The Ontogeny of Exploratory Behavior in the House Rat (*Rattus rattus*): the Mobility Gradient

DAVID EILAM
ILAN GOLANI
Department of Zoology
The George S. Wise
Faculty of Life Sciences
Tel Aviv University
Ramat Aviv, Israel

Infants of rats and other mammals respond to a novel environment by becoming immobile, and then showing a process of motorial expansion called "warm-up." Starting from immobility, new types of movement are incorporated into the stream of behavior according to rather strict rules of order. Once a new type of movement has been performed, the infant reverts to it repeatedly. As a result, the earlier portion of the behavior appears stereotyped, giving the impression of an automatism. Later, as new types of movement are added to the infant's repertoire, the movement becomes increasingly rich and unpredictable, giving the impression of "free" behavior. The same rules of order operate within "warm-up" sequences of movement, and across such sequences, day by day. Concurrently, there is an increase in the amplitude of movements, resulting in a gradual expansion of the portion of the environment explored by the infant. The same rules of order seem to operate in the development of locomotion in more primitive vertebrates. In rats under the action of psychoactive drugs, the "warm-up" sequence is performed in reverse.

When an infant rat is placed in a novel environment, it first becomes immobile and then shows an orderly spread of activity from lateral, to forward, to vertical movements, and a gradual build-up in the amplitude of movements. This kind of behavior, which has been called "warm-up," is the subject of the present study. It was originally described by Golani, Wolgin, and Teitelbaum (1979) in a study of the recovery of exploratory behavior in rats after severe bilateral, lateral-hypothalamic damage. A subsequent preliminary study revealed the existence of "warm-

Reprint requests should be sent to Ilan Golani, Department of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, Israel.

Received for publication 15 September 1986
Revised for publication 3 November 1987

Developmental Psychobiology 21(7):679–710 (1988)
© 1988 by John Wiley & Sons, Inc.
CCC 0012-1630/88/070679-32$04.00

up'' in the ontogeny of normal infant rats and other infant mammals (Golani, Bronchti, Moualem, and Teitelbaum, 1981).

The aim of this study is twofold: To isolate the basic motor patterns of infant rat movement during ''warm-up''; and to formulate general principles of their sequential ordering.

To obtain a reliable description of the behavior of infant rats, in terms of relations and changes of relation between the parts of the body, we used the Eshkol-Wachman (EW) Movement Notation (Eshkol & Wachman, 1958; Eshkol, 1980). This technology of description allowed us to isolate the elementary building blocks of the infant rat's motor behavior, and to formulate the rules of their sequencing.

In this paper we show that infant rat movement in a novel environment, unfolds both in moment-to-moment behavior and in development, along one morphogenetic continuum. In the descriptive Method section and in the Appendix, we explain how we isolate the elementary building blocks of this continuum, so that they will correspond as closely as possible to the morphological reality of infant rat movement. To avoid the use of terms borrowed from ''common speech,'' which are often ambiguous and less informative, we represent the building blocks of movement in terms of EW signs; these represent the complex morphology of movement concisely and unequivocally, in relation to a common interval scale, in a form which can be subjected to quantitative analysis (body parts involved in movement, orientation, amplitude, and timing).

Sequence analysis reveals a process of motorial expansion (Kortmulder, 1983), constrained by rather strict rules of order; these generate both the most stereotyped and most flexible sequences of infant movement. The same rules of order explain the development of locomotion in some primitive vertebrates, the morphology of some forms of adult behavior associated with immobility, and the behavior induced by the administration of psychoactive drugs (Szechtman, Ornstein, Teitelbaum, & Golani, 1985).

Methods

Animals

Infants were obtained from a colony of tame house rats (*Rattus rattus*) established at the Tel Aviv University research zoo. One hundred and sixty-two infants of 22 litters were observed, and their behavior recorded. Table 1 specifies the number and age of the infants which were studied, and the method by which their behavior was recorded.

The Testing Environment

Since pronounced immobility is a prerequisite for the performance of ''warm-up,'' we first had to establish the physical properties of the testing environment that will elicit such immobility: If the contrast between the nest and the testing environment is too small, there is no immobility, and the reference starting point for observation and analysis is lost; on the other hand, in infant house rats, if the contrast is too great, the immobility may last for the whole period of observation.

TABLE 1. Methods of Observation and Number of Observed Infants.

Method of Observation	No. of Litters Observed	No. of Infants Observed	Age (Days)
Tape recording	7	57	0–14
	6	49	Several different ages
Videotaping	2	17	0–14
	2	18	10–14
	1	8	6–10
Filming (16mm)	1	4	0–12
	1	4	0–10
	2	5	11–14
Total	22	162	

In addition, with age, there is a gradual increase in the degree of contrast necessary to induce immobility. Therefore, we had to increase the contrast between the two environments every few days. This was accomplished through the changes which are listed in Table 2, which were found appropriate for house rat infants. Infants were observed on a wooden platform (50 × 70 cm) bounded by a "cliff," a wooden wall, and a wire-mesh wall. A mirror tilted at 45° above the platform, added a top view of the infant. Side and top view were filmed simultaneously by one camera. From day 11 and on, additional filming was carried out on a glass floor (100 × 140 cm). A mirror tilted at 45° below the floor gave a bottom view, allowing a simultaneous observation of trunk orientation and the stepping of all four legs. Observation from this direction was not useful earlier on, because the infants slipped on the glass.

Analysis of Behavior

Methods to record the behavior (Table 1): 1) We made preliminary tape-recorded observations in order to establish the necessary properties of the testing

TABLE 2. Regulation of Contrast between Nest and Testing Environment.

Developmental Day	Testing Environment	Procedure Preceding Observation
0–6	Nest platform	Mother, litter and shavings were removed from nest platform. All infants were placed, huddled, on platform. After a few minutes all infants except one were removed from platform.
7–10	Nest platform	Mother, litter, and shavings were removed from nest platform. One infant was placed alone on nest platform.
11–14	Unfamiliar platform	All infants were placed, huddled, on unfamiliar glass platform. After a few minutes all infants except one were removed from platform.

environment; 2) we then videotaped 8 hr of behavior (28,800 feet of tape). The videotapes were used to establish the movement potential characteristic of each developmental day. We started to videotape during the initial immobility, and finished after several minutes (2–5), when the infant succumbed into prolonged immobility; 3) finally we filmed the behavior with a 16-mm movie camera (2 $\frac{1}{2}$ hr of behavior; 4400 ft; 16 fps until day 5, and 24 fps from day 6 until day 14). The films were used for detailed notation. Filming was started during the initial immobility, but stopped earlier ($\frac{1}{2}$–3 min), when the infant appeared to have exhausted the behavioral repertoire, assessed to be available to it at that age, in the earlier videotaped observations. 28 out of the 56 filmed sequences of movement were notated, frame by frame, with the aid of a stopframe projector, in EW. After the formulation of the rules of warm-up, we assessed their generality by viewing of all the available films and videotapes, frame by frame.

Descriptive Method

An adequate representation of motor behavior should correspond as closely as possible to the morphological reality it attempts to represent. Of the versatile descriptive tools offered by EW we adopted in the course of the present study only those tools which correspond to the morphology of infant rat movement. These tools reflect therefore the properties of the movement material represented by them, and may be taken to form part of the results of this study. A detailed exposition of these tools is presented in the appendix; in this section we confine ourselves to an informal summary of the rationale which guided us in choosing them.

Based on skeletal anatomy, the infant rat's trunk is treated as a linkage of three articulated axes: Pelvis, torso, and head (Fig. 1).

The movements of a single axis of constant length, free to move about one fixed end, are enclosed by a sphere. Therefore, the orientation and changes of orientation of each of the parts of the trunk are described in relation to spherical coordinate systems whose centers are schematically attached to the joints of these axes. Each of the three parts of the trunk has its own individual coordinate system (Fig. 1). The orientation of a part of the body (axis) is read from the center of the sphere outward. The orientation is described in relation to a network of coordinates attached to the surface of the sphere. This network is constructed, like the geographical globe, from the intersection of "lines of latitude" (horizontal circles), and "lines of longitude" (vertical circles).

In pilot Movement Notation analysis we have found that during the first two postnatal weeks, infant rat behavior in the open field consists of movement in two planes: the horizontal and the vertical. The movements along these planes are performed in relatively pure form along one plane at a time; movement along planes which are tilted in relation to the horizontal plane are rare and small, and deviations from the horizontal and vertical paths of movement seem to be insignificant. In other words, the distinction between horizontal and vertical movements which is adopted by us in this study is not an arbitrary abstraction, derived from the projection of more elaborate movements on these planes; rather, it corresponds to the morphological reality of rat movement during the first 2 weeks of life. To adequately represent this reality we notate separately the

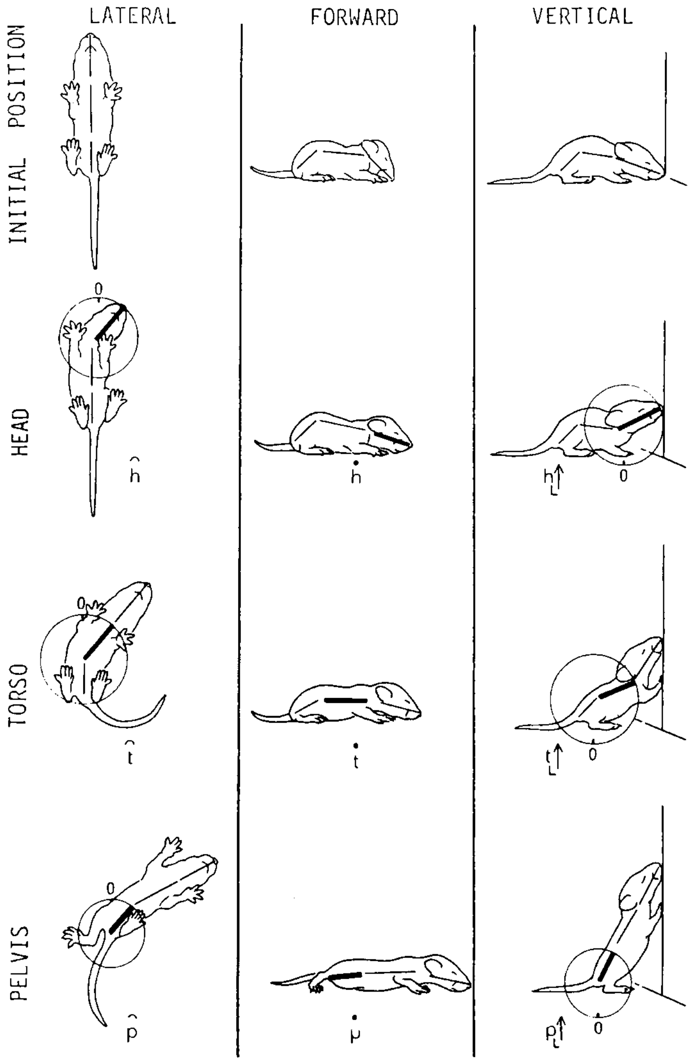

Fig. 1. The infant rat's trunk as a linkage of articulated axes; examples of the effect of movement of a "heavy" part of the trunk on the parts anterior to it. The columns represent the three spatial dimensions isolated in the present study. To reach the postures illustrated in the horizontal row "head" from the postures illustrated in the row "initial position," the infant must move its head; to reach the postures in the row "torso" from the postures illustrated in the row "initial positions," the infant must move its torso, and to reach the postures in the row "pelvis" from the same initial positions, the infant must move its pelvis. Every part of the trunk has its own spherical coordinate system; we illustrate only the sphere of the heaviest part that moved. Its axis is represented by a thick line. Symbols designate the heaviest part that moved and the type of movement: h, head; t, torso; p, pelvis; ⌢, lateral; ·, forward; L↑, vertical movements with loose snout contact on wall; ĥ, lateral movement of head; ṫ, forward transport of torso; p↑, vertical movement on wall of whole trunk (including pelvis), etc.

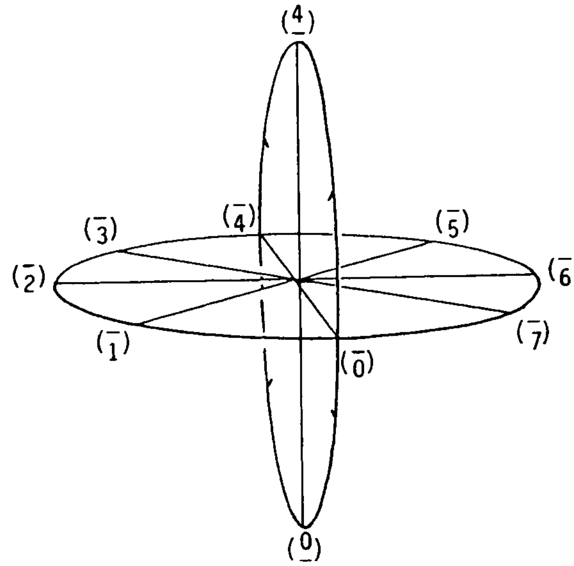

Fig. 2. The horizontal plane and one vertical plane of the E.W. sphere, in scale 1 = 45°. (With permission of the Movement Notation Society, 75 Arlozorov St., Holon, Israel.)

movements of the parts of the trunk in relation to horizontal circles, and in relation to vertical circles (Fig. 1, 1st and 3rd columns; Fig. 2).

The centers of the individual circles are attached to the *caudal* joint of each of the parts of the trunk (Fig. 1), because during the first 2 weeks of life, these parts move exclusively around their respective caudal joints: In side to side horizontal movements, the head and the neck move in relation to the torso, the torso moves in relation to the pelvis, and the pelvis moves in relation to the hindlegs. Also in head raising, torso raising, and rearing on the hindlegs, these parts move on their respective caudal joints (Fig. 1, 1st and 3rd columns).

Reading the orientation of the parts of the trunk in a caudorostral direction also reflects another most important property of the linkage: While movement of the head has no kinematic effect on the locations and paths of movement of the torso and the pelvis, movement of the torso changes the location and path of movement of the head, and movement of the pelvis changes the locations and paths of movement of both the torso and the head (Fig. 1). This mechanical interdependence between the parts of the linkage is called in EW—"the law of heavy and light limbs." The pelvis is regarded as the "heaviest" part along the trunk linkage, the torso is "light" in relation to the pelvis but "heavy" in relation to the head, and the head is the "lightest." This mechanical hierarchy must, of necessity, be taken into account in the organization of movement, and therefore must also be expressed in the representation of movement. In such representation, when movement is indicated in a ("heavy") part of the trunk, it is implied that the locations and paths of movement of the remaining ("light") portion of the trunk rostral to it, were modified as well. This sometimes allows an economy in the representation of movement.

Whereas along the horizontal and vertical planes we notate *spherical* movements, along the third dimension we record the *transport* of the three parts of the trunk along the longitudinal axis of the body. In the course of this study, forward and backward transport along this axis turned out to be morphologically distinct of the other types of movement. Such transport is the compound product of opposite *spherical* movements of the parts of the trunk along the vertical plane and/or of stepping (Fig. 1, 2nd column, and see Appendix).

The direction of stepping of each of the four legs (e.g., forward, backward and sideways) is notated in relation to the longitudinal axis of the body.

In the Appendix we provide a more formal exposition of the EW tools used in the present study.

Results

We divide the "results" section into two parts: First, we describe the regularities observed in *any* sequence of movements, regardless of the developmental day; then we describe the regularities observed *across* the sequences, day by day.

I. The Daily Sequence

a. Serial Order

1. Continuous movement and arrests: The movement that follows the initial immobility is comprised of bouts of continuous movement interrupted by intervals of complete arrest (Fig. 3). The bouts of continuous movement in which the infant does not stop movement for even one frame, are called "phrases"; the sequences comprised of these phrases are called "daily sequences".

2. The spread of activity along the trunk and across the 3 spatial dimensions: Two properties of the daily sequences are demonstrated in Fig. 4: a) There is an

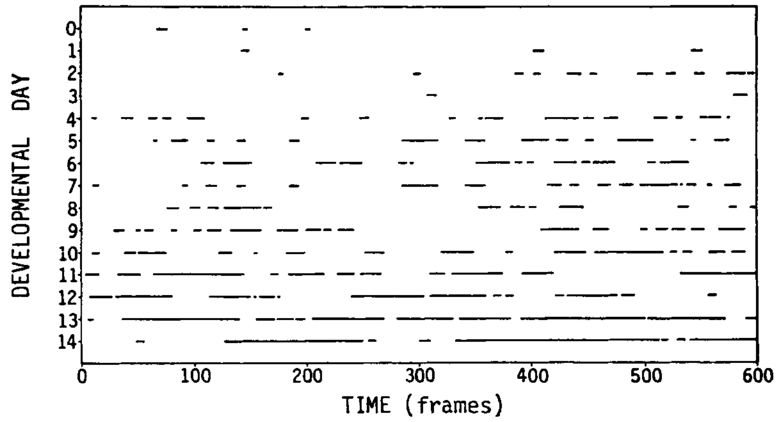

Fig. 3. Intervals of continuous movement (full line) and arrest (empty interval) in the first 600 frames (25 sec) following the initial immobility. One example was chosen at random for each developmental day. Note overall decrease in arrest from top left to bottom right.

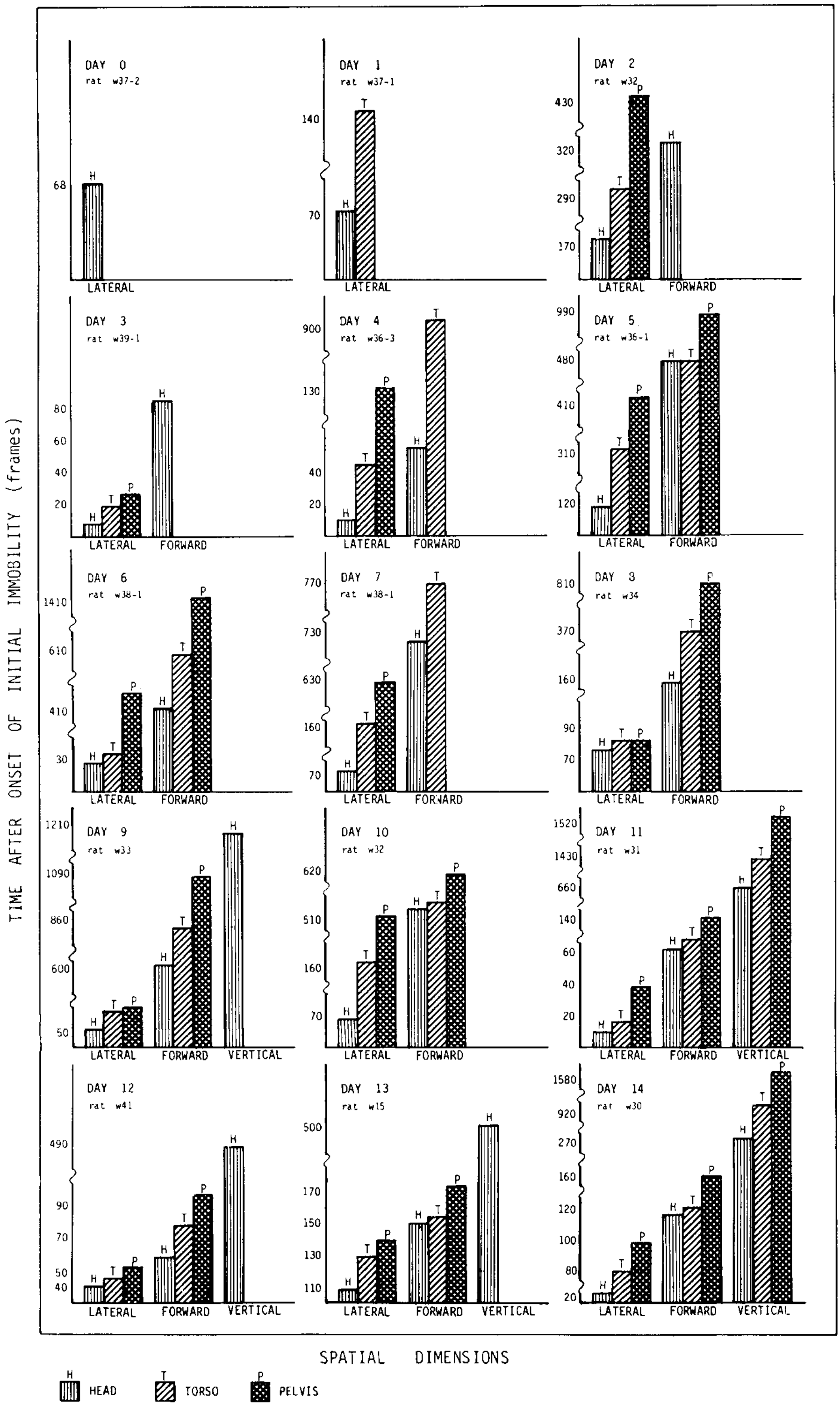

Fig. 4. Timing of first appearance of movement of the parts of the trunk along the three spatial dimensions. One example was chosen at random for each developmental day.

orderly transition of activity from one spatial dimension to the next: movements in the horizontal plane (lateral movements) are performed first, forward transport is incorporated next, and vertical movements last. Furthermore, each part of the trunk separately, moves first laterally, then forward, and only then up. b) Along each of these spatial dimensions separately, there is a cephalocaudal order of recruitment: the head moves first, the torso second, and the pelvis last.

3. Temporal order is preserved in spite of variability in repertoire and timing: Daily sequences which belong to the same developmental day may vary in their content (Fig. 5). The time interval between the incorporation of movement of the next part, along the next dimension, also varies considerably. However, the temporal order of incorporation of the different movement types (which are defined in Fig. 1) is always preserved. These regularities—along the trunk, and across the spatial dimensions—were found in all the sequences listed in Table 1, in the "methods" section.

4. Detailed analysis of one phrase of continuous movement: In Figures 4 and 5 we represented the timing of the first appearance of a new type of movement, but disregarded the movements which are performed in the intervals between such new types. Now we shall present a full and continuous record of two phrases of movement performed at the onset of a daily sequence, and show how regularity is established, movement by movement.

Figure 6 presents the first two phrases of continuous movement, belonging to a daily sequence performed by a 13-day-old rat. The first phrase consists of a single lateral movement of the head (frame 6). After a short period of complete arrest (frames 11–35), the infant moves first laterally (frame 36), and then forward (frame 63). In lateral movement, the head and the torso move first (frame 36), and the pelvis last (frame 74). Cephalocaudal recruitment is also evident in forward transport (head, fr. 63; torso, fr. 68; pelvis, fr. 111).

To visualize the infant's movement, it is necessary to represent the steps which accompany the trunk movements. At first, the trunk movements are not accompanied by stepping; later, as the pelvis joins in turning, the inner hindleg (with respect to the direction of turning) steps backward ([$\underline{\underline{4}}$] $_{\top}$: fr. 74), and the forelegs join in sideways steps ([$\underline{\underline{2}}$] $_{\top}$: fr. 84–106). Finally, as the pelvis joins in forward transport, the infant steps forward ([$\underline{\underline{0}}$] $_{\top}$ fr. 116–139). The end of the phrase is marked by a period of complete arrest (fr. 140–155).

5. Detailed analysis of one daily sequence: In this section we represent the full daily sequence which followed the two initial phrases represented in the previous section.

To represent concisely the sequence of movements, we use the following procedure: The movement of the whole articulated linkage of parts is reduced to a sequence of *initiations* of movements, performed one at a time, by the whole animal. The daily sequence, presented in Figure 7, was derived from full notation scores such as that of Figure 6. It was obtained by leaving in only the symbols which describe the initiation of movement of the most caudal trunk part that moved along any of the spatial dimensions, in proper temporal order. The table thus represents the sequence of initiations of movements of the most caudal part that moved at any one time along any spatial dimension. Because of the caudorostral hierarchy of "heavy" and "light" limbs (see "methods"), an active movement of a part of the trunk implies that the locations and paths of movement

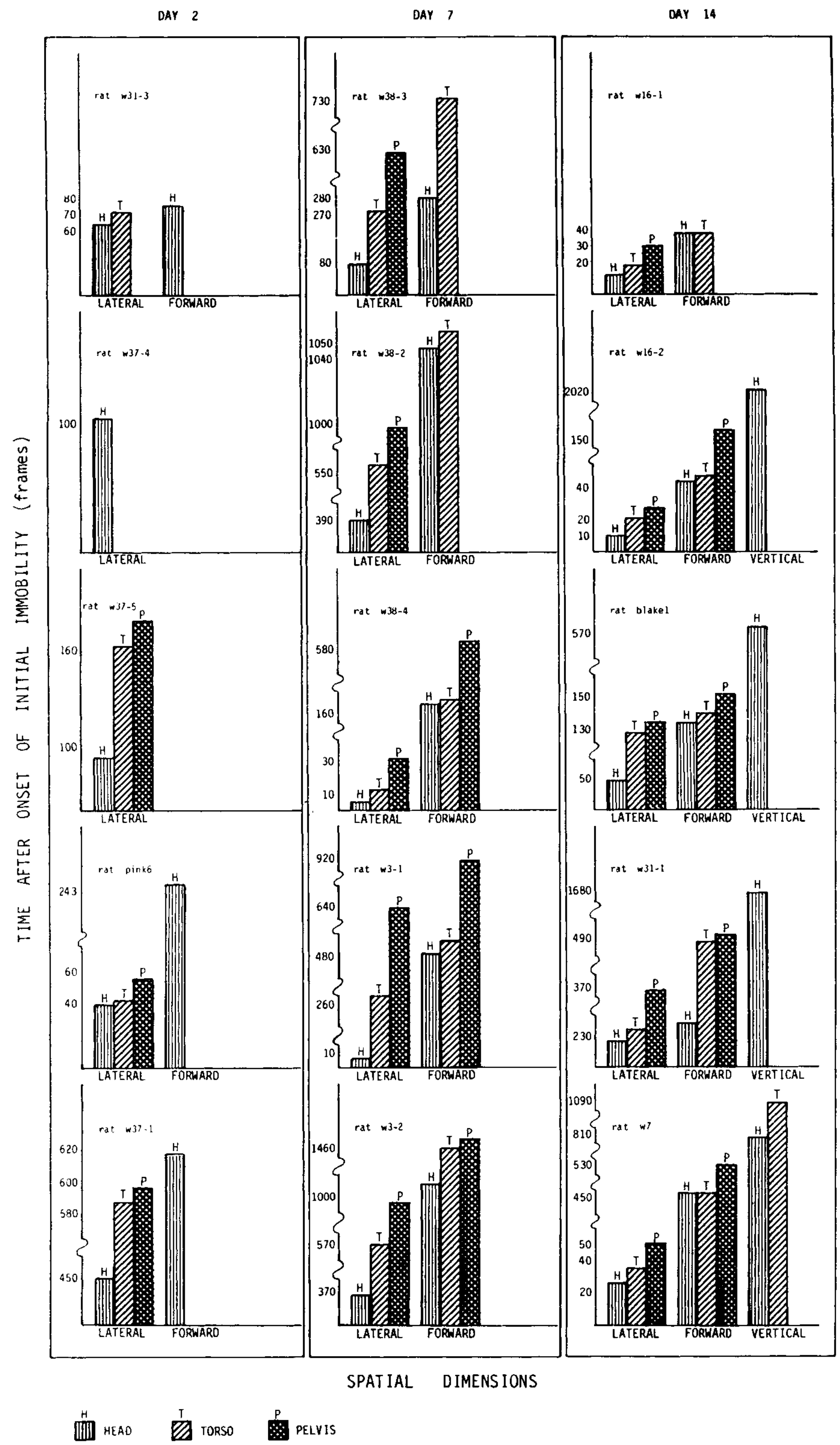

Fig. 5. Timing of first appearance of movement of the parts of the trunk along the three spatial dimensions. Five examples were chosen at random for each of 3 developmental days.

of the remaining portion rostral to it were modified as well (i.e., a movement of the torso implies that the head was carried along, and a movement of the pelvis implies that the torso and the head were carried along).

The symbols are notated between the horizontal lines in proper temporal order, from left to right, the symbol enclosed in the right-hand column included. The horizontal vectors of symbols follow each other temporally, from top to bottom. Horizontal bar-lines represent periods of complete arrest; they mark the end and the beginning of phrases of continuous movement.

The first performance of a movement of a part along a new spatial dimension, never performed before in that sequence, is enclosed in the right-hand column. (In this particular sequence, the first movement, ĥ, is obviously a new one; therefore, the first line consists of only one movement. Also the second movement, t̂, is new, therefore it is also written in the right-hand column; the next four movements consist of reversion to movements which were already performed, therefore, they are written in the next line, on the left of the right-hand column. Following them is a new movement type—ḣ, etc.). Thus, the right-hand column of Figure 7 represents the temporal order in which the parts of the trunk moved along the three spatial dimensions *for the first time* in the course of this particular sequence. The portions of the sequence which consist of "reversion" to movements which have already been performed earlier on in the course of this sequence, are aligned along the horizontal spaces on the left of the right-hand column. Note that once a new movement type has been performed, the infant typically reverts to it time and again.

The first two phrases of this daily sequence were already described in detail in Figure 6. By the end of the second phrase, the incorporation of the three parts of the trunk in movement along the first two dimensions is already accomplished. From the third phrase on, most of the activity consists of reversion to movement along the first two dimensions. In the 9th phrase, forward transport is culminated with forward walking ẇ; movement of the head along the vertical dimension, h̳↑ , is performed for the first time only in the 11th phrase. It constitutes the most "advanced" movement performed by the infant during this sequence.

6. Daily sequences of younger and older infants: Figure 8 represents sequences of younger and older infants. In all the sequences, an infant never moves a part of the trunk along a spatial dimension, unless the part anterior to it has already moved earlier in the sequence along that dimension; and unless that part of the trunk has itself moved along "less advanced" dimensions. In progressing along a sequence, the infant may: (a) repeat the same movement type for a variable number of times; b) "revert" for a variable number of times to movement types performed earlier on; c) proceed to incorporate the next caudal segment in movement along the same dimension; or, d) move with the most anterior segment (the head) along a new, more "advanced" dimension.

The same rules also apply to the order of incorporation of movements *within* phrases (see horizontal vectors of symbols enclosed between lines in Figure 8). When the trunk is already bent laterally at the onset of a phrase (e.g., Fig. 7, phrases 2,9 & Fig. 8, day 14, phrase 15), the phrase may start with a lateral movement of a more caudal part of the trunk. Rarely (Fig. 8, day 14, phrase 13), forward movement may start, in phrases, with a movement of the chest or even the pelvis.

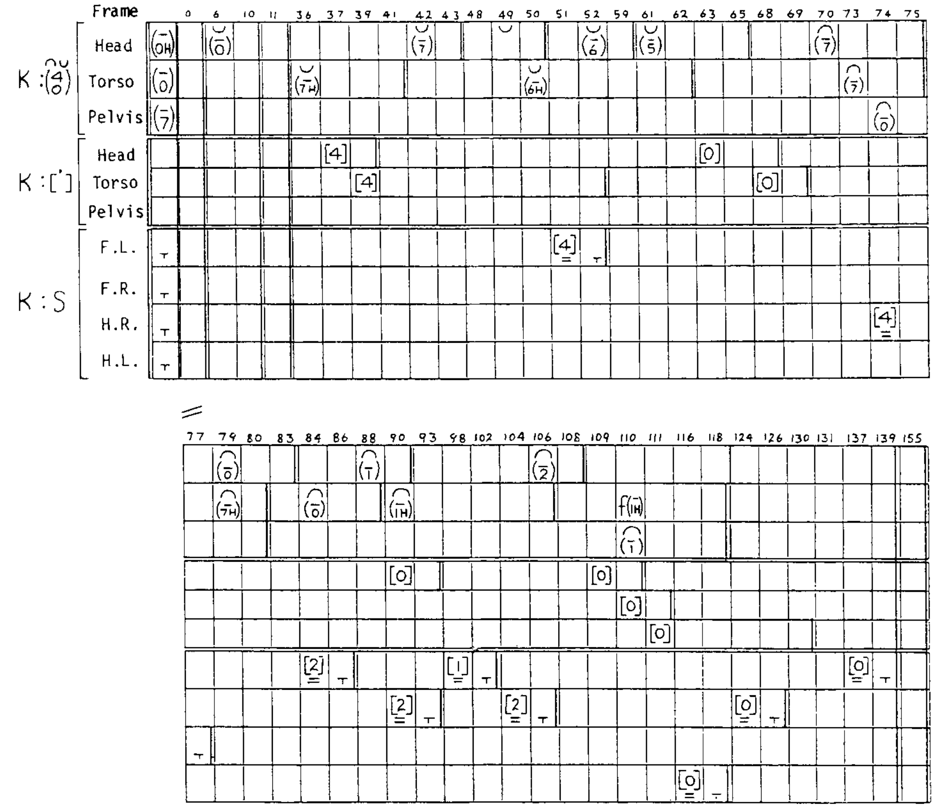

Fig. 6. EW notation score presenting the first two phrases of a daily sequence performed by a 13-day-old rat. Notation was made from film taken at 24 fps.
Structure of manuscript page: The body is represented on a horizontally ruled page. Each horizontal space represents a part of the body. Vertical lines divide the manuscript page into columns denoting units of time (frames on film). The symbols for movement are written (and read) from left to right, and, for each group of serially connected segments, from bottom to top.
Double vertical bar-lines || signify end of movement. Empty spaces following bar-lines signify that the relation to the next caudal segment is kept constant.
Left hand column specifies the initial position of the animal.

***

Here the manuscript page is divided into three parts: The upper part is allocated for lateral (horizontal) movement, the middle part for forward and backward transport, and the lower part for stepping. Each of these parts is signified by a key signature.

K:$(^{4}_{0})$ A key signature which indicates that horizontal movements are notated as rotations (⌒, clockwise; ⌣, counterclockwise), around the vertical absolute axis $(^{4}_{0})$ (see Appendix).

K:[˙] A key signature which indicates that the direction of movement applies to the line traced by the rostral extremity of a part of the body. [ ] signifies that the information specified within the square brackets is to be read "bodywise" (in relation to the adjacent caudal segment). [0] stands for forward, and [4] for backward transport.

K:S A key signature which indicates that the combination of symbols signifies a step. S for step, = for release, and ⊤ for establishment of foot contact with ground. The numeral within the square brackets indicates the direction of the step: [0], forward; [4], backward; [2], sideways to the right. F.L., left foreleg; F.R., right foreleg; H.R. right hindleg; H.L. left hindleg.

Positions: A position in space is specified by two numerals within parentheses; the lower describes the horizontal and the higher the vertical coordinate.

( ) The information within the parentheses is read in the absolute frame of reference.

b. Build-Up in Amplitude

The changes in the amplitude of movements along the lateral and forward dimensions are reflected in the number of steps performed successively along each of these dimensions separately, in consecutive phrases of the same daily sequence. The bouts of stepping are small in earlier phrases, whereas later phrases consist of *both* small and increasingly larger bouts of uninterrupted stepping. There is, across phrases, a gradual increase in the maximal number of steps performed in a bout, interrupted by phrases with bouts of the same numbers (repetition), and smaller numbers of steps (reversion) (Fig. 9).

A detailed illustration of the interrupted growth in amplitude across phrases is given by a comparison of the full scores of the 2nd (Fig. 6) and the 9th (Fig. 10) phrases, which belong to the daily sequence presented in Figure 7. Both phrases consist of a transition from lateral to forward movement; these grow in amplitude from the earlier to the later phrase: from 5 successive steps along the lateral dimension in phrase II (frames 74–106) to 8 successive steps along the lateral dimension in phrase IX (frames 393–426), and from 2 successive steps forward in phrase II (frames 118–126) to 16 steps forward in phrase IX (frames 432–500). These values represent successive peaks along an interrupted process of growth in amplitude: in the phrases performed between the two peaks, the number of steps along each of the dimensions is equal to, or smaller than, that of the first peak. In the sequence presented in Figure 7, stepping along the lateral dimension reaches its peak in the 9th phrase, but forward stepping continues to increase reaching the next peak of 33 steps in the 12th phrase, and the last peak of 34 steps in the 16th phrase. The succession of the daily peaks along the different spatial dimensions is discussed in detail in the section on ontogeny.

c. The Mode of Scanning of the Environment

1. Switching between horizontal directions: In lateral movements, the infant switches repeatedly between clockwise and counterclockwise movements, covering several times the same sections of the absolute horizontal domain, as well as

---

$(\bar{0})$ Signifies that only the horizontal direction, in this case direction zero, is known (see Fig. 2).

$(\bar{0}H)$ The position is zero and a half. The half is added to the specified coordinate in a clockwise direction.

Signs for movements:

$\overset{\frown}{(\bar{7})}$ Signifies horizontal movement to the specified horizontal position. Here, $\frown$ signifies a clockwise movement, to $(\bar{7})$.

$f(\bar{1}H)$ Fixation of position (direction). Here, $(\bar{1}H)$.

How to read the manuscript page: In starting position (left hand column), all four legs are in contact $\top$ with the ground, the parts of the trunk are positioned in the specified coordinates. The infant stays immobile (frames 0–5); then performs a counterclockwise horizontal movement of the head $\smile$ to the position specified under the movement symbol (fr. 6–10); stays immobile again for 25 time units (fr. 11–35); then performs a horizontal counterclockwise movement of the torso (fr. 36–41). Throughout this movement, the head's angular relation to the torso is kept constant (empty space following double bar line, fr. 36–41), i.e., the head is "carried along" passively on the torso. Backward transport of the head (fr. 37) and then of the torso (fr. 39), are successively superimposed on the horizontal torso movement, etc.

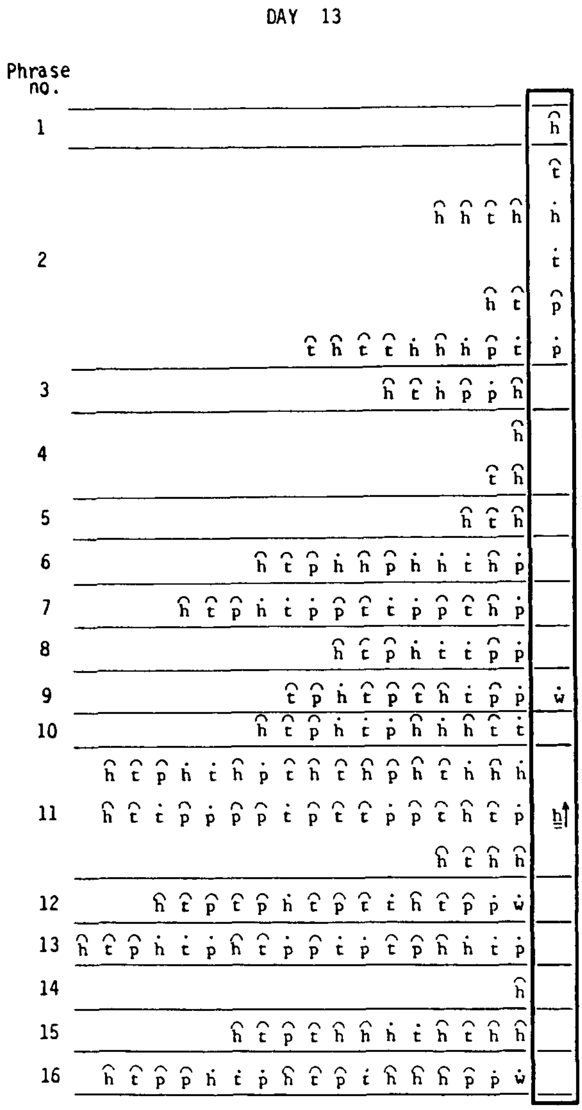

Fig. 7. The sequence of initiations of movements of the "heaviest" part of the trunk, along the three spatial dimensions, in the daily sequence of a 13-day-old rat. The sequence is to be read from left to right and from top to bottom. Horizontal lines distinguish between the phrases. ⌒, signifies horizontal movement; ·, forward transport; =↑, vertical movement up in the air; and ẇ, forward walking. h, *h*ead; t, *t*orso; and p, *p*elvis. Examples of these types of movement are illustrated in Figure 1.

proceeding to scan new sections. Table 3 presents examples of the numbers of alternations of the three parts of the trunk, performed in the course of randomly selected daily sequences. As illustrated, the number is highest in the head, somewhat smaller in the torso, and much smaller in the pelvis. In any case, the switching in the forequarters is typically higher than in the hindquarters. This is

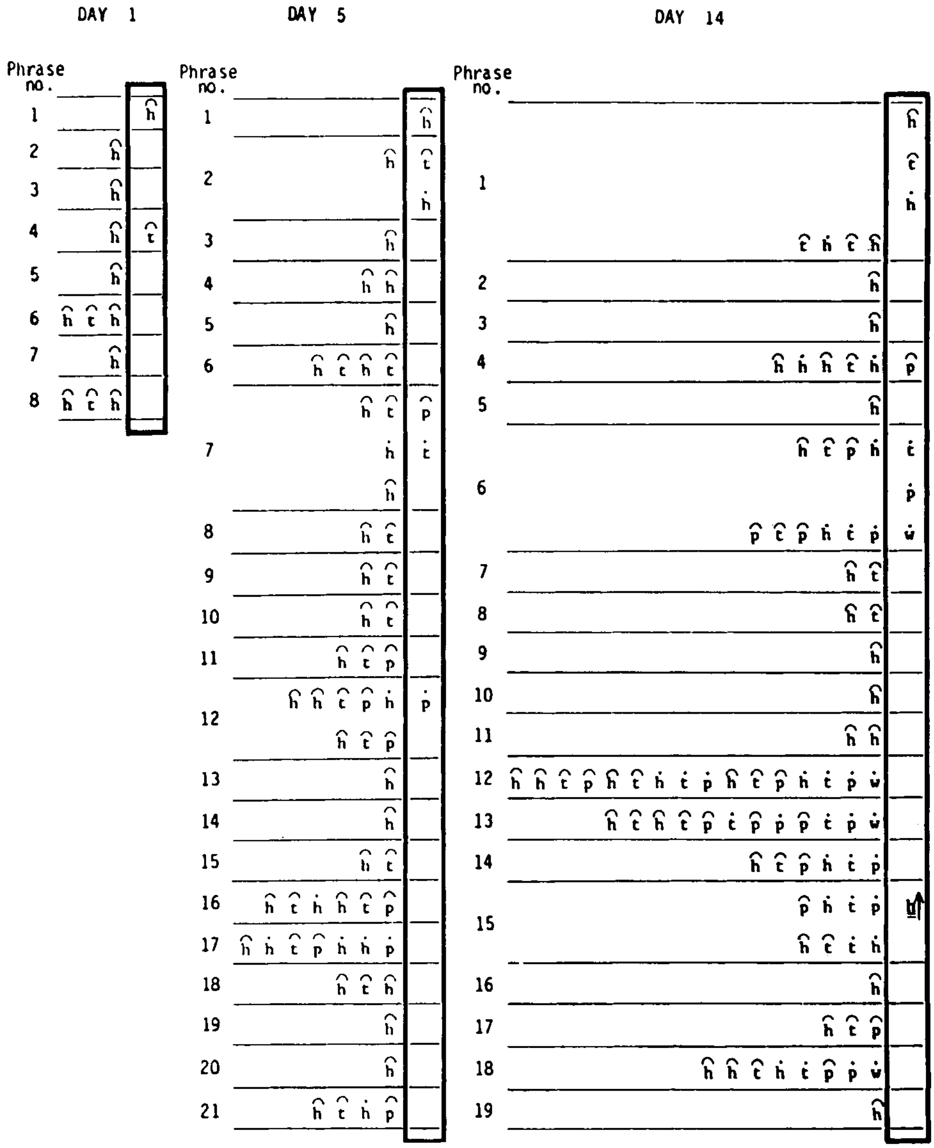

Fig. 8. Daily sequences of 1-, 5-, and 14-day-old rats. For explanation, see Figure 7.

because a) the forequarters move for longer periods of time due to cephalocaudal recruitment, and b) alternations in the hindquarters are also manifested in the forequarters (law of "heavy" and "light" limbs).

The change in the number of alternations along the trunk is illustrated in detail in the first portion of a daily sequence (Fig. 11). During the same period, the pelvis switches directions once, the torso 4 times, and the head 10 times. In addition, the amplitudes of the horizontal sections covered during scanning, are largest in the head, smaller in the torso and smallest in the pelvis.

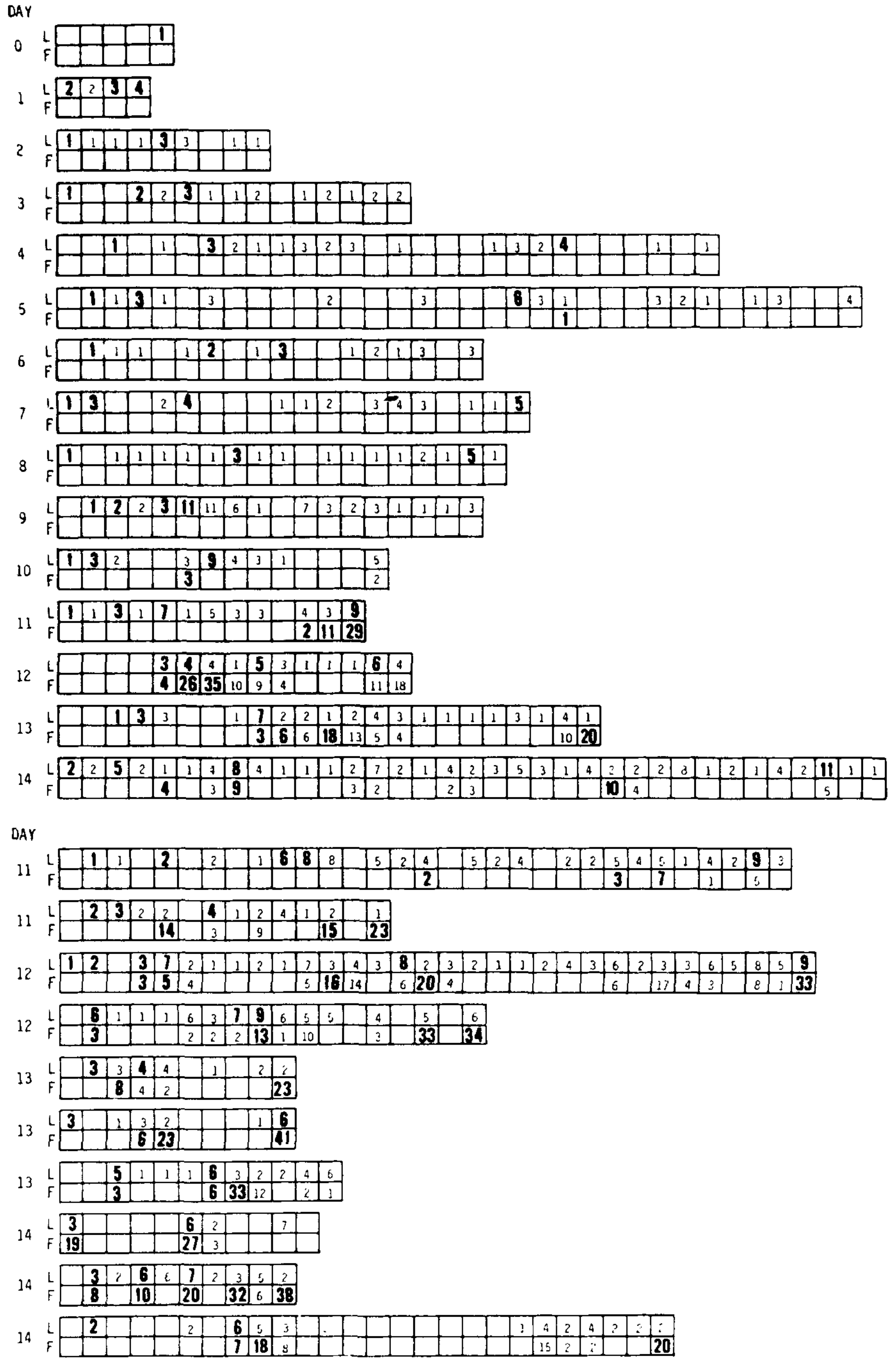

Fig. 9. The interrupted growth in the number of steps performed along the lateral and forward spatial dimensions. Each daily sequence is represented by two horizontal vectors: the upper vector represents stepping along the lateral (L), and the lower along the forward (F) dimension. Vertical lines partition the vectors of the daily sequence into successive phrases, in proper temporal order, from left to right. Each numeral gives the maximal number of successive steps (interval between steps smaller than 6 frames) performed during continuous movement in the same direction. Empty squares indicate that the number of steps along the specified dimension during that phrase was zero. Numerals in *heavy* print stand for new peaks, never performed before in the course of the daily sequence.

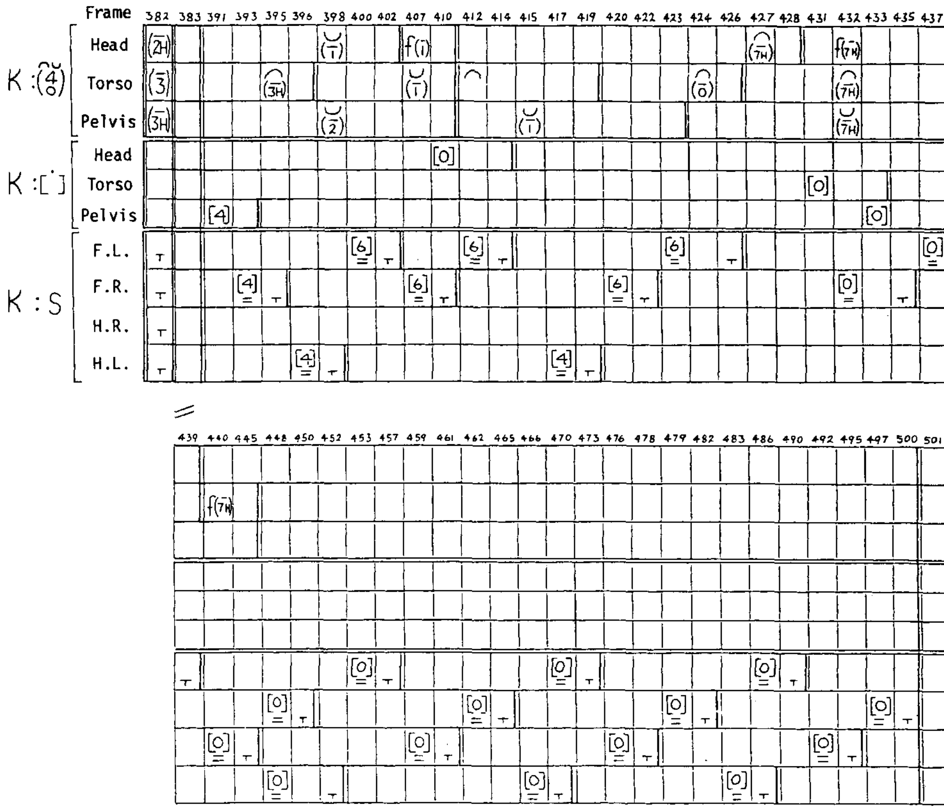

Fig. 10. E–W notation score presenting the 9th phrase of the daily sequence which was represented in Figure 7. Explanation as in Figure 6.

TABLE 3. The Number of Alternations between Clockwise and Counterclockwise Lateral Movements in the Three Parts of the Trunk, per Daily Sequence, in Four Randomly Selected Sequences per Developmental Day.

Postnatal Day	0				1				2				3					4		
Head	2	1	1	0	1	2	1	0	4	3	3	0	4	2	1	2	19	10	9	6
Torso	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	8	3	5	4
Pelvis	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	3	2	2	3
	5				6				7				8					9		
	19	6	16	4	16	9	5	4	18	15	10	8	11	6	6	6	14	10	9	5
	11	3	5	1	8	8	3	1	4	8	3	4	4	5	2	2	4	3	2	4
	5	3	3	1	4	5	2	1	3	7	1	2	2	4	1	1	2	2	0	3
	10				11				12				13					14		
	7	9	7	5	12	7	5	5	12	7	5	4	26	12	7	7	13	11	8	11
	4	2	2	2	4	7	4	3	9	6	3	3	21	5	4	1	5	8	7	5
	3	2	1	0	4	6	2	1	7	4	3	3	5	3	1	1	2	7	5	1

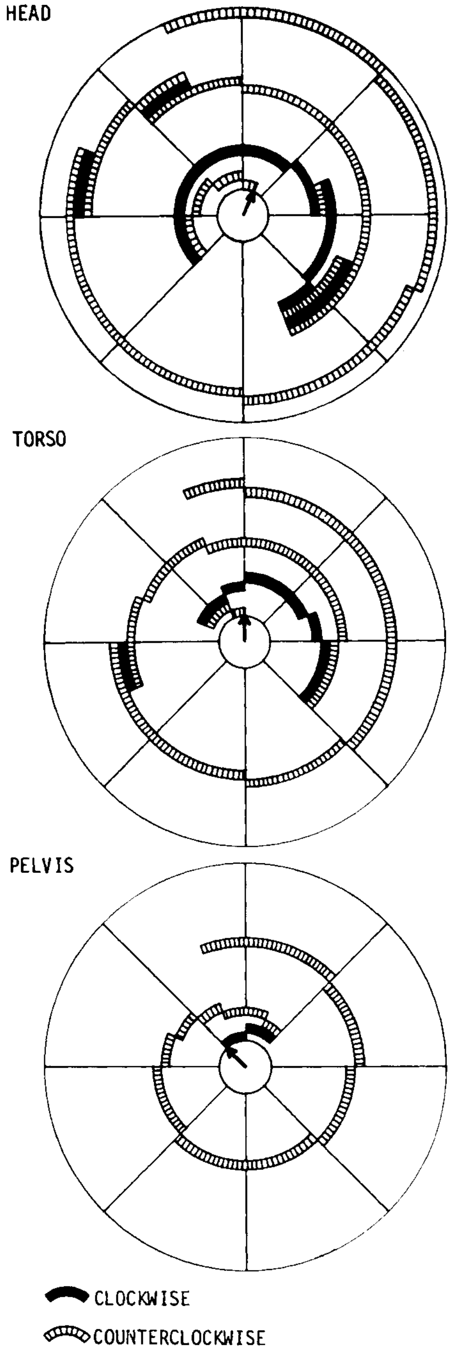

Fig. 11. The sequence of changes of position in the horizontal domain, recorded in a daily sequence of a 13-day-old infant. The record starts from initial immobility and ends with the onset of forward walking. The arrows at the center of the circles describe the initial positions of the respective part of the trunk. Changes of position are described in temporal order, from the center outward.

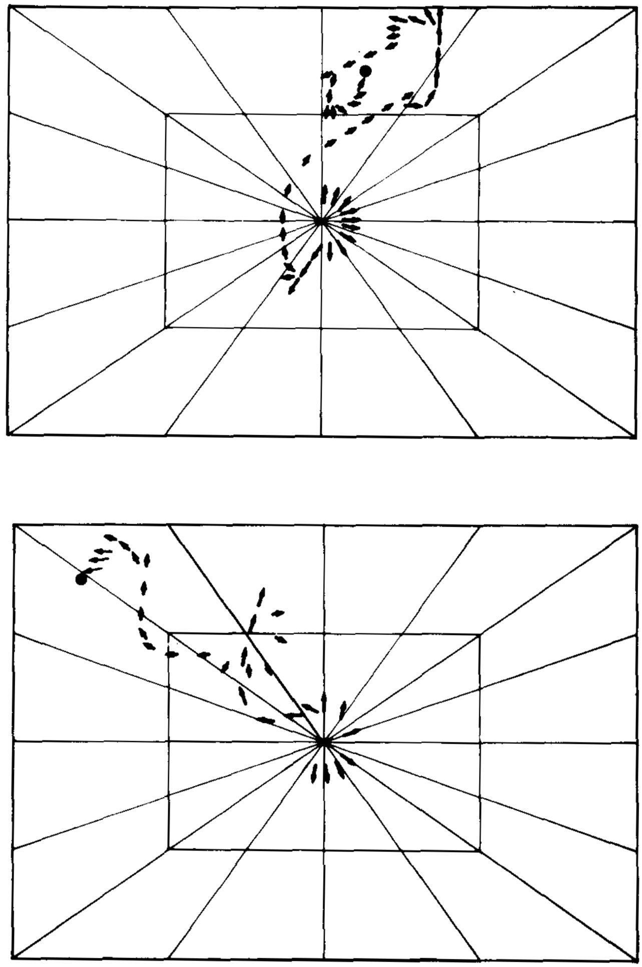

Fig. 12. The locations and positions of the torso on the observation platform are traced from film, in 10 frame intervals, in two daily sequences of 14-day-old rats. Recording started with initial immobility and ended with the performance of the first vertical movement of the head (signified by a circle).

2. *Switching between spatial dimensions:* As soon as forward walking is incorporated into the behavior of the infant, it repeatedly alternates between turning and forward walking, thus scanning increasingly larger portions of the horizontal substrate (Fig. 12). Since vertical scans along walls, and in the air, appear later in the sequence (last movements in Fig. 12), the horizontal substrate is explored for some time before the onset of exploration along the third, vertical dimension. In the presence of, e.g., a vertical wire mesh, the warm-up sequence may even culminate with climbing on all four. As along the other two dimensions, the build-up in amplitude is gradual, and interrupted by repetitions and reversions to smaller amplitudes (see also section on ontogeny).

II. Ontogeny

a. The Progressive Incorporation of New Spatial Dimensions Day by Day

The regularities observed in the daily sequences are also seen on an ontogenetic scale. In Fig. 4, the youngest infants (days 0–1) move only along one dimension (lateral), older infants (days 5–6) move along two dimensions (lateral and forward), and the oldest infants (days 11–14) move along three dimensions (lateral, forward, and vertical) (see also Figs. 7, 8).

b. Incorporation of Spatial Dimensions Is Partly Coupled to Build-up in Amplitude

In Figure 9, in the first few postnatal days (0–4), the infants step only during lateral movement. As the maximal number of steps along this dimension increases across the days, forward steps appear, and increase in frequency with age (days 11–14). The peak of stepping along the lateral dimension typically precedes the peak of stepping forward.

c. Progressive Incorporation of New Types of Movement Day by Day

The rules of the daily sequence guarantee that the spread of activity and build-up manifested in less advanced sequences is contained within the more advanced sequences. This is illustrated in Figure 5: For each developmental day, there is at least one sequence which contains within it the spread of activity manifested in all the other sequences of that day. Therefore, the developmental continuum may be represented by the most advanced daily sequences available for each postnatal day.

In Figure 13 ontogeny is conceived of as a matrix. The most advanced daily sequence, available for each developmental day, is notated from left to right between the horizontal lines, the movement enclosed in the right-hand column included. The first appearance of movement of a part of the trunk along a new spatial dimension, not observed before in that or earlier sequences, is enclosed in the right-hand column, so that the sequence of movements preceding it is represented on its left. When an additional new movement appears in the same daily sequence, it is written below the earlier new movement, and the sequence which was performed between the two new movements is again notated on its left. The behavior following the performance of the last peak is eliminated from the figure because it is composed of repetition and reversion to movements which have already been performed earlier on. The figure thus represents both the movements that culminate the most advanced daily sequences (right-hand column) and the spread of activity and build-up leading to them day by day (horizontal lines).

The two constraining principles of the daily sequence are also manifested in the developmental sequence which is represented in the right-hand column by the movements that culminate the daily sequences: Each part moves in development

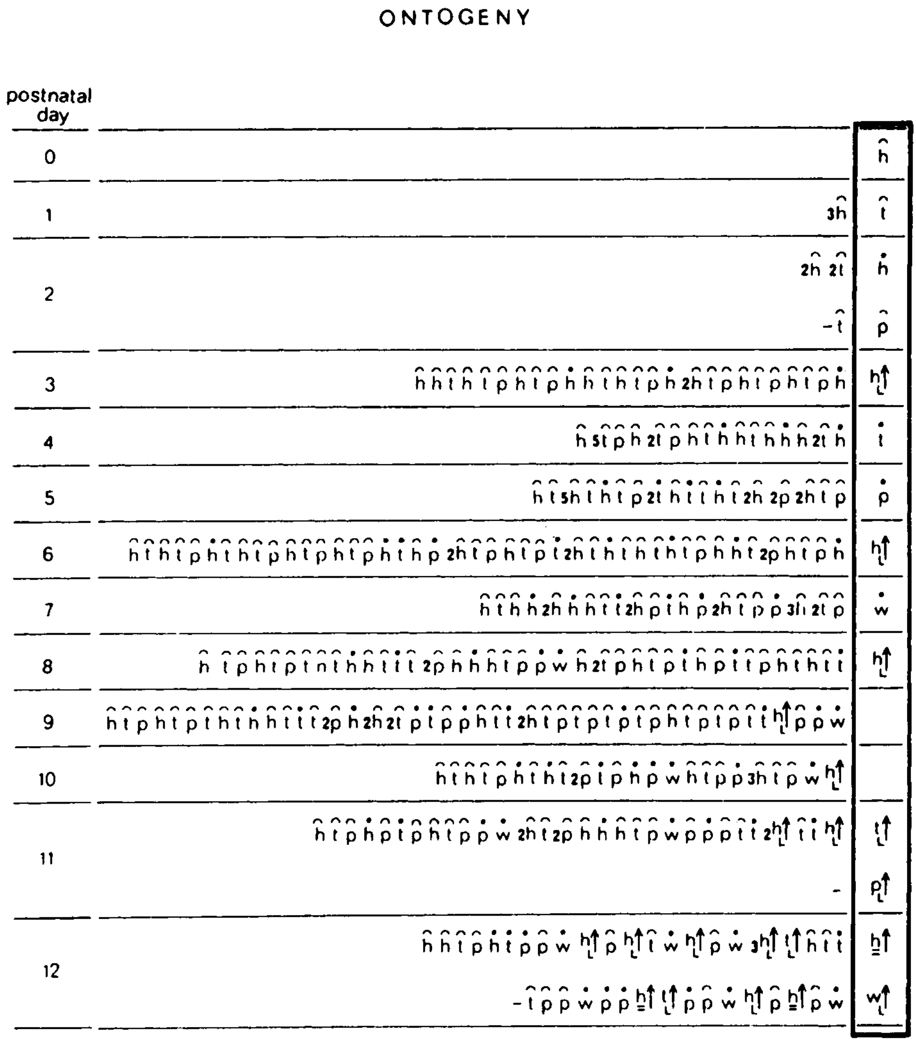

Fig. 13. "Warm-up" in ontogeny. The sequence of initiations of movements of the "heaviest" part of the trunk, along the three spatial dimensions, in the most advanced sequence of each developmental day. Horizontal lines distinguish between daily sequences. (Distinction between phrases is eliminated). ⌒, signifies horizontal movement; •, forward transport; ↑, vertical movement up with loose snout contact; =↑, vertical movement up in the air; ẇ, forward walking; w↑, climbing; h, head; t, torso; p, pelvis. Examples of these types of movement are illustrated in Fig. 1.

first laterally, then forward, and then up; and the parts are incorporated in movement along each dimension separately, in a cephalocaudal order.

As shown in Figure 13, during the first postnatal day, the richest behavioral sequence is composed of lateral head movements, $\hat{h}$, which are bounded by long periods of arrest. Lateral head movements constitute both the daily sequence and the daily developmental peak. In postnatal day 1 the infant starts similarly with lateral movements of the head and culminates the sequence with lateral movement of the torso $\hat{t}$. In day 2, after repeating the movements which have already been performed in the preceding developmental days, it incorporates into the sequence a movement of the head along the next, forward dimension $\dot{h}$; after performing an additional lateral movement of the torso, it completes the cephalocaudal recruitment along the lateral dimension with pivoting laterally, $\hat{p}$, around the hindquarters. From day 3 and on, the infant starts by progressively incorporating the parts of the trunk in lateral movement; forward transport is incorporated in a cephalocaudal order, either after or before exhausting the lateral dimension. The infants' daily sequences consist during these days of switching between lateral movements (which amount to pivoting) and forward stretching. From day 7 and on, the amplitude of forward transport increases further, and all four legs are recruited in forward stepping $\dot{w}$. Up to day 7 the infants spend most of the time in pivoting, switching to short amplitude bouts of forward transport; from day 8 and on, they switch from shorter bouts of pivoting to increasingly larger bouts of forward walking. With the exception of head raising along walls, once a new movement appeared, it was observed in most of the infants in the next day or so. (Head raising along walls was observed in one infant on day 3, and in another on day 6, without being observed again until day 8, when it was observed in many infants (Fig. 13).)

Movement along vertical surfaces typically appears in most of the infants from day 8 and on: On this day, many infants culminate the sequence with head raising along walls; on day 11, the most advanced sequence is culminated in rearing on the hindlegs along walls $p_{\iota}\uparrow$; and on day 12—in climbing $w_{\iota}\uparrow$. Finally, daily sequences are culminated in head raising in the air $\underline{\underline{h}}\uparrow$ on day 12; in sitting up accompanied by release of foreleg contact on day 16, and in rearing up on the hindlegs and then jumping up, on day 25 (not represented in Fig. 13).

Ontogeny is thus conceived of as a matrix of horizontal vectors representing the daily warm-up. The right hand vertical vector consists of the spread of activity manifested in development. Since every behavioral sequence is constrained by the same principles of warm-up which also characterize the whole developmental sequence, it is as though every time the infant moves after pronounced immobility, it recapitulates its ontogeny.

The considerable freedom allowed by the two constraining principles, by the interrupted increase in amplitude, and by the yet unspecified rate of repetition and reversion to less advanced movements, results in a large number of actual sequences of warm-up. These, nevertheless, always abide by the two constraining principles.

Discussion

Summary of Rules of Order

After pronounced immobility, infant rat movement is comprised of phrases of continuous movement interrupted by intervals of complete arrest. Sequence analysis reveals a process of motorial expansion constrained by the following rules: a) every part of the trunk must first move laterally, then forward, then up; b) a part can never move along a dimension unless the part anterior to it has already moved along that dimension; c) once a new type has been performed the infant repeats it and reverts to it unpredictably later on in the sequence; and d) there is a gradual interrupted increase in the amplitudes of movements along the three spatial dimensions. In addition, in horizontal movement, the parts of the trunk switch repeatedly between clockwise and counterclockwise movements; the rate of switching, and the amplitudes of horizontal sections covered during scanning diminish cephalocaudally.

The expansion of movement in space and along the body takes place in three temporal domains: in the phrases of continuous movement, in the longer sequences which are comprised of these phrases, and across the sequences, in ontogeny. This process of build-up and spread of activity results in the scanning of increasingly larger portions of the environment. (The increase in amplitude was demonstrated only *across* the phrases, i.e., in daily sequences, and in ontogeny).

Methodological Considerations

Initial immobility which is a prerequisite for "warm-up," was used as the reference starting point for all observations. Contrary to the common method which demands a constant environment across observations, we substituted environmental constancy with behavioral constancy (initial pronounced immobility), by changing the properties of the testing environment every few days. This procedure minimized the effect of learning (response to a familiar environment) and confined the study to the ontogeny of the infant's response to a novel environment.

The morphology of movement was described in relation to three variables: body (pelvis, torso, head), space (lateral, forward, vertical), and time. By taking into account the mechanical interdependence between the trunk segments ("the law of heavy and light limbs"), we obtained a concise representation of complex movements, without resorting to functional terms, such as orienting, scanning, or sniffing. While the use of such terms may be useful at the end of a study, their premature use may obscure the morphology of the behavior.

The scaling of sequences of movement, i.e., the establishment of gradients, was accomplished by depicting the appearance of new peaks in amplitude, and the first performance of new movement types, never performed before in the examined sequence or in ontogeny. The lawful build-up and spread of activity in all the sequences implies that the behavioral expansion manifested in less advanced sequences is contained within the more advanced sequences of "warm-up." Therefore, the most advanced sequences represent both the maximal expansion observed in a particular developmental day, and the earliest appearance of a new developmental peak. By using this procedure we circumvented the problem of individual variation in the peak reached by particular infants in specific sequences. (A relatively grown-up infant may, for instance, stay immobile throughout the observation period on a particular day, and thus misrepresent its own current potential of movements.)

The Mobility Gradient

To evaluate the method and results of this study consider the following sequence:

AAAAAABABAABABBCBABCBABCACB

The sequence of letters in the last portion of this sequence is unpredictable, yet when the whole sequence is examined, it can readily be seen that the first portion consists of A's, the second of A's and B's, and the third of A's, B's and C's. In other words, A is incorporated into the sequence first, B second, and C last. Furthermore, after the first appearance of a new letter, this and the letters that preceded it appear in no apparent order. As a result, the sequence becomes increasingly unpredictable. The infants' behavior after immobility abides by this regularity along three variables: along the body, A, B, and C may be taken to represent the head, the torso, and the pelvis; in space, these letters may stand for lateral, forward, and vertical movements; and in amplitude, A, B, C etc. represent increasing amplitudes of movement. The coupling between movements is such, that along each spatial dimension separately, the parts of the trunk are incorporated in a cephalocaudal order, and each part of the trunk moves first laterally, then forward and then up. In order words, $T_{i,j} > T_{i-1,j}$ and $T_{i,j} > T_{i,j-1}$, where T stands for the time of first appearance of a movement; i = 1, 2, 3 stand for head, torso, and pelvis, respectively: and j = 1, 2, 3 stand for lateral, forward, and vertical movements, respectively.

The same few rules generate in the portion of the gradient which is adjacent to immobility, relatively stereotyped sequences, and in the portions of the behavior which are temporally remote from immobility, increasingly more variable sequences. Both stereotyped and flexible forms of behavior are thus produced by a rather constrained set of rules. What an infant does in a particular moment depends first and foremost on: a) the preceding temporal sequence which follows immobility, and b) the preceding ontogenetic sequence. Starting with the first lateral movement of the head, there is a gradual increase in the number of degrees of freedom of movement available to the infant at any one time: This process underlies both the most stereotyped "searching automatism" of neonates (Lorenz, 1970, vol. 1, p. 295), and the relatively unpredictable behavior of older infants. The seeds of what appears to the observer as "free" movement are already ingrained in the relatively stereotyped sequences, and unpredictable behavior is gated by the same rules which constrain the matrix from which it unfolds.

Features of the physical environment such as vertical surfaces or cliffs, elicit, or even enhance, particular movement types, *provided* that these are available to the infant at the particular "warm-up" phase. Rearing in a novel environment, for instance, cannot be elicited by a vertical surface on, say, day 3 postnatally, or during the early portion of a "warm-up" sequence on day 12, but can be readily elicited on a later portion of the same 12th day sequence, and performed in the absence of a vertical surface, in the air, on day 17. Our observations were carried out in a static environment; presentation of moving tactile or visual stimuli would conceivably enhance the warm-up sequence.

Morphological Continuity

The chronology of appearance of movement types derived from studies on the development of exploratory behavior in the laboratory rat, is consistent with the order established in the present study (Bolles & Woods, 1964; Altman & Sudarshan, 1975). Williams & Scott (1952) report in house mouse (*Mus musculus*) ontogeny a transition from pivoting (day 4), to walking (day 8), running and hopping (day 12), and a subsequent and concurrent increase in vertical movements (head-raising, day 5; rearing, day 12; jumping, day 16). However, Altman and Sudarshan (1975) challenge the rule of cephalocaudal recruitment of body parts by pointing out that infant rats raise their heads quite late in ontogeny, only after the recruitment of the hindquarters in movement. We show that at the stage of head raising, the hindquarters have moved *only sideways and forward*. In other words, head raising *does* initiate, at this developmental stage, cephalocaudal recruitment of the parts of the trunk along the vertical plane. Prechtl and Schleidt (1950, 1951) report that in kitten (*Felis domestica*) exploratory behavior, sideways sweeping movements are performed simultaneously with creeping forward. In this case, disregard of the precise coupling between body parts and planes of movement seems to have obscured the ordered sequential intercalation of movements of the parts of the trunk along the different spatial dimensions.

Ontogeny of Movement in Other Vertebrates

The morphological continuum established so far may serve as a search image in the examination of other, seemingly unrelated behaviors. The course of motor development in the amphibian urodele *Amblystolma punctatum* (Coghill, 1929) shares several features with the early portion of infant rat postnatal development. In Coghill's account, the entire locomotory repertoire of Amblystoma unfolds—from the simplest change of relation between two adjacent segments, to the greatest possible capacity of performance—through a continuous process of modification of one and the same type of movement.

The first movement to develop in the larva of Amblystoma is a simple lateral bending of the head; when the amplitude of the lateral movement increases, more caudal segments of the trunk are recruited in movement and the larva is seen to coil, and then change its horizontal orientation; when such opposite lateral movements are performed successively, and simultaneously, forward swimming ensues; later, when stepping of all four legs is incorporated into the pattern, the tadpole walks forward.

The whole ontogenetic continuum is generated in the tadpole out of one type of building block: lateral movements. What changes in ontogeny is: a) their amplitude; b) the parts of the body that participate in the movement; and c) the timing of performance of these movements. Furthermore, Coghill comments that "the individual performance (of horizontal movements) recapitulates the history of its performance".

The primacy of horizontal movements (lateral bending, s-waves) over forward progression, and the cephalocaudal order of appearance of horizontal movements in development, are reported in embryos of fish (Tracy, 1926), turtles (Decker, 1967) and chick embryos (Hamburger et al., 1965).

Pathological Behavior

When intact laboratory rats are injected with the dopaminergic stimulants apomorphine or amphetamine, they display a behavioral syndrome which has been reported to consist of increased exploratory locomotion and subsequent perseverative performance of "behavioral stereotypies" (Randrup & Munkvad, 1967; Ellinwood & Balster, 1974; Costall & Naylor, 1975). Several hypotheses have been proposed to explain the bizarre, seemingly incoherent behavior observed under these drugs (Lyon & Robbins, 1975). However, in the absence of a developmental perspective it has been difficult to explain why, during particular phases of drug action, the rats engage in specific types of movement, and not in others. Indeed, Lyon and Robbins frankly point out that a salient weakness of their theoretical conception relates to the questions of "exactly why certain responses dominate 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." The rules established for development suggest a comprehensive hypothesis which seems to explain these phenomena.

Analysis of apomorphine induced behavior in the light of the mobility gradient (Szechtman et al., 1985) shows that several of the effects reviewed by Lyon & Robbins for amphetamine, and observed by Szechtman et al., in rats under apomorphine, reflect a gradual *decrease* in mobility: The order in which movement types are incorporated and then *eliminated* from the rat's behavior is reversed in relation to the order in which they are *incorporated* into behavior in ontogeny and recovery (in relation to "warm-up," elimination proceeds according to the principle "Last In First Out"—"LIFO"). Vertical movements are incorporated and then eliminated first, forward walking next, and large lateral movements last, leaving, in the course of one hour, a residue of small lateral movements of the forequarters on the immobile hindquarters. The same principle operates along the body, as the segments of the trunk drop out of movement in a caudorostral order (pelvis first, torso next, head last).

The change in amplitude is also opposite to that seen in development: starting from normal amplitudes of movement, the apomorphine treated rat first increases the amplitudes of movement along each spatial dimension to an exaggerated peak, and then decreases them to a level much lower than the normal, or even eliminates them completely (Szechtman et al., 1985). In observations not reported in the results section (see also Altman & Sudarshan, 1974), it was found that in development, starting from small movements, the amplitudes increase to an exaggerated peak, and then subside to normal levels (excessive pivoting is seen at days 7–8, excessive forward walking at days 12–14, and excessive rearing at day 17). The same trends in the change of amplitude were observed in recovery from lateral-hypothalamic damage (Golani et al., 1979).

The "warm-up" model thus suggests that under the action of apomorphine, rats undergo a process of shut-down in mobility. This process unfolds concurrently with other processes of behavioral activation which include a disappearance of intervals of complete arrest, an increase in the rate of switching from one movement to the next, and an increase in the speed of movement (Lyon & Robbins, 1975). The shut-down hypothesis, which could not be reached without a comparison to normal ontogeny, provides a unitary explanation for the changes in the types of movement, the changes in the identity of the trunk segments that perform these movements, and the changes in the amplitude of the movement types which take place in the course of the drug's action.

The behavioral shut-down seen under apomorphine might reflect a hitherto unsuspected process of neurological regression (Jackson, 1931; Ey, 1962; Szechtman et al., 1985). One possible mechanism for such regression has been proposed by Jaspers and Cools (in press), who suggest that the shut-down sequence under apomorphine reflects progressive ordered dysfunctioning of the neostriatum and its lower level output stations. According to these authors, "warm-up" in development and lateral hypothalamic recovery, could conversely be mediated by successive involvement, in ascending hierarchical order, of the various output stations of the dopaminergic systems (see also Cools, 1985).

The Mobility Gradient in Normal Adult Behavior

The experimental set-up used in this study ensured an initial period of pronounced immobility, and hence a relatively slow process of "warm-up." If the same infant is tested daily in the same environment, the initial immobility is shortened, the number of repetitions of the same movements is diminished, and the most advanced movement is reached through a condensed sequence of movements, which nevertheless follows the "warm-up" rules.

In many situations which involve a transition between immobility and mobility, mammals perform sequences of movement which show the same hierarchy of movement types seen in either "warm-up" or "shut-down." In such sequences, repetition of the same movement type before the transition to the next type is often completely eliminated: nevertheless, the animals always shift between arrest and forward progression through horizontal movement (pivoting). The ordered spread in mobility is seen in adults in, e.g., moving out of arrest in a new environment; the ordered shut-down is seen in, e.g., lying down to sleep in several mammals.

During agonistic interactions, the proximity of the "superior" animal often induces an arrest in the "inferior." The transition from such arrest to forward progression, and the opposite transition from forward progression to arrest, occur in the majority of cases through pivoting (for a review of the mobility gradient see Golani & Moran, 1983; Yaniv & Golani, 1987). In these contexts and others, the behavior may be respectively interpreted as a condensed version of either "warm-up" or "shut-down" of mobility.

In summary, sequences of motorial expansion and constriction are seen in a variety of vertebrate species, situations and pathological preparations. These sequences extend over a wide range of temporal scales; they share similar basic motor patterns, common rules of order, and perhaps also common neurophysiological mechanisms. This suggests that the organization they reveal is primitive and fundamental.

Notes

Prof. N. Eshkol applied the notation to fit the particular requirements of the present study and devised all the symbols. S. Zeidel acted as liaison with Eshkol. Critical comments on the manuscript were made by Professors P. Teitelbaum, A. R. Cools and D. Todt, and Drs. H. Szechtman and S. Pellis. This study was supported by grants from the US–Israel Binational Science Foundation (BSF) Jerusalem, to I. Golani and P. Teitelbaum, and by a grant to I. Golani from the Alice and Benno Gitter Foundation. Drawings were made by W. Ferguson.

The relevance of "warm-up" in rats to the behavior of primitive vertebrates was brought to our attention by Prof. B. Moore, Dept. of Psychology, Dalhousie University, Nova Scotia, who also furnished the relevant references.

Appendix: EW Movement Notation Principles and Descriptive Tools Used in the Present Study (based on Eshkol, 1980).

System of Reference

The movements of a single axis of constant length, free to move about one fixed end, are enclosed by a sphere. The equatorial plane of the sphere, parallel to the ground, is called the horizontal plane. One direction on it, called absolute zero, is selected as the starting position for all descriptions. By measuring intervals of 45° in a clockwise direction, looking on the plane from above, eight positions (directions) are obtained on the horizontal plane (45° = 1, 90° = 2, etc.). Vertical planes, perpendicular to the horizontal plane, intersect with the horizontal positions. The vertical planes are divided according to the same scale. Vertical direction zero ($\binom{0}{-}$), is the direction of gravity (Fig. 2). The vertical absolute axis is specified by position ($\binom{4}{0}$) (Fig. 14).

Body

The infant rat's trunk is treated as a system of three articulated axes ("limb segments" or "parts of the trunk"): the "pelvis" (including pelvis and few vertebrae anterior to it), the "torso", and the neck-and-head (called "head"). Each of these parts is imagined as a straight line (axis) (Fig. 1).

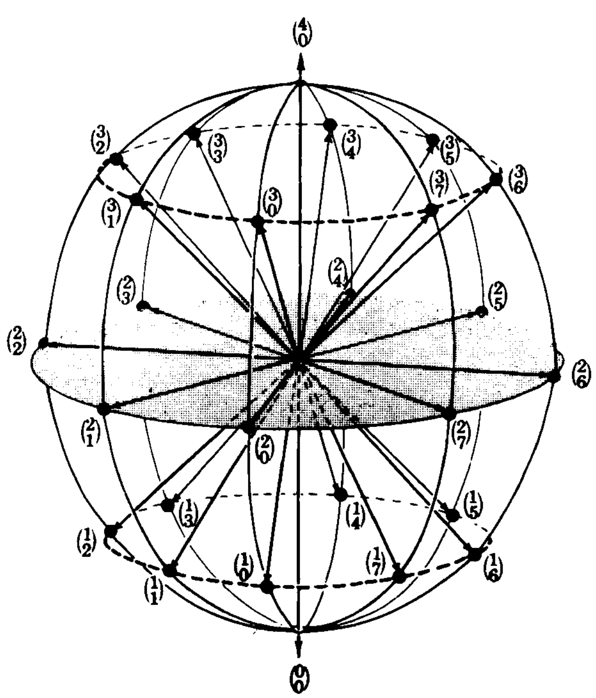

Fig. 14. The EW sphere (with permission of the Movement Notation Society).

Individual Coordinate Systems

Each of the three parts of the trunk has its own individual spherical coordinate system, the centre of which is made to coincide with its more caudal joint. Thus, the pelvis is viewed from the hindlegs rostrad, the torso from the pelvis rostrad, and the head from the torso rostrad. The individual coordinate systems are parallel to each other and to the general System of Reference, at all times (Fig. 1).

Manuscript Page and Mode of Notation

The body is represented on a horizontally ruled page. Each horizontal space represents a part of the body. Vertical lines divide the manuscript page into columns denoting units of time (successive single frames on film). The symbols for movement are written (and read) from left to right, and, for each group of serially connected segments, from bottom to top (Fig. 6).

Separate Notation of Horizontal and Vertical Movements

Initially, movement was notated in relation to the EW spherical coordinate system presented in Figure 14. Notation revealed that during movement on the observation platform, the infants rarely moved the parts of the body in planes which are tilted in relation to the horizontal plane, and the vast majority of movements were performed in relatively pure form in the horizontal or vertical planes. To express this finding in the representation of movement, we adopted an option available in EW, to describe movement in relation to two separate—horizontal and vertical—coordinate systems (Fig. 2). These circular coordinate systems are part of the general System of Reference presented in Figure 14. (See also Fig. 1).

Movement in the Horizontal Plane

As shown in the left-hand column of Figure 1, the coordinates of the horizontal plane are determined in relation to absolute zero, which is fixed at all times in relation to the environment, i.e., in relation to the general System of Reference. A direction (position) of a part of the body on this plane is established by specifying its horizontal coordinate. The numeral designating the position is written in parentheses, e.g., $(\bar{0})$. In EW, there is an option to describe all movements as rotations around specific axes. The axes are defined as positions in the spherical System of Reference. In the present study, horizontal movements are represented as rotations ($\frown$ — for clockwise, $\smile$ — for counterclockwise) around the vertical absolute axes, designated by $(^{4}_{0})$. A movement is described by establishing the initial and final positions of the moving part, and by specifying the sense of the movement. The final position of the movement is written under the sign, e.g., $(\bar{0})$ or $(\bar{1})$, where the numeral designates the final position. The smallest unit of measurement in the present study is 45°/2, designated by the sign H.

Movement in a Vertical Plane

As shown in the right-hand column of Figure 1, the coordinates of a vertical plane are determined in relation to the direction of gravity, which is fixed at all times and designated by vertical zero. A position of a part of the body on a vertical plane is established by specifying its vertical coordinate. The numeral designating the position is written in parentheses, e.g., $(^{4}_{-})$. A movement is described by establishing the initial and final positions of the moving part, and by specifying the sense of the movement— ↑ for up and ↓ for down.

The Mechanical Interdependence Between the Parts of the Body ("Heavy" and "Light" Limbs Hierarchy)

The parts of the body are characterized as active or carried. An actively moving part is called "heavy," and its movements change the locations and modify the paths of movement of any "lighter" part that it carries. During active movement, the lighter part changes its angular relation to its heavy neighbour. During passive movement ("carrying along"), the lighter part maintains a fixed angular relation to its moving, heavy neighbor. Consider the illustrations in the first and third columns of Figure 1: Along the trunk, the most rostral part, the head, is the "lightest": when moving (transition from upper horizontal row to 2nd row) it does not modify the locations and the paths of movement of all the parts that are caudal to it (Fig. 1). The torso is "heavier": its active movements on the pelvis modify the locations and paths of movement of the head (but not those of the pelvis) (Fig. 1, transition from upper horizontal row to 3rd row); the pelvis is the "heaviest": its movements change the locations and the paths of movement of the torso and the head (Fig. 1, transition from upper horizontal row to 4th row).

During the first 2 postnatal weeks, when infants pivot, they do so exclusively around their hindlegs, therefore the "heaviest" part should be the hindlegs: in moving in relation to the ground, the hindlegs modify the locations and paths of movement in all the parts that are rostral to them. However, because of the stocky structure of the infants, we could not assess the relations between the hindlegs and the pelvis. Therefore, the trunk was separated from the legs in the establishment of the "heavy and light limbs hierarchy."

Since infants pivot exclusively around their hindlegs, a specification of the most caudal ("heaviest") part that moved at any one time, *implies* that the locations and the paths of movement of the parts of the body which are rostral to that part, were modified as well.

Forward and Backward Transport

During the maintenance of loose snout contact with the ground, arching (contraction) and unarching (protraction) of a portion of the trunk, causes the whole of the remaining rostral portion of the trunk to be transported along its longitudinal axis backward or forward, respectively. Unarching of the neck causes only the head to be transported forward (Fig. 1, transition from upper to 2nd illustration in middle column); unarching between the pelvis and the torso, with or without forward stepping of the forelegs, causes the torso, and the head to be transported forward (Fig. 1, transition from 2nd to 3rd illustration in middle column); and stretching of the hindlegs as they maintain firm contact with the substrate, causes the pelvis, and hence the whole trunk to be transported forward (Fig. 1, transition from 3rd to 4th illustration in middle column). Backward transport is brought about when the same movements are performed in reverse. These forward and backward "transports" of the parts of the trunk, which are characteristic of rat movement, are brought about by vertical movements of the parts of the trunk in opposite directions (Fig. 1, middle column).

Since many of the films were taken from below, we had no access to the vertical coordinates of the parts of the trunk. Therefore, we focused upon the forward and backward transport of the rostral extremity of the respective part of the trunk. The rostral extremity of a part of the trunk is symbolized by the sign [$\dot{}$], the upper dot signifying the "light" extremity of the axis. In notating transport we merely specify the "heaviest" (most caudal) part of the trunk whose rostral extremity was transported forward, [0], or backward [4] (Fig.1, middle column, darkened axes). Three horizontal spaces were allocated for the three parts of the trunk for the notation of this aspect of movement (Fig. 6). Since we did not notate the vertical coordinates of the parts, this leaves room for a great deal of interpretation regarding their individual movements. When "transport" is indicated in a part of the trunk, it is implied that the remaining portion of the trunk rostral to it was transported as well. In walking, we indicate the direction of stepping of each of the four legs, as well as a transport in the horizontal space allocated for the pelvis.

Stepping

A step is designated by the signs for release, =, and establishment of contact, ⊤, which are written in sequence in the horizontal space allocated for the appropriate leg. Since many of the films consist of a ventral view of the infant, the direction of stepping had to be established by assessing the direction of an imaginary line traced by the paw during the "swing" phase of a step. The orientation of this line is described "bodywise": the reference for the forelegs is the longitudinal axis of the torso, and for the hindlegs—the longitudinal axis of the pelvis. Both are represented by body wise [0]. Bodywise forward steps are designated by ([$\underline{\underline{0}}$] ⊤; backward steps by ([$\underline{\underline{4}}$] ⊤; to the right by ([$\underline{\underline{2}}$] ⊤; and to the left by ([$\underline{\underline{6}}$] ⊤.

References

Altman, J. A., and Sudarshan, K. (1975). Postnatal development of locomotion in the laboratory rat. *Anim. Behav., 23*(4): 896–920.

Bolles, R. C., and Woods, P. J. (1964). The ontogeny of behavior in the albino rat. *Anim. Behav., 12:* 427–441.

Coghill, G. E. (1929). *Anatomy and the Problem of Behavior.* London: Cambridge University Press.

Cools, A. R. (1985). Brain and behaviour: hierarchy of feedback systems and control of input. In: *Perspectives in Ethology, Vol. 6.* (pp. 109–168). P. P. G. Bateson and P. H. Klopfer (eds.) New York: Plenum.

Costall, B., and Naylor, R. J. (1975). Action of dopaminergic agonists on motor function. *Advan. Neurol., 9:* 285–297.

Decker, D. J. (1967). Motility of the turtle embryo *Chelydra serpentina. Science, 157:* 952–954.

Ellinwood, E. H., and Balster, R. R. (1974). Rating the behavioral effects of amphetamine. *Eur. J. Pharmacol., 28:* 35–41.

Eshkol, N. (1980). *50 lessons by Dr. Moshe Feldenkrais.* Israel: The Movement Notation Society.

Eshkol, N., and Wachman, A. (1958). *Movement Notation.* London: Weidenfeld and Nicholson.

Ey, N. (1962). Hughlings Jackson's principle and organo-dynamic concept of psychiatry. *Am. J. Psychiatr., 118:* 673–682.
Golani, I., Wolgin, D., and Teitelbaum, P. (1979). A proposed natural geometry of recovery from akinesia in the lateral hypothalamic rat. *Brain Res., 164:* 237–267.
Golani, I., Bronchti, G., Moualem, D., and Teitelbaum, P. (1981). "Warm-up" along dimensions of movement in the ontogeny of exploration in rats and other infant mammals. *P.N.A.S. USA, 78(11):* 7226–7229.
Golani, I., and Moran, G. (1982). A motility-immobility gradient in the behavior of the "inferior" wolf during "ritualized fighting". In *Recent Advances in the Study of Mammalian Behavior* (pp. 65–94). J. F. Eisenberg and D. J. Kleiman (Eds.). American Society of Mammalogists.
Hamburger, V., Balaban, M., Oppenheim, R., and Wenger, E. (1965). Periodic mobility of normal and spinal chick embryos between 8–17 days of incubation. *J. Exp. Zool., 159:* 1–14.
Jackson, J. H. (1931). The factors of insanities. In Selected Writings of J. H. Jackson, J. Taylor (Ed.). *Vol. II* (p. 411).
Jaspers, R. M. A., and Cools, A. R. (1988). Behavioural correlates of a progressive dysfunctioning of the caudate nucleus: Effects of apomorphine. *Behav. Brain Res:* 193–204.
Kortmulder, K. (1983). Play-like behavior: an essay in speculative ethology. *Acta Biotheoretica, 32:* 145–166.
Lorenz, K. Z. (1970). *Studies in Animal and Human Behavior, Vol. 1.* London: Methuen & Co. Ltd.
Lyon, M., and Robbins, T. (1975). The action of central nervous system stimulant drugs: a general theory concerning amphetamine effects. In *Current Developments in Psychopharmacology, Vol. 2* (pp. 80–163). New York: Spectrum Publications Inc.
Prechtl, H., and Schleidt, W. M. (1950). Auslosende und steurnde mechanismen des saugaktes. I. Mitteilung. *Zeitschrift fur vergleichende physiologie, 32:* 257–262.
Prechtl, H., and Schleidt, W. M. (1951). Auslosende und steurnde mechanismen des saugaktes. II. Mitteilung. *Zeitschrift fur vergleichende physiologie, 33:* 53–62.
Randrup, A., and Munkvad, I. (1967). Stereotyped activities produced by amphetamine in several animal species and man. *Psychopharmacologia, 11:* 300–310.
Szechtman, H., Ornstein, K., Teitelbaum, P., and Golani, I. (1985). The morphogenesis of stereotyped behavior induced by the dopamine receptor agonist apomorphine in the laboratory rat. *Neuroscience, 14(3):* 783–798.
Tracy, H. C. (1926). The development of motility and behavior in the toadfish. *J. Comp. Neurol., 40:* 253–369.
Williams, E., and Scott, J. P. (1953). The development of social behavior patterns in the mouse, in relation to natural periods. *Behaviour, 6:* 35–65.
Yaniv, Y., and Golani, I. (1987). Superiority and inferiority: a morphological analysis of free and stimulus bound behavior in Honey Badger (*Mellivora capensis*) interactions. *Ethology, 74:* 89–116.