Proc. Natl. Acad. Sci. USA
Vol. 78, No. 11, pp. 7226–7229, November 1981
Psychology

"Warm-up" along dimensions of movement in the ontogeny of exploration in rats and other infant mammals

(motor development/subsystems/akinesia/lateral hypothalamic recovery)

ILAN GOLANI*, GIL BRONCHTI*, DAVID MOUALEM*, AND PHILIP TEITELBAUM†

*Department of Zoology, Tel Aviv University, Tel Aviv, Israel; and †Department of Psychology, University of Illinois, Champaign, Illinois 61820

Contributed by Philip Teitelbaum, July 31, 1981

ABSTRACT When some infant mammals are placed outside their nest, a sequence of exploratory behavior occurs, displaying a regular buildup and spread of activity. This "warm-up" involves repetition of movement along specific dimensions and an orderly transition from one dimension to the next, with cephalocaudal recruitment of body and limb segments. A similar principle of organization applies to neurological recovery from lateral hypothalamic akinesia.

In a recent analysis of lateral hypothalamic akinesia in adult rats (1), use of the Eshkol–Wachmann movement notation system (2) revealed a "warm-up" phenomenon. This consists of a regular buildup in amplitude of head movement trajectories along specific dimensions which appear successively every time the animal starts to move after prolonged arrest. Head trajectories may involve head and neck alone or head and neck carried along by more caudal body and limb segments.

Normal infantile development often parallels adult recovery after brain damage (1, 3–7). We now show that warm-up does indeed exist in exploratory locomotion in normal infant rats and in several other species. We also highlight some differences between the warm-up of ontogeny and that of recovery.

The damage that produces the lateral hypothalamic syndrome (8) typically includes the nigrostriatal bundle, a dopaminergic pathway running from the substantia nigra to the striatum (9). Destruction of this system also occurs in Parkinsonism (10), and many symptoms, such as somnolence, akinesia, and catalepsy, are common to both (11). After recovery from the immobility produced by large lateral hypothalamic lesions, an adult rat can walk around, appearing relatively normal (but see ref. 1 for specific deficits in locomotion and exploration revealed by movement notation analysis). When removed from its cage and placed on the ground, however, its movements cease. After such an arrest, a specific warm-up sequence occurs (1). First, small repetitive lateral head and neck movements appear, followed by lateral movements of larger amplitude involving also the forelegs and upper torso. Moments later, the lateral head trajectories increase to 360 degrees or more as the animal pivots using only one hind leg, that ipsilateral to the direction of pivoting, in backward steps. Then, forward stepping with the contralateral hind leg is added to the pivoting pattern. Movement along the longitudinal dimension (backward/forward), also recruiting limb and body segments cephalocaudally, appears only after the onset of lateral movements. In small-amplitude longitudinal movements, only the head and neck flex and extend; as the amplitude increases, the forelegs step forward or backward as the torso flexes and extends. Ultimately, the hind legs are also recruited and the animal walks forward. Up to this point, no vertical scans are elicited when a vertical surface is encountered. Then, vertical tactile scans appear, also increasing in amplitude, as body and limb segments are recruited cephalocaudally. Finally, the steady snout contact with the substrate is intermittently released as the animal rears its head upwards away from surfaces along increasingly larger vertical trajectories. The entire process takes at most a few minutes.

Movements along the various dimensions emerge in recovery day by day in the same order as in warm-up, their amplitude also increasing gradually. Because the overwhelming majority of these movements appear in pure form and in a definite order along these dimensions both during specific sequences and in recovery (1), they may constitute relatively independent behavioral subsystems. Similar motor subsystems have been described in the extrapyramidal system by Jung and Hassler (12). To summarize, warm-up in recovery has three aspects: (*i*) a regular successive appearance of head movement trajectories along specific dimensions; (*ii*) a gradual buildup in amplitude through repetition of movement along each dimension; and (*iii*) progressive cephalocaudal recruitment of the limb and body segments that carry the head along these dimensions (1). In this brief report, we compare the warm-up in ontogeny with that seen in neurological recovery.

METHODS

Forty Wistar laboratory rat pups from five litters were studied intensively from birth (which was defined as day 0) for 17 days. One hundred other rat pups were observed less systematically over the same age range. Each pup's movements were observed for 5 min daily after it was placed outside the nest on a horizontal surface. The behavior was recorded on film, on videotape, or by written notes. Two thousand feet of film were used for frame-by-frame analysis in a stop-frame motion-data analyzer. In addition, 20,000 feet of videotape were checked to confirm the results. For comparative analysis, infants of several other species were studied. These included 20 house rats (*Rattus rattus*; 1000 feet of film, 10,000 feet of videotape); 8 wild cats (*Felis lybica*; 600 feet of film, 5000 feet of videotape); and 3 common badgers (*Meles meles*; 1000 feet of film).

A conceptual framework derived from Eshkol–Wachmann movement notation (2) was used for comparative analysis. This notation system has been adapted for the study of animal motor behavior. In brief, this adaptation involves a simultaneous notation of the same behavior in several polar coordinate systems. The coordinates of each system are determined with reference to the environment, to the animal body midline axis, and to the next proximal or distal limb or body segment. By transforming the description of the same behavior from one coordinate system to the next, invariances in that behavior may emerge in some coordinate systems but not in others. Thus, the behavior may be invariant in relation to some or all of the following: the animal's longitudinal axis, gravity, or bodywise in relation to the

---

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U. S. C. §1734 solely to indicate this fact.

next proximal or distal segment (1, 13–15). A detailed documentation of infantile warm-up will be published elsewhere.

RESULTS AND DISCUSSION

First, we describe warm-up in the infant rat at day 11, when it is quite similar to that seen in the adult brain-damaged animal. At this age, an infant rat can move along all dimensions seen in the normal adult: along the lateral dimension by pivoting, along the longitudinal dimension by backward or forward walking, and vertically by scanning upwards along a vertical surface or by merely lifting its head vertically without surface contact. However, as illustrated in a typical sequence (Fig. 1), when removed from its nest and placed outside on a horizontal surface, it arrests its movement, and then it never walks forward before pivoting and never pivots or raises its head before performing lateral head scans. The warm-up principle is evident throughout early development. It involves a buildup in movement amplitude along at least two relatively independent dimensions, with partial coupling between them. After arrest, the lateral dimension is used first; with repetition, movements grow in amplitude along it. Only after the initial lateral movements, do longitudinal movements set in, also growing in amplitude.

This principle operates throughout development, but the behavioral sequences at a given age are determined by several concurrent developmental trends which we have isolated in rat ontogeny:

(*i*) At birth and for about 3 days, infants move along all the dimensions seen in normal adults, using a variety of hind leg stepping patterns. Then, for several days they become relatively immobile, tracing only small lateral head trajectories, minimal or no movements longitudinally, and none along the vertical. From day 5 or 6, movement reemerges cephalocaudally day by day, increasing in amplitude along the dimensions we have described and following the same general order of emergence of stepping patterns seen in recovery.

The infantile warm-up observed during the period of transient immobility (days 3–4) and the reemergence of movement (from day 5 on) resembles most closely the warm-up seen in recovery from adult lateral hypothalamic akinesia. In contrast, the early postnatal period of freedom of movement is not evident in adult recovery. In a sense, recovery parallels infant development, but only from the stage of relative infantile akinesia.

Furthermore, even when the parallel is closest and the pattern of stepping in warm-up closely follows the order of emergence in recovery, the infant always has a richer repertoire of stepping patterns. Thus, two hind leg stepping patterns never observed in recovery (sideways double-stepping of both hind legs in pivoting, and backward stepping of both hind legs in backing) are also present.

(*ii*) As the infants emerge from immobility, backward stepping with both hind legs along the longitudinal dimension appears. At first, such backward walking may initiate the warm-up; later, it is performed after lateral movements. Ultimately, at about day 10, it disappears. In contrast, lateral hy-

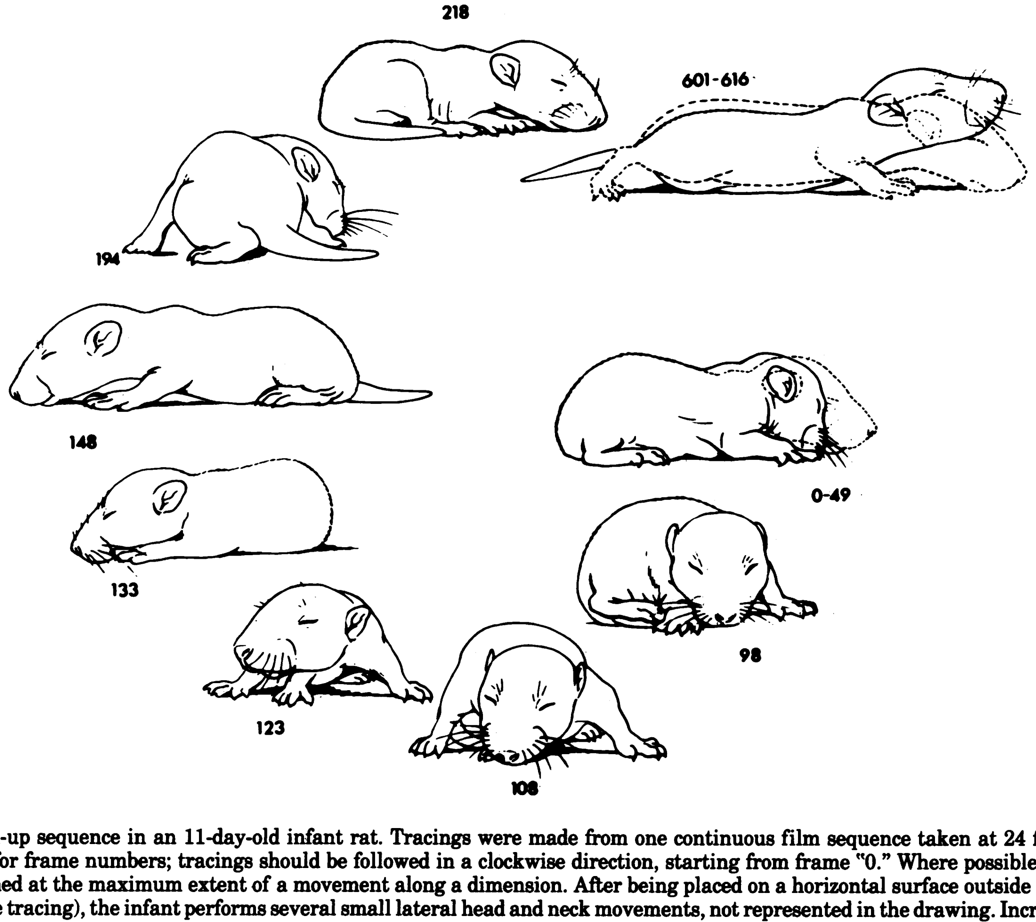

FIG. 1. Warm-up sequence in an 11-day-old infant rat. Tracings were made from one continuous film sequence taken at 24 feet per second. Numerals stand for frame numbers; tracings should be followed in a clockwise direction, starting from frame "0." Where possible, tracings show the position reached at the maximum extent of a movement along a dimension. After being placed on a horizontal surface outside the nest (frame 0, interrupted line tracing), the infant performs several small lateral head and neck movements, not represented in the drawing. Increasingly larger lateral head trajectories follow as the infant recruits first head, neck, and one foreleg in a sideways step (frame 49, continuous line tracing); then head, neck, and both forelegs in sideways stepping and the ipsilateral hind leg in backward stepping (frame 98); and then all four legs—forelegs to its right, hind legs to its left (frames 108, 123). Pure minimal head raising in air then occurs (frame 123), and after lowering its head, the infant continues to pivot (frames 133–218). Movement forward along the longitudinal dimension then sets in as the infant walks for several steps, stops (frame 601, interrupted line tracing), and then raises its head away from the surface (frame 616, continuous line tracing).

pothalamic animals never show any longitudinal backward walking in the warm-up sequence (1).

(*iii*) Unlike head-raising in recovery, where exploratory vertical movement independent of surfaces never appears before the animal walks forward, head-raising in ontogeny follows a more complex pattern. First of all, it appears before the period of transient akinesia (days 0–2), disappears during it (days 3–4), and reemerges afterwards. In addition, it may appear in warm-up after lateral and longitudinal trajectories. Only towards the end of the developmental period in which warm-up can still be observed (the first 2.5 weeks) is it shifted to the end of the exploration sequence, thus culminating the warm-up as in the lateral hypothalamic animal.

(*iv*) Throughout early development, after arrest in the open field, lateral always precedes longitudinal movement. At first, only small lateral head, neck, and foreleg movements precede forward progression; later (from day 6 on), large amplitude pivoting involving all four legs is engaged in before forward progression appears. In adult recovery (perhaps due to lesion variations), different animals may vary in the amplitude of lateral movement that they perform before forward locomotion appears (1).

(*v*) Towards the end of early development (from day 11 on), warm-up shortens progressively. Movements of the same amplitude and dimension are eliminated, and elements of the sequence may be skipped entirely. The prescribed order is always followed, but only a few movements need be performed before forward locomotion appears. Similar shortening of warm-up is

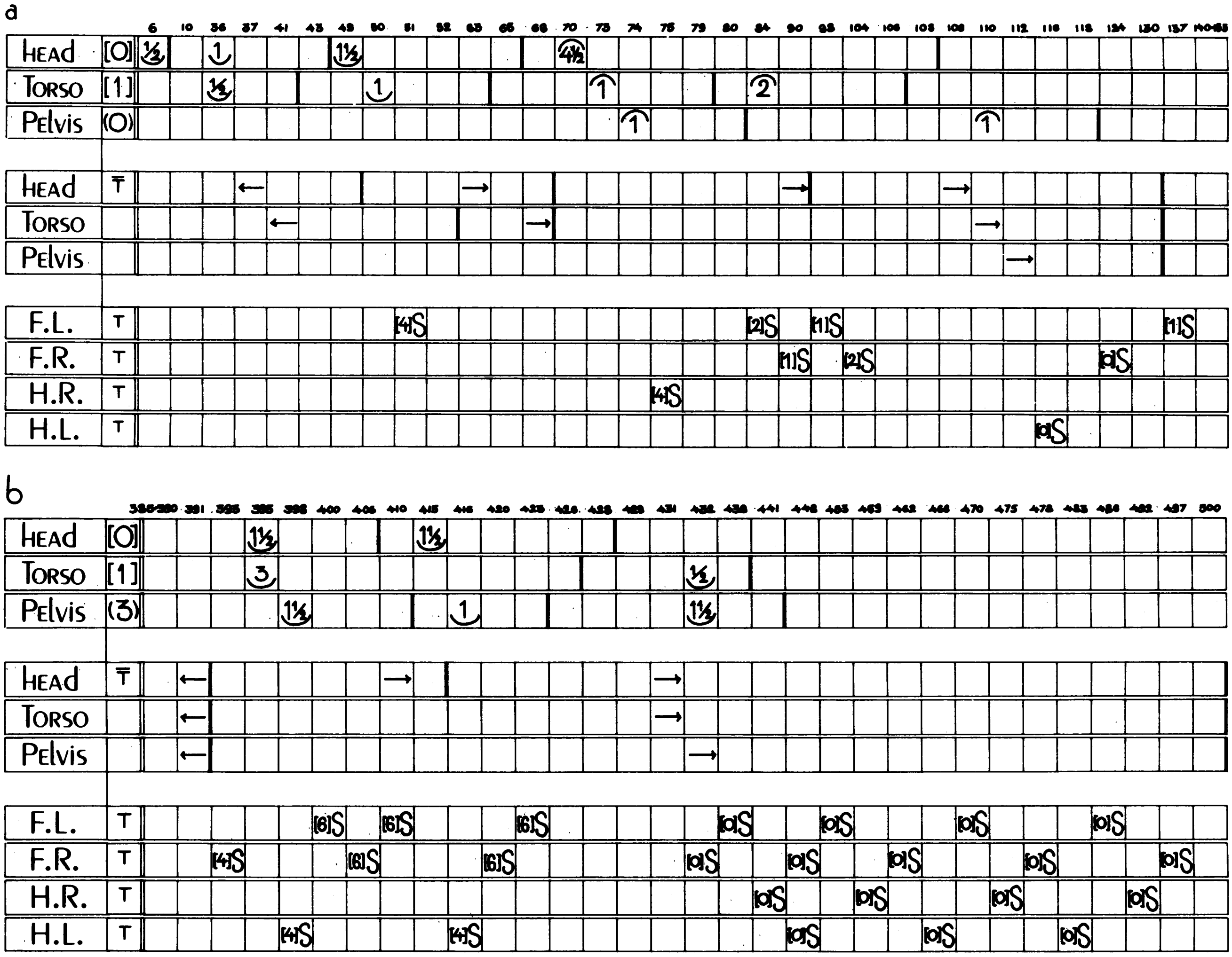

FIG. 2. Eshkol–Wachmann movement notation motor scores representing initial exploratory behavior upon being placed outside the nest (*a*) and later stages of the same behavioral sequence (*b*). Notation was made from film taken at a speed of 24 feet per second. Numerals on top indicate frame number on film. The three top horizontal lines describe angular displacements of respective body segments. Displacements were calculated irrespective of whether they involved actual movement of a segment in addition to that of the caudally adjacent segment or merely being carried along due to movement of more caudal segments. ⌒ and ⌣ stand for clockwise and counterclockwise displacements, respectively, and indicate initiation of displacement; heavy bars indicate termination of displacements; the number within each sign indicates amount of displacement, where 1 = 45°. The three middle lines describe backward, ←, and forward, →, transportations; the four bottom lines stand for right and left forelegs (F.R., F.L.) and right and left hind legs (H.R., H.L.). S stands for step, and numerals in brackets indicate the direction of the step in relation to the longitudinal axis of the body, where [0] stands for forward, [1] for 45° clockwise to right, [2] for sideways to right, [4] for backward, [6] for sideways to left, etc. The first column on the left describes the initial arrested position of the rat: T stands for contact with ground, T̄ stands for light contact, and the numerals describe the orientation of the body segments in the same polar coordinate system as described above. In *a* the infant starts with lateral angular displacements and continues with increasing amplitudes involving first head, then also torso, then also pelvis. Backward and then forward transportation of segments also involves cephalocaudal recruitment of segments. Foreleg stepping precedes hind leg stepping in ensuing pivoting with ultimate forward stretch. Transient arrest follows and then—(not represented in the score)—the infant continues to both pivot and stretch, up to excerpt *b*. In *b* large amounts of pivoting, involving extensive stepping, turn for the first time in this sequence into actual forward locomotion. Only much later in the sequence (again not represented), in frame 714, the first vertical head movement away from the surface appears.

seen late in lateral hypothalamic recovery.

There are, of course, enormous differences in motor capacity between recovering adults and developing neonates. Lateral hypothalamic animals have fully developed limbs, which are kept under the body, maintaining firm ground contact and stable equilibrium throughout recovery (1, 16). In contrast, infants undergo dramatic anatomical and functional development, which proceeds both proximodistally and cephalocaudally (17). Nevertheless, in development and recovery, activity is still distributed along the same dimensions and in much the same order. The animals may crawl, stagger, or walk, but always along the same dimensions. This suggest that the warm-up phenomenon reveals a basic principle of organization of both behavior and the neural activity mediating it. There should be a buildup and spread of activity, involving the aspects of repetition, dimensionality, and cephalocaudal organization not only at the behavioral level but also at the neural one.

Although warm-up is most evident outside the nest, it is also present in the home cage in the first few postnatal days when an infant finds itself isolated from mother, littermates, and nest. Therefore, this sugggests that it is not an artifact imposed by the particular observational procedures used in the present study.

To test the generality of warm-up, the ontogeny of locomotion in an open field was also studied in house rats, wild cats, and common badgers. Warm-up is markedly evident in all of them. Fig. 2 represents excerpts from the first 20 seconds of exploratory behavior of a house rat, 13 days old, upon being placed outside the nest. In this representation, the infant starts to move by performing purely lateral movements, then shifts to backward movements, and only then incorporates forward movements that ultimately turn into an actual forward walk. Movement amplitudes along each of these dimensions increase, involving progressive cephalocaudal recruitment of limb and body segments (Fig. 2). Of the four species examined, each highlights a different aspect of warm-up. The badger is nidicolous, seldom coming above ground before 8 weeks of age (18). Whereas in the laboratory rat forward locomotion disappears for only 2–3 days, in the badger, after culminating the warm-up in the first few days postnatally, longitudinal movement disappears for as long as 7 weeks and only then reemerges gradually. In further contrast, the house rat does not show the freedom of movement characteristic of both the common badger and the laboratory rat during the first 2–3 days postnatally. Instead, it shows very little movement, only along the lateral dimension, in these first few days. Then, movements emerge in much the same order and along the same dimensions. It is as though the house rat is born at a later stage of development—that of transient akinesia.

Because warm-up is seen in early life in a variety of mammals, we suggest that the organization it reveals is primitive and fundamental.

We thank W. Ferguson for the drawing and the zookeepers of the Canadian Center for Ecological Zoology at Tel Aviv University for their assistance. The research was supported by a grant to I.G. from the US.–Israel Binational Science Foundation, Jerusalem, Israel, and by National Institutes of Health Grant NS11671 to P.T. P.T. was a Fulbright Fellow at Tel Aviv University, on leave from the University of Illinois.

1. Golani, I., Wolgin, D. L. & Teitelbaum, P. (1979) *Brain Res.* **164**, 236–267.
2. Eshkol, N. & Wachmann, A. (1958) *Movement Notation* (Weidenfeld & Nicolson, London).
3. Teitelbaum, P. (1971) in *Progress in Physiological Psychology*, eds. Stellar, E. & Sprague, J. M. (Academic, New York), Vol. 4, 319–350.
4. Teitelbaum, P., Cheng, M. F. & Rozin, P. (1969) *J. Comp. Physiol. Psychol.* **67**, 430–441.
5. Cheng, M. F., Rozin, P. & Teitelbaum, P. (1971) *J. Comp. Physiol. Psychol.* **76**, 206–218.
6. Teitelbaum, P., Wolgin, D. L., De Ryck, M. & Marin, O. S. M. (1976) *Proc. Natl. Acad. Sci. USA* **73**, 3311–3314.
7. Twitchell, T. E. (1965) *Neuropsychologia* **3**, 247–259.
8. Teitelbaum, P. & Epstein, A. N. (1962) *Psychol. Rev.* **69**, 74–90.
9. Ungerstedt, U. (1971) *Acta Physiol. Scand. Suppl.* **367**, 95–122.
10. Hornykiewicz, O. (1973) *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **32**, 183–190.
11. Levitt, D. R. & Teitelbaum, P. (1975) *Proc. Natl. Acad. Sci. USA* **72**, 2819–2823.
12. Jung, R. & Hassler, R. (1960) in *Handbook of Physiology, Section 1: Neurophysiology*, eds. Field, J., Magoun, H. W. & Hall, V. E. (Am. Physiol. Soc., Washington, DC), Vol. 2, pp. 863–927.
13. Golani, I., in *Issues in Behavioral Development: The Bielefeld Interdisciplinary Conference*, eds. Immelman, K., Barlow, G. W., Petrinovich, L. & Main, M. (Cambridge University Press, London), in press.
14. Golani, I. (1976) in *Perspectives in Ethology*, eds. Bateson, P. P. G. & Klopfer, P. H. (Plenum, New York), Vol. 2, pp. 69–134.
15. Ganor, I. & Golani, I. (1980) *Brain Res.* **195**, 57–67.
16. Schallert, T., Whishaw, I. Q., De Ryck, M. & Teitelbaum, P. (1978) *Physiol. Behav.* **21**, 817–820.
17. Hughes, A. (1968) in *Growth of the Nervous System*, eds. Wolstenholme, G. E. W. & O'Connor, M. (Churchill, London).
18. Neal, E. G. (1977) *Badgers* (Blandford, Poole, England).