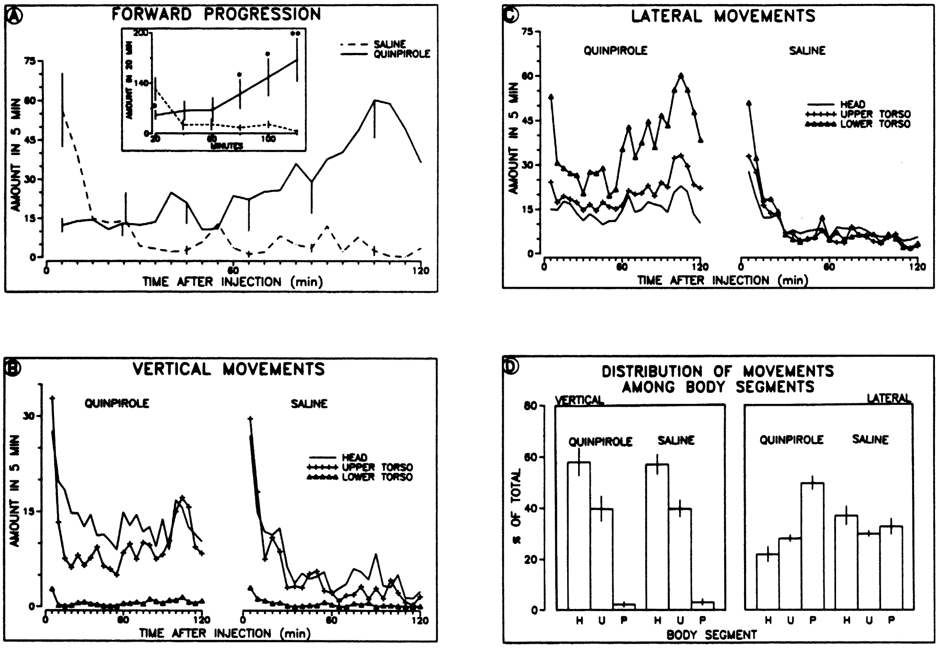


Fig. 5. Time course of the effect of QUIN on forward (A), vertical (B), and lateral (C) movements of body parts (head, upper torso and lower torso), and the proportion of vertical and lateral movements performed by each body part (D) (Eilam et al., 1989).

than those shown with APO and AMPH. Surprisingly, the pronounced hyperactivity is not accompanied by a shut-down of any of the three collective variables (Eilam et al., 1989; Fig. 5).

Chronic administration of QUIN enhances the rat's hyperactivity several folds, but it does not eliminate any of the collective variables (Eilam et al., 1989). A reduction in the number of collective variables is, thus, not to be taken for granted during hyperactive behaviour. The behaviour observed under QUIN appears highly stereotypic in spite of the fact that the number of collective variables is not reduced. As will be shown below (end of Section 4 and Section 5.1, this is because of other features of stereotypy exhibited.

The collective variable of the trajectory in locale space. QUIN (0.5 mg/kg) induces intense hyperactivity, but does not eliminate the collective variable of the path in locale space throughout the 1-h session (Eilam et al., 1989). Again, although chronic administration of QUIN (two injections per week for 5 weeks) enhances the rat's hyperactivity, it does not eliminate the regularity of the path traced by the animal in relation to the environment. In other words, even after chronic treatment, knowing the rat's location is informative about where it came from and where it is going next (Szechtman et al., 1998).

In summary, a list of the collective variables that are included in the animal's repertoire is a useful criterion for phenotyping stereotypies because it compresses the apparent variability into a few criteria that can be used to both differentiate and highlight commonalties among species-specific, strain-specific and preparation-specific stereotypies.

4. Changing the range of values collective variables can take

A horizontal movement initiated by the head does not necessarily propagate along the whole rat's body. It may be confined to the head (as in a lateral head scan), to the head and the chest, or to the head, the chest, and the forelegs..., etc., or else it may include the whole body (as in turning). We ask how constrained the rat's repertoire is in terms of the portion of its body that participates in movement within a given time period. A rat whose movement is mostly confined to the head is relatively stereotyped. Similarly, a rat whose head movements almost always propagate along its whole body (as in a whole-body turn) is stereotyped. In contrast, a rat whose head movement may be followed by the recruitment of any number of parts of the trunk is relatively free.

When placed outside their nest, 1-day-old infant rats, for example, perform only lateral head movements. As the root of the movement shifts caudad, the range of body parts engaging in lateral movements increases daily (Eilam and Golani, 1988). In adult intact rats all the anatomically possible propagation patterns can be observed within a single 5-min bout of lateral movements (Golani et al., unpublished data).

Eliminating forequarter-scanning movements. We use the time elapsed since the injection of AMPH (5 mg/kg) as a parameter and observe how it affects the range of body parts that participate in lateral movement. Once a head movement away from the straight midline position commences, we record the parts of the body that participate in that movement (head, chest, each of the forelegs, pelvis, each of the hind legs). We ascertain that the parts of the body indeed join in a cephalo-caudal order, and then estimate the probability for a part of the body to move laterally, given that its anterior neighbor has just moved laterally. This reveals that there is a long stage in which a lateral movement of the head is mostly followed by a lateral movement of the rest of the body in the same direction. Lateral movements that are confined to the anterior part of the body are rare, and sometimes even absent for periods of several minutes (this stage ends just before lateral rhythmic side-to-side movements set in (Taylor et al., 1974; Adani et al., 1991; Fig. 6).

Eliminating whole body movements. In LH rats, a part of the body does not recover movement within, say, the horizontal dimension (variable) unless the part anterior to it has already recovered movement along that dimension. The same rule applies to forward and vertical movements. Therefore, a specification of the most caudal part of the body that moved within the most ‘‘advanced’’ dimension provides a summary of the range exploited that far, an overall compressed measure of the recovery accomplished that far, and more generally, a measure of the rat’s global stereotypy (Golani et al., 1979).

Eliminating large amplitude movements of body parts. In normal rat behaviour, the amplitudes of lateral movement of an anterior part of the body, just before the movement propagates to the next caudal part, vary greatly. During the transition from immobility, for example, rats perform a very large movement of the head and the neck before the chest is recruited in movement, and a very large chest movement before a foreleg steps, etc. Later on in the warm-up process, smaller angles of recruitment become a majority (Golani et al., unpublished manuscript).

Once again, we demonstrate a reduction in the range of variation in the amplitude of lateral bending preceding recruitment in AMPH stereotypy. When more than one part participates in a movement away from the midline, we record the angle between the axis of the moving part and the axis of the next caudal part of the trunk, just before the caudal part joins the movement: the angle between the head and the chest just before the chest starts to move, and the angle between the chest and the pelvis just before the pelvis starts to move (Fig. 7a and b). During the stage of increased propagation along the body, these angles are significantly reduced (Fig. 8).

The behaviour of the AMPH rats is stereotyped, also because large amplitude steps are eliminated from the rat’s repertoire (Fig. 9; Adani, 1990).

Finally, the most striking feature of QUIN stereotypy at the level of inter-limb articulation is that it constrains lateral bending (Golani et al., 1997): QUIN rats tend to perform whole-body turning-in-place in the horizontal plane, with a straight or relatively straight trunk.

Eliminating small amplitude movements of body parts. One feature of the stereotypy characterizing LH rats is the very large amplitudes of lateral and forward movements of the anterior ‘‘movable’’ anterior part(s) of the body. Small amounts of lateral bending are practically absent during the early stages of recovery (Golani et al., 1979).

Reducing the number of stops per excursion. The upper limit on the number of stops per excursion is in the range of 5–14 stops. This upper limit is stable in normal hooded rats: we could not reduce it by reducing the size of the arena explored by the rats (from 8 × 8 to 2 × 2 m; Golani et al., 1993). When the effect of 5 mg/kg AMPH on tame wild rats throughout a 1-h session is used as a parameter, the number of stops per excursion is gradually reduced, reaching a maximum of 1–3 stops per excursion (Eilam and Golani, 1990, 1994).

5. Changing the predictability of behaviour

A priori, behaviour can unfold within all the above listed collective variables and yet be completely predictable. On the other hand, it may be constrained within a single collective variable and take a narrow range of as few as two values and yet be as unpredictable as a random sequence written in binary code. It may also spread over a wide range within each of many collective variables and yet be fully predictable. In other words, the predictability criterion is orthogonal to the other two criteria of the animal's repertoire contents.

5.1. Increasing the predictability of the rat's path in locale space

The parameter is the time elapsed since an injection of 5 mg/kg AMPH. In normal rat behaviour (Fig. 10), the identity of a visited place does not predict the identity of the next place to be visited.

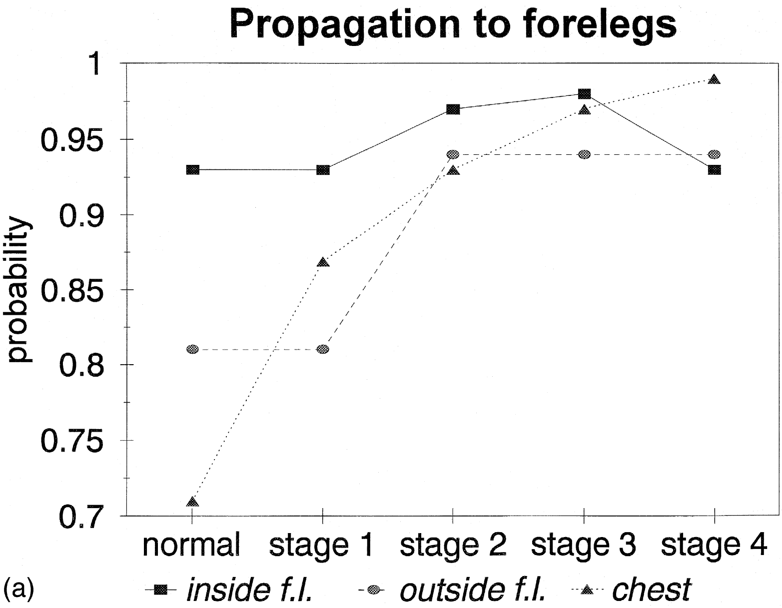


Fig. 6. (a) The estimated probabilities of an inside foreleg (f.l.) step, an outside foreleg step, and a chest movement, following a horizontal movement of the head. (b) The estimated probabilities of an inside hind leg (h.l.) step, an outside hind leg step, and a pelvis movement, following a horizontal movement of the chest. (c) The estimated probabilities of a chest movement following a head movement and a pelvis movement following a chest movement.

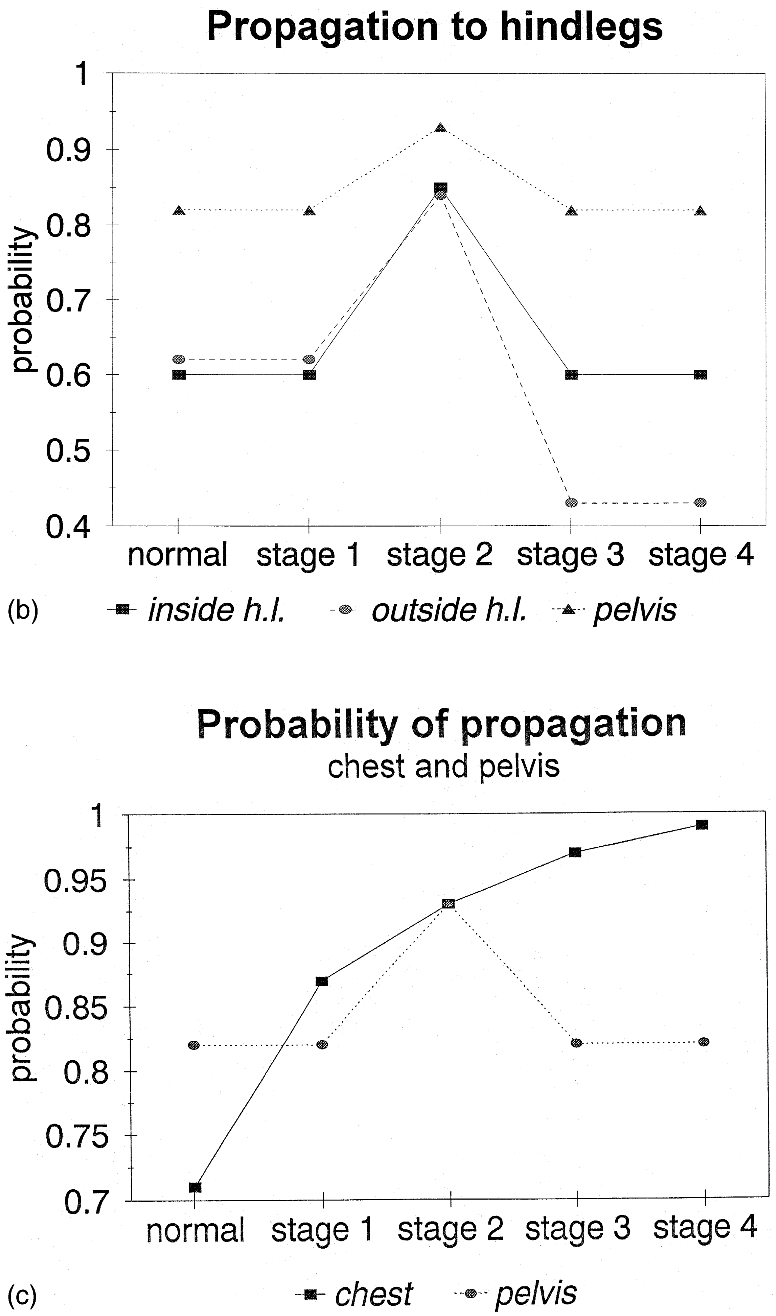


Fig 6 (continued).

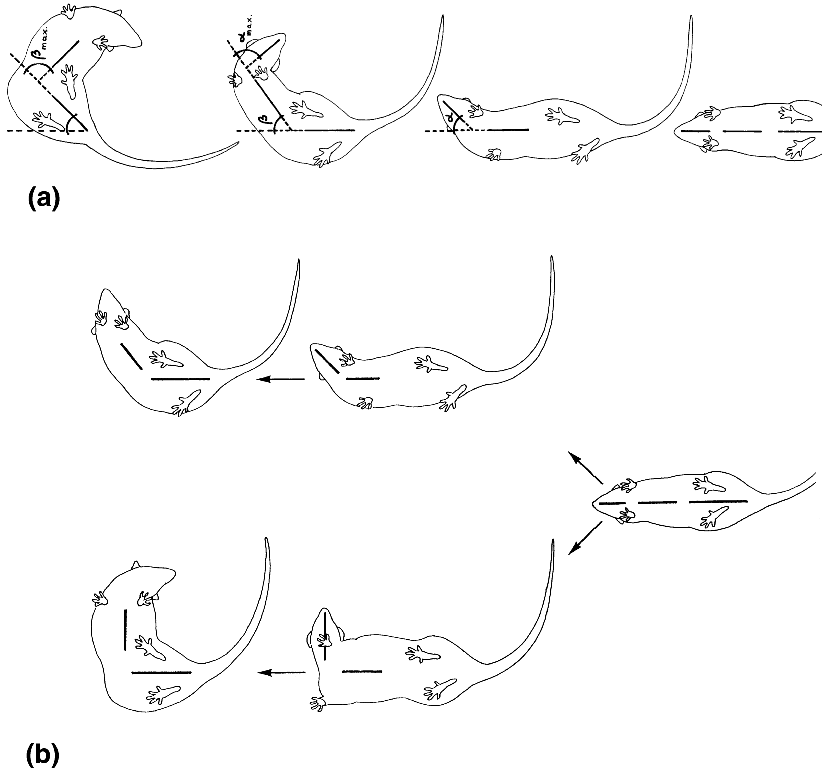


Fig. 7. (a) Ventral view of lateral bending in place. From right to left: straight initial position, lateral bending of head, lateral bending of chest and of head, and maximal bending of chest. Bar-lines represent the longitudinal axes of the head, the chest, and the pelvis. The angles measured in this study are: α — the angle of recruitment of the chest, α_{max} — the maximal angles obtained at the end of the bending process of the chest, β — the angle of recruitment of the pelvis and β_{max} — the maximal angles obtained at the end of the bending process of the pelvis. (b) Ventral view of lateral bending in normal (bottom) and AMPH-treated rats (top). The bending process proceeds from right to left. The heavy bars represent the longitudinal axes of the relevant parts of the body. The rat on the right shows the straight initial posture; the middle and left rats in the bottom row of b show the selected angles of recruitment from normal behaviour and finally the middle and left rats in the upper row of b depict the largest corresponding angles of recruitment that could be found during the second AMPH stage.

Under AMPH (Fig. 11), the identity of a stopping place increasingly predicts the identity of the place of the next stop, leading for example to the fully predictable sequence presented in Fig. 11, block E. The places of stopping within excursions become gradually consolidated into routes with specific identities: chunks which are performed in a fixed order en bloc. The identity of the places included in a chunk is arbitrary, in the sense of being idiosyncratic to that rat — a relatively complex individual habit acquired in the course of drug action. In Fig. 11, the path is consolidated into a single route, but with lower doses the path may be consolidated into as many as four routes. The behaviour within a route becomes increasingly more predictable, but the sequence of routes is typically unpredictable throughout the process. We have here a process of emergence of a new collective variable, idiosyncratic to the animal. The routes are the stable patterns included within this variable. In one rat the variable consolidates (or is compressed) into a single route or pattern, in another it consolidates into several routes. In many cage stereotypies the collective variable of the animal's path consists of one to several such consolidated patterns which are idiosyncratic to the performing animal.

As elaborated elsewhere (Eilam and Golani, 1994), the consolidation of exploratory behaviour into packages or chunks of stopping places is reminiscent of similar processes of chunking taking place during learning in humans (Miller, 1956). Chunking has been considered a strategy of coping with an increasing load on information-processing capacity in the context of the establishments of habits, and in the consolidation of memory (Murdock, 1961; De Grot, 1965; Simon, 1974; Moats and Shumacher, 1980).

That predictability is not a function of repertoire size is nicely illustrated in 0.5 mg/kg QUIN stereotypy induced by chronic treatment. In this preparation (Eilam and Szechtman, 1997), the repertoire of visited places is very small, yet within this repertoire the predictability of the places which are visited during shuttling between the two home bases is low, in spite of the intensive "knob-turning" produced by chronic treatment (Fig. 12). A similar phenomenon has been observed in nightingales during song acquisition in ontogeny: the birds establish packages, each package including a limited number of songs. During a singing bout a bird first sings the songs belonging to one package, then those belonging to another, etc., yet the sequencing of songs within a package is relatively unpredictable (Hultsch and Todt, 1989).

5.2. Increasing the predictability of sequences of patterns belonging to different collective variables

A rat treated with 5 mg/kg AMPH may be seen to, say, rear to the west and pivot clockwise in place A, scan forward to the north in place B, perform a side-to-side head movement in place C, and then repeat this sequence time and again (Eilam, 1987). A more constrained version of such correlation between specific movements and specific locations is seen in rats treated chronically with 0.5 mg/kg QUIN (Szechtman et al., 1998). The rat's current location predicts with high probability its current movements. Movement patterns and visits to particular places become consolidated into an idiosyncratic itinerary.

Similar itineraries are commonly observed in cage stereotypies: head weaving at particular locations in horses, side-to-side or circular pacing along the ‘‘well trodden path’’ (Hediger, 1964) in canids, and stopping at a particular place along a circular path, perhaps the vestige of a home base, in horses. Activities are organized around itineraries also in the wild. After leaving the den an animal follows the ‘‘familiar path’’ (von Uexkull, 1934) along which it performs at specific locations particular behaviours. In place A it scent marks, in B it takes a rest, in C it forages, etc. (Hediger, 1964).

Given the appropriate knob, the predictability of such itineraries can be manipulated: as horizontal side-to-side head movements emerge under 5 mg/kg AMPH, some of the rats first perform these movements at a particular place, then in several specific places, and finally indiscriminately all along the route. A similar phenomenon of initial restriction and subsequent spreading of a behaviour in locale space has been observed by us in a young captive honey badger (*M. capensis*). In the course of several weeks, while running around in its cage, this animal first log-rolled in one place, then in several places, and finally all over the floor of the cage (unpublished observations). A similar ability to partly restrict compulsive movements and vocalizations to particular places is known in humans suffering of *Gilles de la Tourette* syndrome. Obsessive Compulsive Disorder (OCD) patients sometimes show a similar predictability in the performance of a particular ritual in a particular place (H. Hermesh, Gehah Psychiatric Hospital, personal communication).

6. Predictability as stability in a dynamic non-linear system

Until now we have not defined what we mean by the term ‘‘predictability’’. The meaning of the word used here is the same as that used in weather forecasting. That is, the amount of certainty with which we can guess, from knowledge of the past and of the present, what will happen in the near future. It is important to stress, however, that high

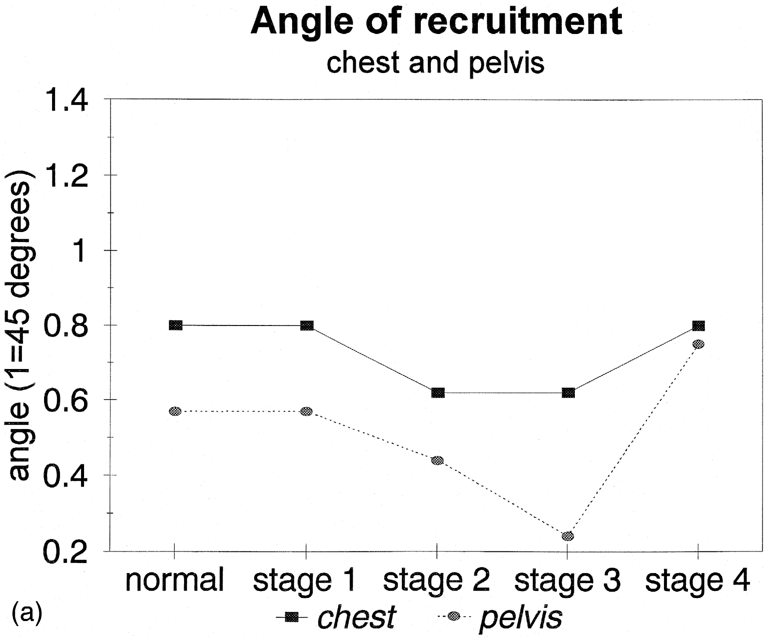
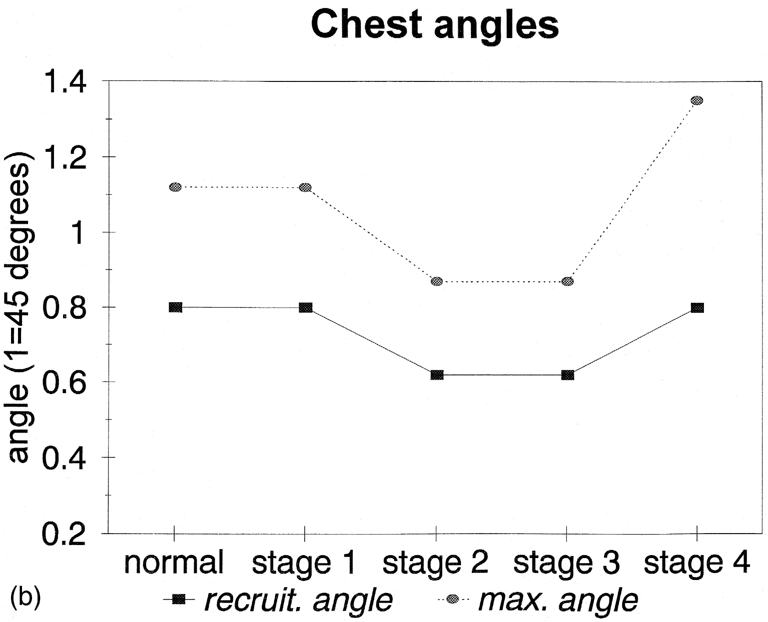


Fig. 8. (a) Expected angles of recruitment of chest and pelvis. (b) The expected angles of recruitment and the corresponding maximal angles obtained during lateral bending of the chest. (c) The expected angles of recruitment and the corresponding maximal angles obtained during lateral bending of the pelvis.



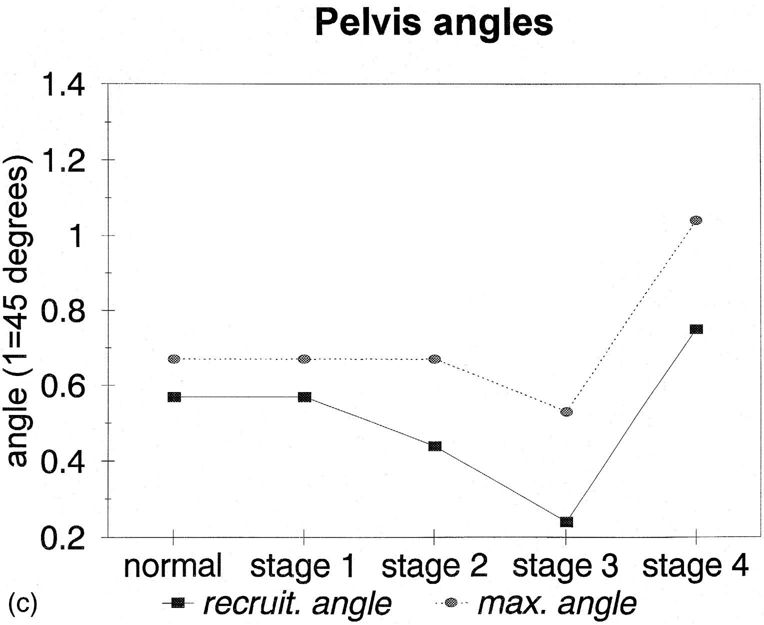


Fig. 8 (continued).

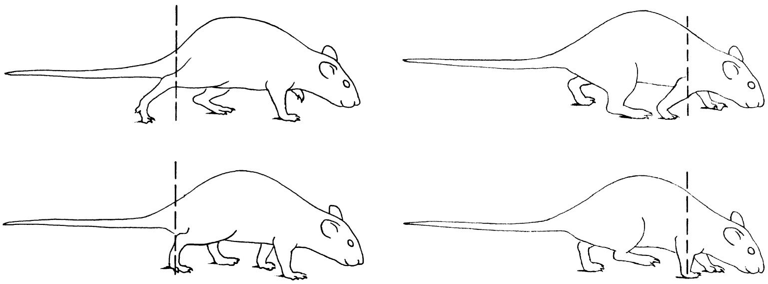
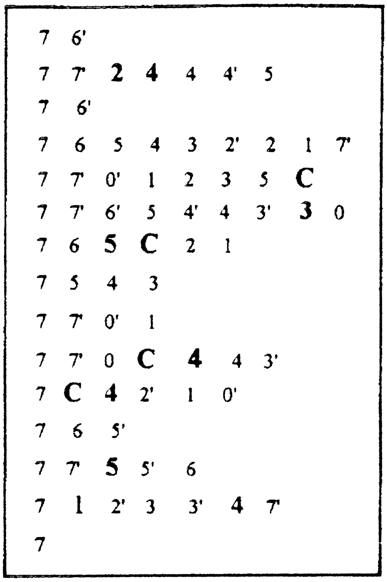


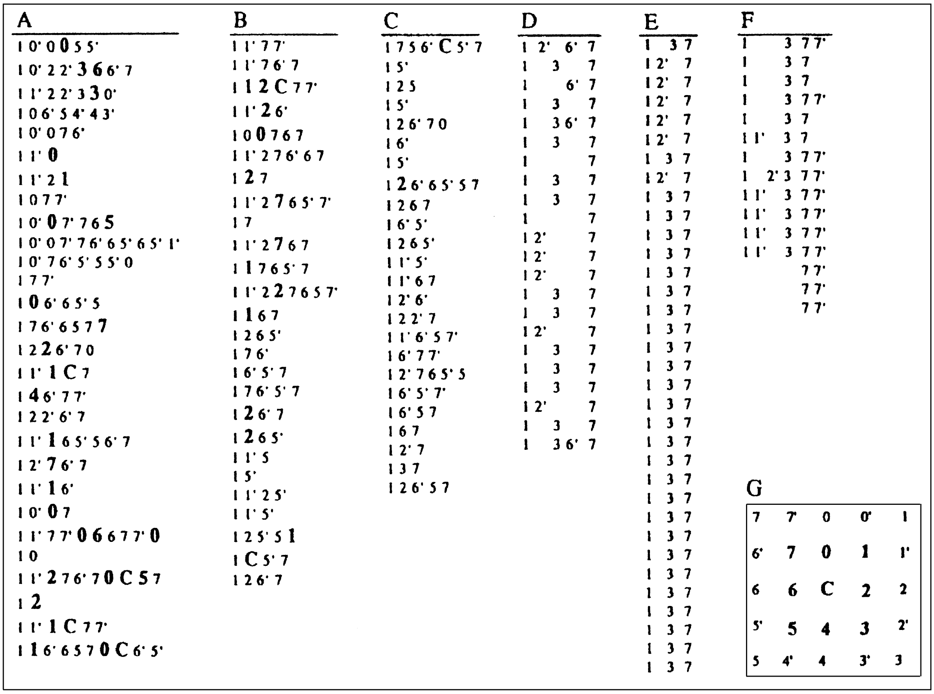
Fig. 9. The reduction in step size in AMPH-treated rats. The angles at the shoulder and hip joints at the instant of transition from support phase to swing phase in normal (top two drawings) and AMPH-treated rats (bottom two drawings). An interrupted vertical line designates the focal leg. In normal rats the lower arm and metatarsus proceed far behind the vertical absolute before the foot releases contact with the ground. In the AMPH rats foot contact is released as soon as the forearm or metatarsus reach the vertical absolute, thus eliminating the second half of the support phase.

predictability does not necessarily imply what we generally view as stereotypic behaviour. In the mathematical theory of Dynamical Systems it has been shown that completely deterministic processes (that is, with absolute predictability) may create seemingly very complex and variable sequences.



7 6'
7 7' **2** **4** 4 4' 5
7 6'
7 6 5 4 3 2' 2 1 7'
7 7' 0' 1 2 3 5 **C**
7 7' 6' 5 4' 4 3' **3** 0
7 6 **5** **C** 2 1
7 5 4 3
7 7' 0' 1
7 7' 0 **C** **4** 4 3'
7 **C** **4** 2' 1 0'
7 6 5'
7 7' **5** 5' 6
7 1 2' 3 3' **4** 7'
7

Fig. 10. The temporal sequence of stopping places written in the order of their occurrence, from left to right and from top to bottom. The sequence is partitioned into excursions from home base performed by an intact rat in the course of a 1-h session after being introduced to a novel arena. The numerals designate places in the arena (see block G in Fig. 11). The numeral 7 designates home base location.



A

1 0' 0 **0** 5 5'
1 0' 2 2' **3** **6** 6' 7
1 1' 2 2' 3 **3** 0'
1 0 6' 5 4' 4 3'
1 0' 0 7 6'
1 1' **0**
1 1' 2 **1**
1 0 7 7'
1 0' **0** 7' 7 6 **5**
1 0' 0 7' 7 6' 6 5' 6 5' 1'
1 0' 7 6' 5' 5 5' 0
1 7 7'
1 **0** 6' 6 5' 5
1 7 6' 6 5 7 **7**
1 2 **2** 6' 7 0
1 1' **1** **C** 7
1 **4** 6' 7 7'
1 2 2' 6' 7
1 1' **1** 6 5' 5 6' 7
1 2' **7** 6' 7
1 1' **1** 6'
1 0' **0** 7
1 1' 7 7' **0** **6** 6 7 7' **0**
1 0
1 1' **2** 7 6' 7 **0** **C** **5** 7
1 **2**
1 1' **1** **C** 7 7'
1 **1** 6' 6 5 7 **0** **C** 6' 5'

B

1 1' 7 7'
1 1' 7 6' 7
1 **1** **2** **C** 7 7'
1 1' **2** 6'
1 0 **0** 7 6 7
1 1' 2 7 6' 6 7
1 **2** 7
1 1' 2 **7** 6 5' 7'
1 7
1 1' 2 **7** 6 7
1 **1** 7 6 5' 7
1 1' 2 **2** 7 6 5 7'
1 **1** 6 7
1 2 6 5'
1 7 6'
1 6' 5' 7
1 7 6' 5' 7
1 **2** 6' 7
1 **2** 6 5'
1 1' 5
1 5'
1 1' 2 5'
1 1' 5'
1 2 5' 5 **1**
1 **C** 5' 7
1 2 6' 7

C

1 7 5 6' **C** 5' 7
1 5'
1 2 5
1 5'
1 2 6' 7 0
1 6'
1 5'
1 **2** 6' 6 5' 5 7
1 2 6 7
1 6' 5'
1 2 6 5'
1 1' 5'
1 1' 6 7
1 2' 6'
1 2 2' 7
1 1' 6' 5 7'
1 6' 7 7'
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D

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E

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F

1 3 7 7'
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1 1' 3 7
1 3 7 7'
1 2' 3 7 7'
1 1' 3 7 7'
1 1' 3 7 7'
1 1' 3 7 7'
1 1' 3 7 7'
7 7'
7 7'
7 7'

G

7	7'	0	0'	1
6'	7	**0**	**1**	1'
6	**6**	**C**	**2**	2
5'	**5**	**4**	**3**	2'
5	4'	4	3'	3

Fig. 11. The sequence of all places in which an AMPH-treated rat stopped in the course of an hour, following the injection. A map of the places is provided in block G. The numerals in blocks A–F represent successive time intervals across the session. For further explanations see Fig. 10. As shown, the number of stops per excursion gradually decreases, the repertoire of places of stopping decreases and the predictability of the next stopping place is gradually increased, up to the consolidation of an idiosyncratic route — a chunk — in block E.

This kind of predictability is demonstrated in the coordination between side-to-side head movements and stepping in rats injected with 5.0 mg/kg AMPH. As the head reaches an extreme lateral position, the contra-lateral foreleg executes a ‘‘crossing step’’ (with reference to the other leg), and lands under the head. We call this pattern of coordination Contra Lateral Pattern (CLP). The pattern lasts for short time periods, but then there is a faux pas: the rat performs an indeterminate step with poor timing, then, say, two ‘‘open steps’’ in which the foot lands under the head, but the head is on the wrong, ipsilateral side of the stepping leg. Then, the stable pattern is resumed. This phenomenon is known as relative coordination (von Holst, 1937). The foreleg steps seem to be attracted to a specific phase of the head cycle, but from time to time they ‘‘run away’’. In the traditional approach, the three steps that violate the rule would have been discarded as mere noise, or else the CLP stereotypy would have been described as enigmatically heterogeneous. Within the framework of coordination dynamics (Schoner and Kelso, 1988; Kelso, 1994) however, both the stable and transient aspects are intrinsically related.

QUIN (0.5mg/kg), inj #11

30	35					
30				50		
30			45			
30		40	45			4
30		40				4
30		40				
30	35	40				4
					10 6	
30	35					
30	35					
30		40				
30		40				
	35	40				4
		40				
30		40				4
					10 2	
30						4
30		40				
30		40				4
30			45	50		4
30			45			4
30		40				
30			45			4
30						4
			45			4
30		40				
30		40			5	4
				50		4
30		40				
30						4
30					3	
30						4
30						4
					10 7	4
30						4
		40				
30		40				
30	35					

30	35				4	
					1	4
30		40				
30			45			
30				50		4
30	35					
30		40				4
30		40				4
30			45	50		4
30			45			4
					0	4
30		40	45			4
30						4
				50		4
30		40				4
30		40				
30			45			4
30						4
30				50		
30		40				4
30						4
					0	4
30						4
		40				
30				50		4
30						4
30						4
		40				4
30		40		50		4
30			45			
30						4
30						4
30			45			4
30					0	4
30						4
30						4
		40				
30		40				4
30						4
					3	4

Fig. 12. The sequence of places of stopping, from left to right and from top to bottom, of a rat treated chronically with QUIN (see text) in the course of an arbitrarily selected time interval. The rat shuttles between two presumable home bases, stopping in-between in a small number of places in a relatively unpredictable order (Courtesy of Szechtman and Eilam).

In this section we will show how it is possible to model both the CLP and the variable relative coordination situation with the same dynamical system. Moreover, by continuously turning a parameter knob in the model, it is possible to get coordination that is more stereotypic or less stereotypic (Kafkafi et al., 1996).

To examine the coordination between the head and the legs we use two collective variables: the phase of the right foreleg's landing in the head cycle, and the phase of the left foreleg's landing in the head cycle (for example, when the right foreleg lands as the head reaches the extreme left, this is plotted as head phase 0.5, given that head phase equals zero when the head is in the extreme right). By plotting the second collective variable against the first, we get a curve *f* (Fig. 13a). By plotting the first collective variable against the second we get another curve *g* (Fig. 13b).

When the curves f and g are plotted together in the same state-plane (Fig. 14), one can trace the coordination which emerges. If the right foreleg lands in, say, phase 0.25 of the head movement (i.e., the head is straight while moving leftward), then the left foreleg landing time (relative to the head cycle) can be found by drawing a vertical line from the horizontal axis until it meets curve f (point A in Fig. 14). In order to find when the right foreleg will subsequently land (relative to the head cycle), draw a horizontal line from that point until it meets the curve g (point B), and so on (points C and D).

It is easy to see that, starting from any point in the state-plane (that is, any possible configuration of the two collective variables), we quickly reach the point when the two curves meet each other, and then stay there. This point designates the CLP: the right leg lands when the head is at 0.5 (i.e., the peak of its movement to the left) and the left leg lands when the head is at 0.0 (the peak of its movement to the right). This explains the observed stability of the CLP.

If, however, some perturbation takes the system any small distance to the left and down of the CLP point, it continues to flow left and down until reaching again the CLP point from above. The system always flows leftward and downward, because g is above f in all parts of the state-plane. This means that the next landing of each foreleg will always be in an earlier head phase, except upon reaching the CLP, when the landing phase does not change anymore. This explains why, when the CLP is lost, the step cycle is always faster than the head cycle.

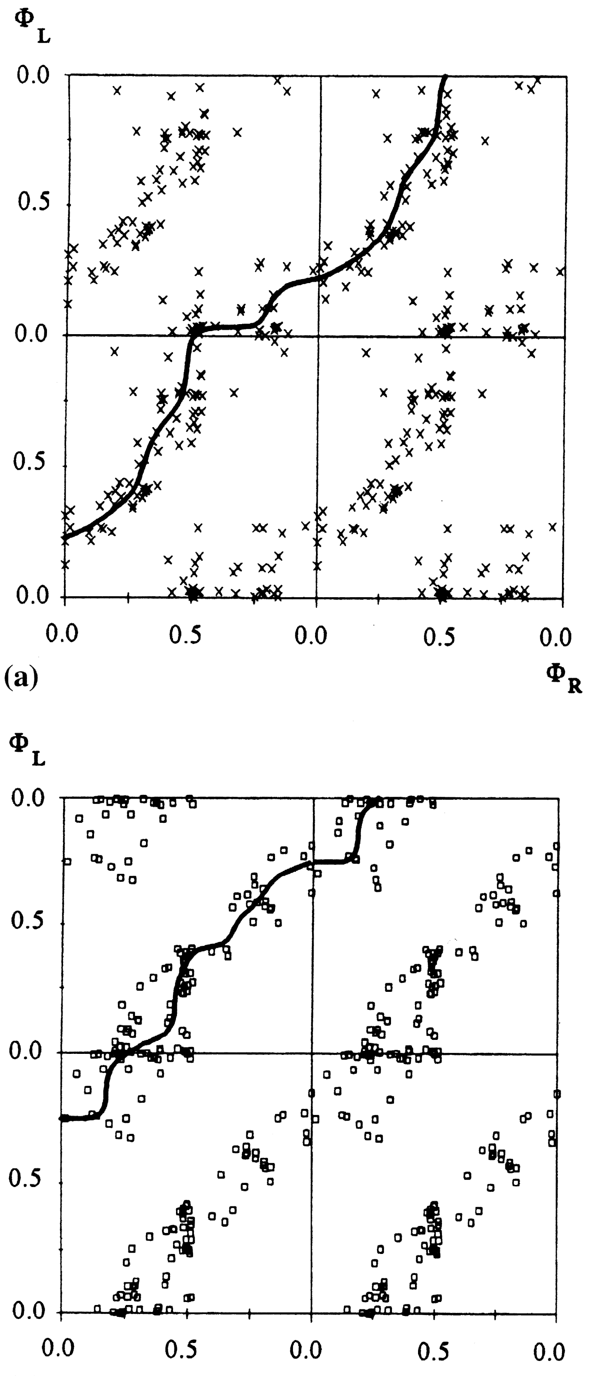
If we model the curves f and g with some simple equations (say, by using sinus functions) we can switch the system from fixed to relative coordination by continuously changing one parameter of the curves' equations. In one setting of the parameter the curves may intersect at the CLP point (Fig. 15c). The intersection then forms a point attractor, i.e., an equilibrium point that is stable from both above and below. In this setting of the parameter the CLP will be very stable and the behaviour will seem very stereotypic.

If, however, this parameter is now continuously changed until the curves no longer intersect (Fig. 15b), the system will always flow leftward and downward. If the curves are still closer to each other near the CLP point, then relative coordination arises, since the flow is slower in the CLP region, making this phase relation a little more stable than the others.

This example shows how, within the mathematical theory of Dynamical Systems it is possible to get a switch from more stereotypic to less stereotypic situations by changing one parameter of the same system (for a basic text in Dynamical Systems see Sandefur, 1990, and for applications to motor behaviour see Kelso, 1995). By using the concepts of Dynamical Systems and the right set of collective variables, it may be possible to show that seemingly non-stereotypic behaviours are in fact predictable.

7. Conclusion

Consider a horse performing side-to-side head movements at a particular place along a fence. When examined in isolation, the behaviour appears enigmatic and even bizarre. A classical ethologist would consider it a priori as a distinct stereotypic pattern, label the


Φ_L
0.0
0.5
0.0
0.5
0.0
0.0
0.5
0.0
0.5
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(a)
Φ_R
Φ_L
0.0
0.5
0.0
0.5
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0.0
0.5
0.0
0.5
0.0
(b)
Φ_R

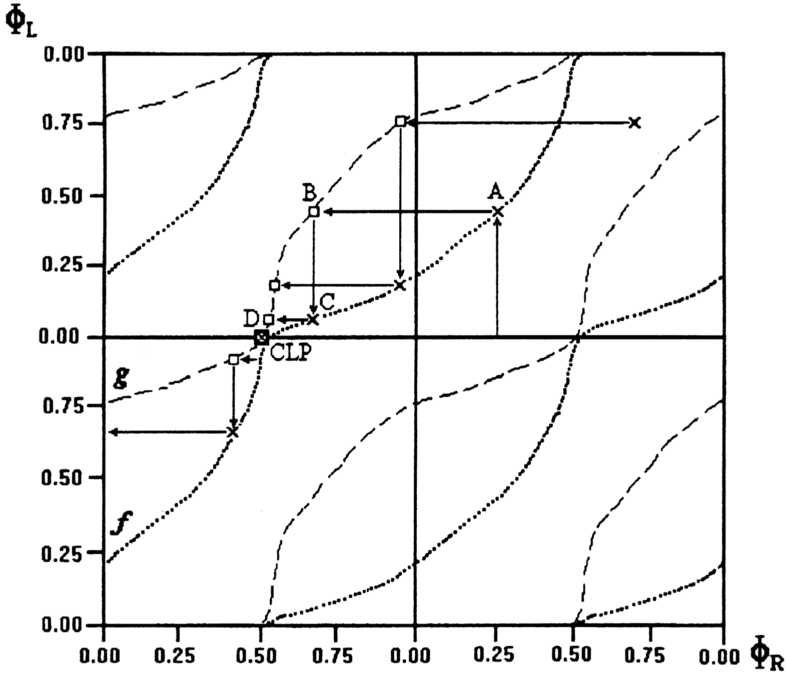

Fig. 14. A phase-plane representation of the model behavior. It consists of four replicates of the phase-plane of $\varnothing_R$ and $\varnothing_L$, tiled 2×2, to show the continuity of phase. The curves f and g are suggested according to the data from all rats. Vectors illustrate the flow of the system (see text for details).

behaviour as, for example, stationary head-swing (Meyer-Holzapfel, 1968); characterize it as preservative, aimless, circumscribed in space, etc.; proceed to record its occurrence by using some sort of an event recorder; quantify the observations by using the standard procedures summarized in Martin and Bateson (1986); perhaps even assess the information redundancy of this behaviour (Stolba et al., 1983); and move on to study the gross features of the environment associated with the appearance of this behaviour (Ödberg, 1987), its underlying motivation (Rushen et al., 1993), neurobiology (Cabib, 1993), or function (Dantzer and Mittelman, 1993).

Within the perspective of the present review, however, this behaviour is as bizarre or as self evident as any other behaviour lying along the gradient between free and stereotypic behaviour. Based on the thesis of the present review, our working hypothesis

Fig. 13. (a) $\varnothing_L$, the head phase of the left foreleg landing, as a function of $\varnothing_R$, the head phase of the previous landing of the right foreleg, in one rat. The graph is replicated and tiled 2×2 to show the continuity of phase. The number of data points (before replicating) is 101. An estimation curve for f is shown for one of the repetitions. (b) $\varnothing_R$, the head phase of the right foreleg landing, as a function of $\varnothing_L$, the head phase of the previous landing of the left foreleg, in the same rat. Note that the independent axis is the vertical axis, in order to show both f and g in the same coordinate system. The graph is replicated and tiled as in (a). The number of data points (before replicating) is 101. An estimation curve for g is shown for one of the repetitions.

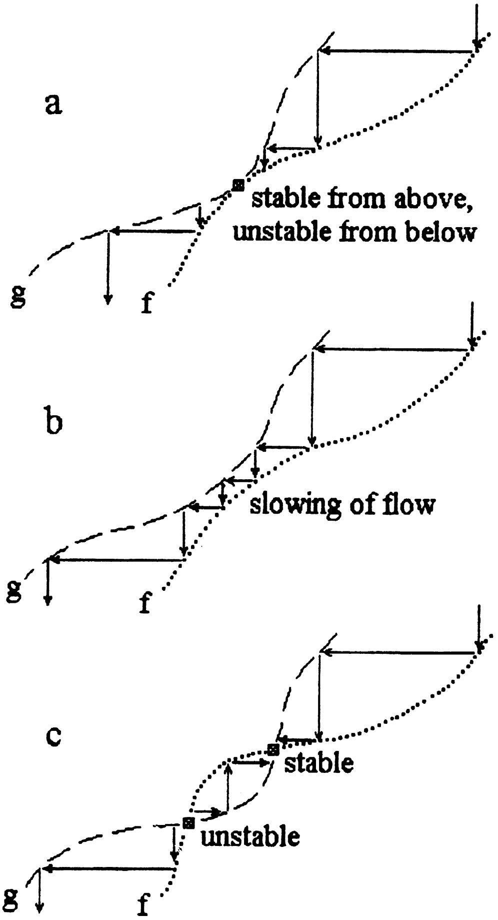

Fig. 15. A structurally unstable situation (a), with f and g exactly tangent. The Equilibrium State at the point of tangency is stable from the right and above and unstable from the left and below. Decrease or increase of the parameter that controls the amount of inflexion of f and g will result with two structurally stable situations, b or c, respectively. In (b) there is slowing of the flow but no equilibrium point. In (c) there are two equilibrium states at the intersections of f and g, where the upper is stable and the lower is unstable.

would be that there should be an observable gradient leading from free behaviour to side-to-side head movements.

The time elapsed since the horse's introduction to the arena can be viewed as our parameter or knob. Based on the collective variables that were demonstrated here, and on the course of transition from normal to stereotyped behaviour observed by us in other situations and preparations, we can predict that, as this time progresses, the horse's behaviour will involve:

(a) a gradual reduction in the range of the terrain covered by the horse,

(b) a gradual increase in the predictability of its trajectory,

(c) a gradual elimination, first of rearing on forelegs (Golani, 1992a,b), then of rearing on hind legs, then of forward progression (pacing),

(d) a gradual elimination of hindquarter horizontal movements.

Ultimately, the horse will be left with a residue of (lateral) forequarter side-to-side movements that are performed in one and the same place.

Within this framework there is clearly no distinct borderline between ''free'' behaviour and stereotypy. The relevant issue is, furthermore, not that of distinguishing between normal and stereotyped behaviour, but rather that of phenotyping the rules of transition between most free and most stereotyped behaviour.

Anyone using the framework presented in this paper as the eyeglasses, as it were, for observing a horse's behaviour can readily see that during side-to-side movements the coordination of the head cycle with the stepping pattern is similar to that described above for the rat's CLP. It can also be readily observed that during the crossing of the midline plane of the pelvis, the head does not slow down.

The CLP is brought about in the horse's case by the time elapsed since the animal's introduction to the arena, and in the AMPH-treated rat's case by the time elapsed since injection. It is defined in terms of the animal's action repertoire, and not in relation to this or that parameter. In other words, the same degree of stereotypy, consisting of similar kinematics, might be generated by a variety of parameters.

An exposition of presumable brain processes mediating the gradient from free to stereotyped behaviour has been presented elsewhere (Golani, 1992a,b), and is beyond the scope of the present review. We will, however, present a single example in order to illustrate how kinematic detail can have important phenotyping and hence important physiological implications.

The distinction between a stereotypy involving side-to-side forequarter movements organized around a point attractor located in the midline plane of the pelvis (zero velocity in the midline plane) and a CLP stereotypy, has considerable pharmacological implications. The first pattern implicates the dopaminergic system: it is observed under the D2/D3 agonist QUIN (Golani et al., 1997). The second pattern implicates the serotonergic system: it is ascribed to the 5-hydroxytryptamine (5-HT) syndrome, elicited with high doses of AMPH (Ernst, 1967, 1969; Taylor et al., 1974; Kuczenski and Segal, 1988), but also with a 5-HT receptor agonist injected into the superior colliculus. Since this last rat preparation exhibits low visual distractibility (Boulenguez et al., 1995), it could hint at both the mediation (serotonergic) and function (low distractibility; focus on internal context) of the horse's side-to-side forequarter movements.

The fine-tuning of the micro KDFs involved in this behaviour by the immediate physical properties of the environment would again require a detailed study. Proximity to edges, for example, is a prerequisite for the performance of the AMPH-induced CLP (but not of the APO-induced side-to-side forequarter movement), which is otherwise immediately transformed into whole body pivoting (I. Golani et al., unpublished data).

Finally, while we used drug-induced behaviour to support our thesis, the rules of transition from normal to stereotyped behaviour clearly apply to the general organization of behaviour. Furthermore, since the main site of action of the dopaminergic drugs used to generate this transition was the striatum, it may be useful to examine any action repertoire mediated by the basal ganglia and its descending output stations in terms of the framework presented in this paper. The subject of this paper might thus be considered to be a specification of the functional demand made upon the basal ganglia and its descending output pathways (Golani, 1992a,b).

The contribution of the basal ganglia to the modulation of predictability of action repertoires has received increasing attention in recent years. It has been shown that in humans, the neostriatum (caudate nucleus and putamen) is essential for the gradual, incremental learning of associations that is characteristic of habit learning (Knowlton et al., 1996). It has also been demonstrated experimentally that cortically derived information is re-coded within the striatum, chunking thereby the representations of motor and cognitive action sequences so that they can be implemented en bloc as performance units (Graybiel, 1998). In other words, the process of chunking, demonstrated at the level of whole animal unrestrained stereotypy (Eilam and Golani, 1994), can now also be demonstrated at the mediating electrophysiological level.

In summary, in response to the plea formulated in the introduction (Mason, 1993), we suggest that a three-fold specification of good collective variables, range and predictability provides a well-defined account of stereotypy. Such definition furnishes stereotypies with sharp borders, accounts for a substantial part of the observed diversity and defines the immediate proximate ‘‘goal’’ of a stereotypy as the stable value(s) taken by its collective variable(s).

Acknowledgements

This paper was presented at the Wood-Gush Memorial Lecture of the 31th Congress of the International Society for Applied Ethology in Prague. This work was supported by a grant from the Israel National Academy of Sciences and Humanities. We thank David Eilam for critical reading of the manuscript.

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