

POSTNATAL DEVELOPMENT OF SYNCHRONOUS STEPPING IN THE GERBIL (*GERBILLUS DASYURUS*)

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Summary

During the first two postnatal weeks, Wagner's gerbil (*Gerbillus dasyurus*) pups employed stepping sequences considered to be more basic than in the later stages of development and displayed alternate stepping of the legs in each girdle. In the third postnatal week, the adult mode of locomotion, the bound, became prominent and synchronous stepping dominated locomotion, gradually replacing alternate stepping. Motor performance of the gerbil pups corroborates previous studies in following a developmental motor *gestalt* termed 'warm-up', which involves an ordered incorporation of movements along three distinct spatial dimensions. In the present results, the

validity of warm-up has been extended to a quantitative perspective: the order in which movement types reached their peak performance was identical to the order of their emergence in ontogeny. Transient modes of locomotion were also employed by gerbil pups during postnatal development, in accordance with changes in body morphology, indicating that there exists a causal link between body design and specific modes of locomotion.

Key words: locomotion, walking, running, bound, stride, warm-up, rodent, gerbil, *Gerbillus dasyurus*.

Introduction

The relatively low degree of complexity of behaviour in newborn animals makes them a very attractive model for experimental analysis (Campbell and Marbey, 1972; Groothuis, 1993; Eilam, 1994b). Altricial rodents are typically born furless, have closed eyes and ears, are relatively immobile and are poorly supported by their limbs. Within 2–3 weeks, fur covers the body, the eyes and ears open and well-developed legs support the body. At this time, the pups exhibit marked hyperactivity to a degree that is rarely matched later in life (Spear and Barke, 1983). In the present study, we used this period of extensive changes to determine how gerbils develop their specialized mode of locomotion, in what order the movement types emerge and how the synchronous stepping typical of gerbils evolves in ontogeny.

The morphology of an animal limits the range of movements that it may execute, thus providing a constraint to certain locomotor activities (Taylor, 1989). Since the morphological, physiological and behavioural demands imposed by walking and running increase markedly as speed, endurance and body size increase (Garland, 1983; Hildebrand, 1980, 1989), it is assumed that each animal will utilize its specific morphology to optimize locomotion (Alexander, 1989, 1992; Dagg, 1973; Eilam, 1994a). Rodents are an excellent group for assessing functional morphology, as they display a variety of body morphologies (Mendelssohn and Yom-Tov, 1987) and modes

of locomotion (Djawdan and Garland, 1988). Since body mass and body morphology undergo extensive changes during the postnatal development of rodents, it is intriguing to determine whether motor performance is also transformed in the course of ontogeny. Consequently, the present work was aimed at studying the postnatal development of quadrupedal activity in Wagner's gerbil (*Gerbillus dasyurus*).

Gerbils, like other small cursorial mammals, run using a specialized mode of saltatory locomotion termed the 'bound' (Dagg, 1973; Gambaryan, 1974). In bounding, gerbils leap with their relatively long hindlegs and land on their relatively short forelegs, with each pair of legs acting synchronously. Bounders typically store elastic energy in their trunk, by arching it dorsoventrally when landing on the forelegs and unarching it when thrusting with the hindlegs in order to leap (Biewener, 1989). In accordance with this mode of locomotion, bounders share a typical body morphology: their hindlegs are longer than their forelegs and their trunk is arched in order to position the centre of body mass above the hindlegs, thus reducing yaw, pitch or roll torque (Dagg, 1973; Gabriel, 1984). While previous studies of postnatal behaviour in gerbils concentrated on the emergence of reflexes (Fox, 1964; Kaplan and Hyland, 1972) or on general biological perspectives (Valentine and Baudoin, 1980; Cabana *et al.* 1990), the present work focuses on describing the development of the bound and

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the accompanying morphological changes during the course of the postnatal period of gerbil pups.

During the postnatal development of mammals, new movement types emerge according to a motor *gestalt* termed warm-up (Golani *et al.* 1981; Eilam and Golani, 1988) or the mobility gradient (Golani, 1992). The segments of the trunk (i.e. head, upper torso and lower torso) are incorporated in a cephalocaudal order of movement along the lateral, then the forward and finally the vertical dimension. While this general plan of the development of movement in mammals has been analyzed so far only in terms of sequential (qualitative temporal) order, the present work tested the warm-up model from a quantitative temporal perspective. Specifically, in the first description of warm-up (Golani *et al.* 1979), it was proposed that the different types of movements would reach their peak performance in the same order in which they emerged. Such a proposal implied that lateral movements would be the first to peak in performance, followed by forward movements and finally vertical movements. Quantification of these movements in the postnatal development of gerbils was employed in the present study to investigate the assumption that the order of emergence and the order of peak performance are identical.

A study of the development of the motor behaviour of the hindlimbs of the toad (*Xenopus laevis*) revealed that alternate hindleg kicks were gradually replaced by synchronous limb action. In other words, synchronous hindlimb action gradually developed from alternate limb action (Hughes and Prestige, 1967; Hughes, 1968). An opposite pattern of development of synchronous limb action was described in turtles (*Dermochelys coriacea*), which swam with synchronous limb strokes immediately after hatching (Davenport, 1987), suggesting that synchronous limb action developed directly. A study of the development of stepping in gerbils may therefore demonstrate whether synchronous stepping emerged directly or evolved gradually to replace the more basic alternate stepping.

Materials and methods

Animals

Wagner's gerbil (*Gerbillus dasyurus*) is a small (24±4 g) rodent which inhabits rocky arid habitats (Harrison, 1972). Ten pairs (male and female) of gerbils were housed in separate cages (80 cm×50 cm×50 cm), under natural (uncontrolled) light and temperature. Subjects for this study were 10 litters, comprising 31 pups (males and females).

Apparatus

The 'open field' observation area (Walsh and Cummings, 1976) consisted of a 100 cm×100 cm transparent glass table surrounded with 30 cm high wooden walls. A mirror was placed 5 cm below the glass, tilted at 4°, to provide an image of the pup from below simultaneously with the top view. We found this setting to be optimal for evaluation of the horizontal and vertical orientation of the trunk and of the stepping of

limbs (in terms of losing and establishing contact with the ground). Five litters were also tested on sand (in addition to the glass table). Testing on sand took place in a cylindrical (diameter 1 m, and height 25 cm) tank, containing a 5 cm layer of sand.

Filming procedure

Filming was conducted between 10:00 and 14:00 h. Filming of each litter was started during the first 24 h after delivery (day 0), and then on every alternate day, until postnatal day 20. All pups were brought to the filming room in a small box filled with straw taken from their nest. Each pup was isolated from its littermates, placed gently in the centre of the open field, and its behaviour was continuously recorded for 5 min.

Behavioural analysis

Synchronized binary and digital time codes were recorded on the videotapes together with the picture (Telcom Research T800 and T5020 time code generators). The digital time code allowed accurate identification of each frame on screen, whereas the binary code was read by a computer through an interface card (Telcom Research PC 600) and custom-built program that allowed the computer keyboard to function as a real-time event marker at any playback speed. A specific computer key was assigned for each behavioural category. Once a key had been pressed, the respective frame number (time) was automatically recorded in the computer with the character of the assigned key. These data were then sorted and analyzed in order to calculate the incidence and duration of each behavioural category, as well as the order of stepping.

Movements of gerbil pups were assessed by activities which encompass the whole trunk, while movements of parts of the trunk (see Eilam and Golani, 1988) were ignored (i.e. lateral head movements were not scored, but lateral movements of the whole trunk were scored as pivoting). The following behavioural categories were analyzed.

Pivoting

Pivoting was defined as a change in the horizontal posture of the trunk by at least 45°. A change in horizontal position during walking was not considered as pivoting, but as walking along a circular path. Turns of less than 45° were not included. Pivoting was quantified by calculating the accumulated amplitude of pivoting during each developmental day for each pup. Amplitude was presented in units, where 1 unit equals 45°. Pivoting is a result of lateral movements of the parts of the trunk (Eilam and Golani, 1988) and a typical stepping sequence (Eilam, 1982; see Altman and Sudarshan, 1975, and Eilam *et al.* 1992, for further descriptions of pivoting and displacement).

Distance

The distance traversed by each pup during the 5 min observation period was used as a measure of the amount of forward progression. Distance was measured in units of body length.

Rearing

Loss of contact with the substratum by both forelegs when the head and the trunk were perpendicular to the substratum was scored as rearing. The number of incidents of rearing for each pup in each observation was recorded; rearing consisted both of supported rearing, when the pup leaned vertically on the walls of the observation area, and air-rearing, when rearing took place away from the walls.

Jumping

This category was recorded when, after rearing, the pup pushed with both hindlegs and jumped up into the air. Jumps typically occurred along the walls.

Grooming

An episode of grooming was scored as any movement of either forelimb in conventional face grooming (Golani and Fentress, 1985). Grooming was measured as the number of grooming episodes and by the cumulative duration of grooming in each daily behavioural observation.

Tumbling

Tumbling was recorded whenever the pup lost its balance and tumbled on its back with its four feet in air; it was measured as the number of episodes.

Digging

Digging is a typical action of the forelegs and hindlegs (Kaplan and Hyland, 1972), which the pups performed in the corners of the observation area, and was measured by the number of incidents and the cumulative duration of episodes.

Footfall patterns

On postnatal days 0–4, when episodes of forward locomotion were relatively few, the entire forward locomotion displayed by the pups was analyzed. On postnatal days 6–20, only four bouts of forward locomotion were selected in the following procedure for the analysis of footfall sequences. During initial viewing of the video tapes, periods of continuous forward progression were identified. For each pup, the four longest (in terms of distance) bouts of forward locomotion were selected for analysis. Frame-by-frame analysis was performed on each selected bout, with only one foot being analyzed during each viewing of the sequence. This procedure ensured that the observer concentrated only on the foot being scored and was not aware of the actual sequence of steps. The footfall sequence was obtained by sequencing the data chronologically. Inspection of these stepping sequences revealed that a period (bout) of locomotion consisted of strides of different footfall patterns (a stride is a sequence of four steps; one step per foot). Analysis was therefore performed at the level of the stride.

In the present study, the classification of strides was based on the order in which the feet lost contact with the ground. The swing phase (the period for which a leg is off the ground)

ranged from two to four frames (1 frame = 40 ms), with a maximum of 1–2 frames' phase lag between the establishment of contact by the stepping foot and the loss of contact by the successive stepping foot during walking and running. Simultaneous loss of contact by the feet with the ground in the same frame, with establishment of contact in the same frame or after one frame's delay, was considered as simultaneous stepping. Consequently, the selection of bouts of continuous walking and running resulted in the following phase relationships in the footfall sequences.

Lateral walk (HL, FL, HR, FR)

In this sequence, legs stepped in succession, with not more than 50% of overlap of the swing phase of two successive steps.

Trot (HL+FR, HR+FL)

Simultaneous stepping of diagonal feet, which implies simultaneous loss of contact and 75–100% overlap of the swing phase of diagonal feet.

Bound (HL+HR, FL+FR)

Simultaneous stepping of both hindlegs, followed by simultaneous stepping of both forelegs. This implies simultaneous loss of contact and 75–100% overlap of the steps executed by each girdle.

Half-bound (HL+HR, FL, FR or HL+HR, FR, FL)

Simultaneous stepping of both hindlegs, followed by successive stepping of the forelegs. This implies simultaneous loss of contact, 75–100% overlap of hindleg steps and up to 50% overlap of foreleg steps.

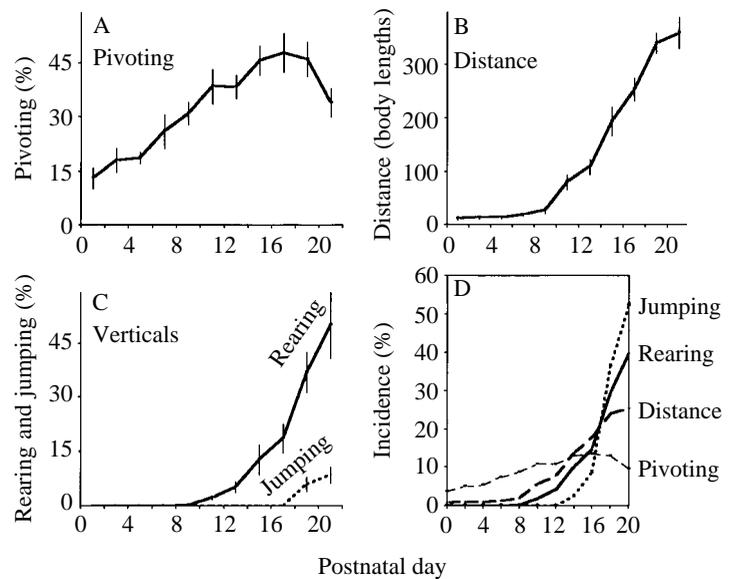
The numbers of each of these types of strides were counted for each pup throughout the bouts selected in each daily observation. Only sequences which adhered firmly to the above definitions were counted. For instance, a delay of one frame in the loss of ground contact by one of the pairs of diagonal legs was enough to exclude such a sequence from the trot. Nevertheless, the selection of bouts of continuous locomotion and the low speed of videotaping (25 frames s^{-1}) resulted in less than 10% of footfall sequences being categorized as other than lateral walk, trot or bound. The other sequences mainly include the half-bound or occasions when one diagonal pair of legs was synchronized, and typically preceded the performance of common sequences (diagonal walk, trot or bound), indicating that these could be transitional sequences.

The effect of foot posture on the stepping sequence was not considered since, starting on postnatal days 4–5, the pups maintained their trunk elevated from the surface during walking and running. Thus, in the present study, classification of diagonal walk, trot and bound was solely based on the footfall sequence and the phase relationships described above and did not consider other features of these gaits.

Morphological measurements

After each daily observation, the following measurements

Fig. 1. The mean \pm s.e.m. ($N=10$ litters) incidence of pivoting (A), the distance moved (B) and the incidence of rearing and jumping (C) over the course of 21 postnatal days. Pivoting is described in units of 45° and undergoes a significant increase ($P<0.001$) in the course of ontogeny. Distance is described in units of body length and undergoes a significant increase ($P<0.001$) in the course of ontogeny and significant increases ($P<0.05$ before Bonferroni correction for repeated tests) between postnatal days 8 and 10, 12 and 14, 14 and 16, and 16 and 18. Rearing and jumping are described by the mean number of incidents and both undergo a significant increase ($P<0.001$) across ontogeny. The order of emergence and the order of achieving relative peak performance are depicted in D. Each behaviour is expressed as a percentage of the total number of incidents of that behaviour. The order of peaks (y-axis), which is indicated on the right-hand side, is identical to the order of emergence in the course of ontogeny (x-axis).



were taken for each pup: body mass (in g); body length, tail length, length of forelegs and hindlegs, and width of the trunk at the chest (all in mm). In addition, days of pigmentation appearance, fur cover and opening of eyes were recorded for each pup.

Statistics

Statistical and graphical analyses were conducted at the level of the means of the litters, not on the measurements from individual pups. This procedure was necessary since pups were not marked individually (in gerbils, marking could have interfered with maternal care, causing neglect or cannibalism by the parents). However, applying statistics at the level of litter means could have reduced variation, as compared with applying statistics to data for individual pups, and this would have resulted in unjustified significant differences. In order to allay fears from such a possibility, a one-way analysis of variance (ANOVA) was conducted between the variation among individual pups and the variation among litters, revealing that, for most measurements, the variation within each litter was significantly larger than the variability among litters. In the few measurements for which variation among littermates was not significantly greater than that among litters, no statistical differences were evident between variations. Therefore, work with litter means did not appear to bias the data and seemed to be a legitimate procedure for statistical analysis.

ANOVA with repeated measures was employed in a search for a significant ($P<0.05$) changes in each behavioural category over the course of postnatal development. Paired t -tests were then conducted between successive observations to test for significant changes ($P<0.05$ before Bonferroni correction for multiple tests).

Results

Movement along the lateral, forward and vertical dimensions

Quadrupedal locomotor activity comprised pivoting and forward progression. Fig. 1 shows an increase in the mean accumulated amplitude of pivoting (Fig. 1A) and an increase in the mean distance traversed by the pups (Fig. 1B) in the course of postnatal development. Both pivoting and forward progression were displayed by neonates (day 0), yet pivoting increased in the following days, whereas a marked increase in distance traversed occurred only on postnatal day 12. In the vertical domain, rearing and jumping were first displayed on postnatal days 10 and 16, respectively, and their performance then increased abruptly (Fig. 1C).

In order to compare the relative rates of performance of the above movements, it was necessary to eliminate units of measurement that were different for each type of movement. For this purpose, the number of occurrences of each type of movement for each developmental day was calculated as a percentage of the total number of occurrences of that behaviour accumulated during the course of postnatal development. For instance, the amount of pivoting on postnatal day 8 was 10% of the total amount of pivoting displayed by the pups over the course of the 11 observations. The results are depicted in Fig. 1D, revealing that the order of emergence of the different types of movement (intersection with x-axis) is the same as the order of the relative peak performance of the types of movement (highest values on the y-axis) during the postnatal age of testing. Pivoting was the first activity to reach its peak performance, followed by forward locomotion (distance traversed), rearing and finally jumping. This order was identical to the order of the first performance of these movements in the course of postnatal development. The above results therefore indicate an overall increase in movement along the lateral, forward and vertical dimensions. This increase involved an ordered incorporation, and then an

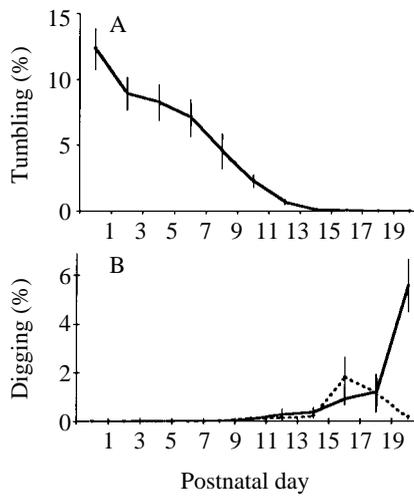


Fig. 2. The mean \pm S.E.M. ($N=10$) incidence of tumbling (A) and digging (B) with only the forelegs (dotted line) or with both forelegs and hindlegs (solid line). As shown, the incidence of tumbling and digging with both forelegs and hindlegs change significantly ($P<0.001$) in the course of postnatal development.

increase to a peak performance, of movements along the different spatial dimension.

Fig. 2A shows that the mean incidence of tumbling at delivery (maximal on day 0) gradually diminished to zero (by postnatal day 14). Digging with both forelegs and hindlegs (Fig. 2B) was first displayed on postnatal day 10, increasing abruptly on postnatal day 18.

Stepping sequences

Gerbil pups displayed three footfall patterns in the course of ontogeny: lateral sequence, trot and bound. The mean incidence of each of these patterns is depicted in Fig. 3A,B,C. Lateral walking and trot were present at delivery, whereas bound was first displayed on postnatal day 12. The incidence

of lateral walking was consistently low (note the scale), reaching its peak by day 6. Trot incidence reached its peak on postnatal day 12, and the highest incidence of bound was measured on the last observation day (day 20).

Fig. 3D describes the proportion of pups in each litter displaying each of the stepping sequences. As shown, 50–60% of the pups displayed the lateral walk and trot strides on the day of delivery, and by postnatal days 10–12, all pups displayed these sequences. Bound was first displayed on postnatal day 12, by 20% of the pups, and on day 18 was displayed by all pups.

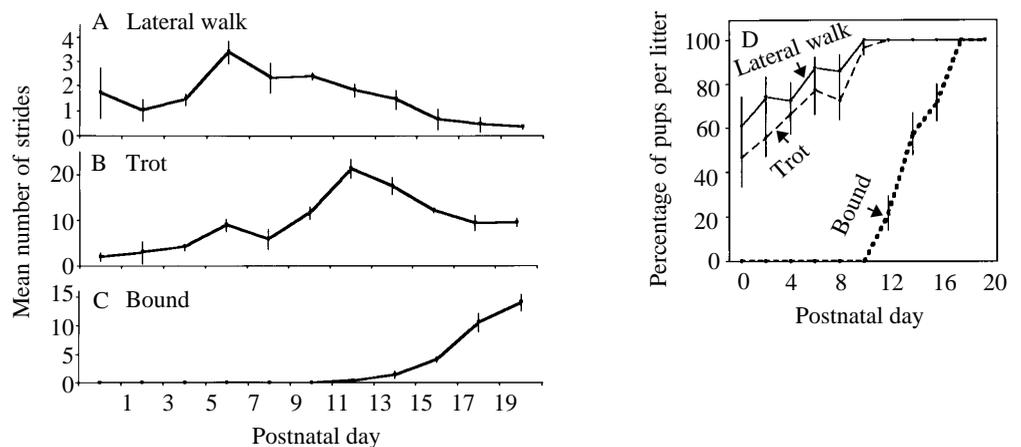
The performance of bound was preceded by a ‘half-bound’ sequence, in which hindleg stepping is synchronized while the forelegs step alternately. The incidence of this sequence was low (a peak incidence of 3.13 ± 0.68 strides per pup on postnatal day 18; data not shown). A ‘trot-like’ sequence, in which one pair of diagonal legs stepped synchronously while the other pair stepped in succession, was also displayed at low incidence (a peak incidence of 2.7 ± 0.51 strides per pup on postnatal day 4; data not shown) in the first postnatal days. These two stepping sequences were displayed by only some of the pups and diminished when the performance of trot and bound increased.

Morphometry

The body mass, trunk length, tail length, trunk width and length of the forelegs and hindlegs increased linearly in the course of the first three postnatal weeks (Fig. 4). However, the rate of increase in hindleg length was greater than that of foreleg length. Thus, while the length of forelegs and hindlegs was almost equal at delivery (1 and 1.3 cm, respectively), hindleg length on postnatal day 20 was twice that of foreleg length (2.4 and 4.8 cm, respectively).

Fig. 5 illustrates the morphological changes which the gerbils underwent in postnatal ontogeny. From having a horizontal trunk, forelegs and hindlegs of equal length and a

Fig. 3. (A) The mean \pm S.E.M. ($N=10$ litters) incidence of lateral walk (A), trot (B) and bound (C), showing that both lateral walk and trot are present on postnatal day 0, whereas bound is incorporated on postnatal day 12. Similarly, the order of peak performance is lateral walk on postnatal day 6, trot on postnatal day 12 and bound on postnatal day 20. The decrease in the number of incidents of lateral walk and trot after peak performance and the increase in the number of incidents of trot and bound before peak performance are all significant ($P<0.05$). (D) The mean \pm S.E.M. ($N=10$ litters) percentage of pups in each litter which, on a given postnatal day, displayed each gait at least once. 60% of the pups in each litter displayed lateral walk on postnatal day 0, and on day 10, all pups in all litters exhibited lateral walk. Less than 50% of the pups in each litter displayed trot on postnatal day 0, yet on day 12, all pups displayed trot. Bound was displayed on postnatal day 12 by 20% of pups and on postnatal day 18 by all pups.



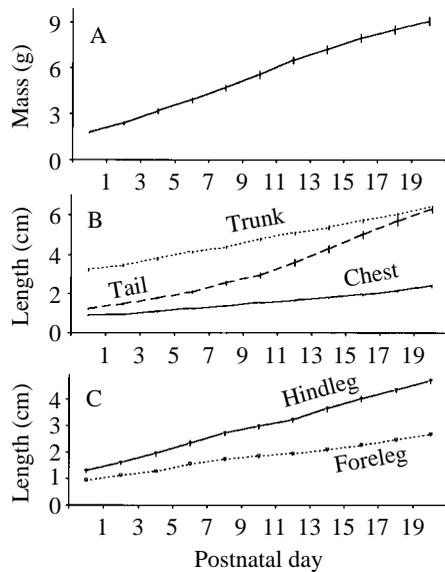


Fig. 4. A significant increase ($P < 0.001$) over the course of postnatal development and between successive observations was measured in body mass (A), in the length of the trunk (dotted line, B) and tail (dashed line, B) and in the width of the chest (solid line, B), as well as in the length of the forelegs (dotted line, C) and hindlegs (solid line, C).

sprawling leg posture, the pups developed an arched trunk, hindleg length twice that of foreleg length and the legs gathered beneath the trunk.

Pigmentation of the skin appeared in all pups on postnatal day 3, and fur cover was observed on postnatal day 8. Eye-opening typically occurred on postnatal day 16 (in 19 of 31 pups). Seven pups opened their eyes on postnatal day 15, and five pups opened their eyes on postnatal day 14.

Behaviour on sandy platform

In addition to testing on the glass platform (results described above), five litters were also tested on a sandy platform. A comparison of the behaviour of these five litters on both



Fig. 5. Body morphology and posture of 2-day-old (left), 12-day-old (centre) and 18-day-old (right) gerbil pups. The horizontal, unarched shape of the trunk, the relatively equal lengths of the forelegs and hindlegs and the sprawling leg posture are evident in postnatal day 2. On postnatal days 12 and 18, the pup has an arched trunk, hindleg length about twice that of the foreleg length, and the legs gathered underneath its trunk. On postnatal day 12, however, the hindlegs have a plantigrade posture and the eyes are closed. On postnatal day 18, the hindlegs attain a digitigrade posture and the eyes are open.

platforms revealed that the sandy platform affected behaviour, reducing motor activities such as distance moved and the incidence of rearing, and increasing activities such as grooming and digging. The differences that were statistically significant ($P < 0.05$ for interaction between platform type and age of pups in a two-way ANOVA with repeated measures) are listed in Table 1.

Discussion

Vertebrate adaptations for locomotion have been a cardinal field in the study of form and function (Hildebrand *et al.* 1985; Alexander, 1992). The locomotor benefit of a specific design is usually discussed for adult animals (Alexander, 1989, 1990; Biewener, 1989; Biewener and Taylor, 1986; Brown and Yalden, 1973; Dagg, 1973), where form, body mass and the mode of locomotion are relatively stable. During ontogeny, however, form, body mass and also the mode of locomotion change over the course of a few weeks, posing the question of whether a dynamic correspondence between body morphology and the mode of locomotion exists. In the following discussion, we will first describe parallels between changes in body morphology and the morphology of locomotion. We will then discuss the development of synchronous locomotion in gerbils,

Table 1. The effect of the type of testing platform (glass or sand) on motor activity described by the general trend and a representative mean for one postnatal day

Activity	Effect on sand compared with glass	Change in means from glass to sand		Day
		Glass	Sand	
Amplitude of pivoting in postnatal days 0–7	Increased	26.1±4.8	19.98±2.27	6
Amplitude of pivoting in postnatal days 8–21	Decreased	33.9±4.09	17.88±5.4	20
Distance travelled in postnatal days 14–21	Decreased	360.14±30.26	169.8±37.42	20
Tumbling	Decreased	12.35±1.61	5.41±1.69	0
Incidence of rearing	Decreased	20.8±5.29	3.9±2.4	20
Incidence of jumping	Decreased	8.49±2.4	1.5±1.37	20
Grooming	Earlier appearance	Day 8	Day 6	
Synchronized digging	Appeared earlier	Day 10	Day 8	

Table 2. Alternation and synchronization between girdles and within girdles in the different modes of progression displayed by gerbils during postnatal development

	Alternation		Synchronization	
	Between girdles	Within each girdle	Between girdles	Within each girdle
Lateral walk	+	+	-	-
Trot	+	+	+	-
Bound	+	-	-	+

and the application of the mobility gradient in the behaviour of vertebrates to the development of locomotion in gerbils. Finally, we will compare the postnatal development of locomotion in gerbils and rats in order to highlight how gerbils develop a more specialized mode of locomotion over the same period during which rats develop less specialized locomotion.

The correspondence between changes in body morphology and the mode of locomotion

Newborn gerbil pups feature a relatively horizontal trunk and have forelegs and hindlegs of almost the same length (Figs 4, 5). Within 2 weeks, the pups develop an arched trunk and hindlegs twice the length of the forelegs. Body mass increases from 1.78 ± 0.08 g at delivery to 9.05 ± 0.32 g on postnatal day 20 (or from 8% to 38% of adult body mass; see Lee *et al.* 1991, for a discussion of birth weight and weaning weight). These changes are accompanied by a transition from lateral walk and trot to trot and bound. The performance of lateral walk and trot and the lack of bound in early postnatal development seem to meet the morphological constraints described by Dagg (1973): the horizontal trunk and the relatively equal length of legs required for trotting are present, while the arched trunk and hindlegs longer than forelegs required for the bound are absent (see Fig. 5). The later manifestation of bound also meets Dagg's criteria, since the emergence of bound is accompanied by the acquisition of an arched trunk and the longer hindlegs required for bounding (see Fig. 5). Yet, there is the puzzling presence of trot on day 20, when pup morphology is atypical of trotters: the hindlegs are twice the length of the forelegs and the trunk is arched, but the trot still constitutes about 50% of the strides displayed by the pups. The incidence of trot is, nevertheless, higher when pups have a horizontal trunk and forelegs and hindlegs of almost the same length. Thus, in gerbil pups, the trot is not necessarily constrained by the body morphology that characterizes it in adult mammals. Unlike the trot, the bound is presumably linked to the development of the morphology typical of bounders.

Over the course of ontogeny, there is a transition from relatively slow modes of progression (lateral walk and trot) to faster modes (trot and bound). Despite the transition to faster modes of progression, the incidence of tumbling decreases, indicating an increase in stability. Poor stability in early ontogeny may thus account for the use of slower, yet more stable, modes of progression (Gray, 1968; Hildebrand, 1980).

In other words, it is possible that newborn gerbil pups are capable of locomoting more quickly, but that they employ the slower gaits of lateral walk and trot in order to reduce the apparently high incidence of tumbling; thus, they exchange speed for stability (Peters, 1983). Indeed, in the first postnatal week, the pups have a sprawling limb posture that does not allow bounding, yet provides a better support against tumbling (note the lateral position of the legs in Fig. 5). Later, limb posture is changed to give an erect posture (note that the legs are underneath the trunk in Fig. 5), and bounding is possible. However, the argument that posture and support dominate the change in the mode of progression needs to be further investigated since other factors (e.g. the development of the neural control; see, however, Cazalets *et al.* 1990; Atsuta *et al.* 1988, for evidence of the early establishment of neural control of locomotion) may affect the change in the mode of progression. Force production and the tuned action of distal muscles may also affect the performance of specific gaits. The corresponding changes in body morphology and mode of locomotion are, nevertheless, evident in the present results, regardless of the underlying mechanism.

The development of synchronous stepping

Changes in stepping in the course of postnatal development may be described in terms of alternation and synchronization of stepping within and between the anterior and posterior girdles. In the lateral walk, the legs in each girdle step alternately, and alternate stepping also occurs between girdles: in each girdle, a step of one leg is followed by a step of the other leg, and a step of a foreleg is followed by a step of a hindleg and *vice versa*. In the trot, the limbs in each girdle step alternately, yet there is synchronization between girdles, as diagonal legs (foreleg and opposite hindleg) step simultaneously. In the bound, there is synchronous action in each girdle, but alternate stepping of forelegs and hindlegs: stepping of both forelegs is followed by stepping of both hindlegs. The transitions between alternate and synchronous stepping are summarized in Table 2. According to these definitions and the order of performance during the postnatal ontogeny of gerbils, synchronous stepping is first performed between girdles and then within each girdle.

A transition from alternate to synchronous limb action was described in the swimming of the toad *Xenopus laevis* (Hughes and Prestige, 1967; Hughes, 1968; Stehouwer, 1992). During metamorphosis, the tadpoles switch from undulatory swimming to propulsion with alternate strokes of the hindlegs. The alternate strokes of the hindlegs are then gradually replaced by the synchronous action of both hindlegs. The performance of alternate strokes diminishes in parallel with an increase in the performance of synchronous strokes and, ultimately, swimming is based solely on the repetitive synchronized hindleg kicking typical of adult toads and frogs. The transition from alternate to synchronous limb action in gerbils and toads seems to be similar. Such similarity in a kinematic process between phylogenetically remote species such as the toad and the gerbil suggests that a transition from

alternate to synchronous limb action may be a general feature of locomotion in vertebrates (Eilam, 1994b). In contrast to the transition from alternate to synchronous stepping seen in gerbils and toads, Davenport (1987) showed that turtles (*Dermochelys coriacea*) display swimming with synchronous limb strokes immediately after hatching. However, this will invalidate the proposed uniformity of the transition from alternate to synchronous stepping only if it can be demonstrated that there is no prehatching stage of alternate limb strokes in turtles.

In gerbils, performance of the bound is preceded by a brief performance of the half-bound, in which the hindlegs step synchronously, but the forelegs step in succession. Dagg (1973) argued that the half-bound differs biomechanically from the bound by the extended duration of landing. Small mammals may bound, since their forelegs are strong enough to support their relatively small body mass on landing. Middle-sized mammals use the half-bound, since their forelegs cannot support landing of their heavier trunk and may collapse. According to this explanation, it could be that the earlier use of the half-bound in gerbils is not a transitional stage in the development of synchronization, but rather a mechanism to prevent the pup from collapsing when landing on the forelegs. A few days later in ontogeny, when the forelegs are strong enough to carry the load on landing, the bound replaces the half-bound. In summary, synchronous stepping between girdles precedes synchronous stepping within girdles, and the development of synchronous modes of locomotion (trot and bound) is preceded by a brief transitional stage when only one pair of legs is synchronized.

The biomechanical advantage of synchronous stepping of longer hindlegs in a hopping toad or a frog is that both legs contribute to take-off (Gray, 1968). However, in a bounding mammal, synchronous stepping also increases the restoration of elastic energy by the trunk (Biewener, 1989). On the basis of this difference, it could be argued that these are independent processes. Nevertheless, if we ignore the biomechanical ('functional') explanation, and consider only form, then changes are regularly ordered: development involves a transition from alternate to synchronous stepping.

'Warm-up' in movement along three spatial dimensions in the ontogeny of gerbils

The incorporation of lateral, then forward and finally vertical movements is a feature of a motor *gestalt* termed warm-up (Golani *et al.* 1979, 1981; Eilam and Golani, 1988; Golani, 1992). This *gestalt* characterizes an increase in mobility comparable with that described here in the ontogeny of gerbils. The orderly transition from one spatial dimension to the next has so far only been described in qualitative (sequential) terms (Eilam and Golani, 1988). The present results illustrate that, in the course of the first three postnatal weeks, the order in which movement types reach their peak performance (Fig. 1) is identical to the order of their emergence. Therefore, the present study adds a temporal-quantitative perspective to the previous temporal-qualitative regularities in warm-up.

Table 3. *A comparison of the postnatal development of the wild house rat (Rattus rattus) and Wagner's gerbil (Gerbillus dasyurus)*

	Gerbils	Rats
Pregnancy	22 days	21–22 days
Mean number of pups per litter	3	7
Pigmentation	Postnatal day 3	Postnatal day 3
Fur cover	Postnatal day 8	Postnatal day 7
Eyes opened	Postnatal days 14–16	Postnatal day 16
Nesting period	21 days	21 days

Some of the data are taken from Mendelssohn and Yom-Tov (1987).

A comparison of the development of locomotion in gerbils and domestic cats

The development of posture and gait in gerbils is remarkably similar to a previous description of the postnatal development of domestic kittens (Peters, 1983). In both species, the early gait in neonates is the lateral walk, the trot is incorporated next and finally the asymmetrical adult gait. Since a similar order of emergence of gaits was proposed for the history of tetrapod locomotion (Hildebrand, 1976), Peters (1983) suggested that the ontogeny of gaits may recapitulate the evolutionary need for an increase in locomotor versatility. This hypothesis is further supported by the gradual transition from the slower and less specialized to the faster and more specialized modes of progression seen in gerbil pups.

Both gerbils and cats seem to meet Dagg's criteria (1973) for the linkage between body morphology and the mode of locomotion. Cats gallop and therefore display isometric leg growth: a 2:3 ratio between foreleg and hindleg length is preserved from delivery to maturity. Gerbils bound, and therefore display allometric leg growth: a 3:4 ratio at delivery, changing to 1:2 within 2 weeks. Peters (1983) also described changes in the 'functional length' of the leg: the initial 'sprawled leg' posture of neonates is followed by a plantigrade posture. These postures, and the consequent low centre of gravity, form stable supports for younger kittens. A few weeks later, neuromuscular maturity and a digitigrade posture are achieved. A similar transition is evident in gerbils, in which the legs are first extended laterally in a sprawled posture followed by plantigrade and then digitigrade postures.

These parallels between body morphology, posture and mode of locomotion in gerbils and cats corroborate the rationale of the present work, that the search for a causal link between form and function in locomotion may be found through studying the postnatal development of mammals, during which body morphology, body mass and gait change extensively.

A comparison of the development of locomotion in gerbils and rats

The present results illustrate that a more specialized mode of locomotion in gerbils replaces less specialized modes of

locomotion. A comparison with the development of locomotion in rodents, which differ in their adult mode of locomotion, may reveal general components of the development of quadrupedal locomotion. For this purpose, we compare the development of locomotion in gerbils (present results) and rats (Altman and Sudarshan, 1975; Eilam, 1982; Eilam and Golani, 1988).

The duration of pregnancy and the postnatal nesting period (from delivery to the first exploration out of the nesting burrow) are similar in both rats and gerbils (see Table 3). However, during the same period, gerbils and rats develop different motor capabilities: gerbils bound, while rats locomote using the lateral walk and do not display the bound during the nesting period (Eilam, 1982; Eilam and Golani, 1988), but only as adults (Gambaryan, 1974) or when treated with psychostimulant drugs (Szechtman *et al.* 1994). The development of locomotion in gerbils is condensed compared with that in rats. Both rats and gerbils start with a similar mode of quadrupedal activity, pivoting. Alternate stepping in the lateral walk, which develops in rats only on postnatal days 7–10 (Altman and Sudarshan, 1975; Eilam, 1982; Eilam and Golani, 1988), is seen in newborn gerbils throughout the first postnatal week. On postnatal days 10–14, when rats display their peak performance of the alternate lateral walk (Altman and Sudarshan, 1975), gerbils start to exhibit synchronized stepping; i.e. there is a similarity in the order, but not in the pace, of development of locomotion in rats and gerbils. Moreover, both species have a roughly similar period over which they practice the adult mode of locomotion, from postnatal day 10 until the end of nesting on postnatal day 21. In addition, in both gerbils and rats, eye-opening occurs about 5 days before the first exploration out of the nesting burrow. Eye-opening is accompanied by a significant increase in the amount of locomotion in both rats (Altman and Sudarshan, 1975; Bolles and Woods, 1964) and gerbils (Fig. 1B; see, however, Foreman and Althaha, 1992, for a discussion of the linkage between eye-opening and the increase in quadrupedal activity).

On the basis of the above similarities, it is tempting to propose (1) that the pace of ontogeny of locomotion is condensed or extended to enable the pups to achieve the adult mode of locomotion at the time of their first exploration out of the nesting burrow, as a necessity for survival; (2) that altricial rodents with different modes of locomotion as adults display similar periods of practicing the adult mode of locomotion; (3) that eye-opening occurs about 5 days before the end of nesting and that, at the same time, there is an abrupt increase in the amount of locomotion. Our recent preliminary observations on dormice (*Eliomys melanurus*), voles (*Microtus socialis*) and merions (*Merions tristrami*) confirm that these proposed developmental regularities characterize species with different adult modes of locomotion (voles, dormice and gerbils), with different adult body sizes (merions and gerbils) and of different zoogeographical origins (gerbils and dormice *versus* merions and voles). However, further analyses and studies of additional species are also required.

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