

## POSTNATAL DEVELOPMENT OF BODY ARCHITECTURE AND GAIT IN SEVERAL RODENT SPECIES

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### Summary

Observations on five species of rodents, vole (*Microtus socialis*), gerbil (*Gerbillus dasyurus*), jird (*Meriones tristrami*), dormouse (*Eliomys melanurus*) and jerboa (*Jaculus orientalis*), revealed that, during the period when their neonates share a matching morphology, they also share the same forms of quadruped locomotion (gaits). The order in which the different gaits develop is similar in all species, beginning with the basic gaits of lateral walk and trot. Gaits and body morphology do not undergo further changes in voles, whereas the other species incorporate more specialized gaits later in ontogeny, when the adult body morphology has been attained. Gerbils and jirds incorporate a bounding gait, dormice incorporate galloping and jerboas incorporate bipedal running. Species with more specialized locomotion thus undergo more developmental stages than those with less specialized locomotion. Except for the jerboa, the nesting period was roughly the same for all species, but those with more

specialized locomotion exhibited earlier onset of the basic gaits as if condensing their development in order to reach the adult gait within the same nesting period. Consequently, the adult gait emerges approximately 10 days before the end of nesting, regardless of nesting duration. Since growth rate does not seem to account for the differences in morphology and onset of gaits, the heterochrony in the observed species probably stems from differences in the duration of growth, which seems to be the key factor in the diversion from the basic common morphology. The present results reconfirm the traditional generalities of functional morphology derived from cross-species comparisons. In addition, they provide another perspective by comparing form and function within the same individuals in the course of ontogeny.

Key words: walk, run, bound, gallop, stride, footfall patterns, rodents, ontogeny, development.

### Introduction

This study was designed to examine the postnatal development of form and function both across a variety of rodent species and during the postnatal development of each individual species, when morphology, anatomy and locomotor behavior undergo extensive transformations. The working hypothesis was based on my preliminary observation that the young of different rodent species are born in a similar altricial state and with similar morphology. It was hypothesized that, when newborn rodents of different species share a similar morphology, they will also share the same form of progression (gait). Each species is then expected to diverge to its typical form of progression as it develops its characteristic morphology.

Rodents are an excellent group for assessing functional morphology as they vary greatly in body morphology and forms of progression. For instance, voles (*Microtus socialis*) feature a cylindrical and relatively elongated trunk with forelegs and hindlegs of relatively short and even length, locomoting in basic quadrupedal gaits. In contrast, the jerboa (*Jaculus orientalis*) represents a very different morphology and

locomotion: its body is short and the hindlegs are four times the length of the forelegs. The jerboa is a bipedal walker (like humans), although it can also progress by bipedal leaps (somewhat similar to those of the kangaroo). Between these two extremes, there is a large variety of forms. Despite these adult differences in gaits and morphologies, the young of the above species are all born in a similar altricial state and with similar morphology, which makes it hard to distinguish between the newborn of different species. From this ancestral state, they achieve rapid postnatal development, during which each species gains its typical gait and body morphology. The present study was aimed at describing the changes which take place during postnatal development and determining whether changes in body morphology are involved in reciprocal changes in gait.

Locomotion is largely discussed in terms of the reciprocal appropriateness of a specific body design for a specific gait (Dagg, 1973; Peters, 1983; Hildebrand *et al.* 1985; Taylor, 1988; Blumberg-Feldman and Eilam, 1995). At the physiological level, optimality in structural elements in order

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to meet the requirements of functional systems has been termed 'symmorphosis' (Taylor and Weibel, 1981) and was proposed as a unifying principle for the anatomy and explanation of scaling relationships. At the anatomical and behavioral levels, it has been assumed that the morphology of an animal limits the range of the movements that it may execute, thus providing a constraint to certain locomotor activities (Dagg, 1973; Carrier, 1983; Garland, 1985; Taylor, 1988; Bertram and Biewener, 1992). The present study concentrates on behavior (e.g. stepping sequences) and anatomy (e.g. leg length), but not on physiology, and therefore does not refer to the problem of optimality.

In the ontogeny of gaits, it has been shown that the more specialized galloping gaits develop only after the more basic gaits such as lateral walk and trot (Peters, 1983; Blumberg-Feldman and Eilam, 1995). This order in the development of gaits supported the idea of uniformity in the development of locomotion in ontogeny and in phylogeny (Eilam, 1995) and the implication of such order for studies of the neural control of locomotion (Blumberg-Feldman and Eilam, 1995). From comparative behavioral testing, the present study rephrased the question of how more specialized gaits, such as the bipedal walk of the jerboa, the leaping of the dormouse and the bounding of the jird, develop during ontogeny. In a recent discussion of the ontogenetic limits on locomotor performance, Carrier (1996) proposed the need to study (1) how locomotor performance varies ontogenetically and (2) how components of the locomotor system change during growth. The present work approaches these issues from a behavioral perspective.

## Materials and methods

### Animals

Successful breeding in captivity was a prerequisite and the main criterion for choice of species. Rodent species of the Israeli fauna were kept in the research zoo of the Department of Zoology at Tel-Aviv University, and five species which bred successfully were included in the study. An additional seven species were not included since they failed either to breed or to rear their pups under the experimental procedure of daily separation of the pups from the dam. Consequently, a larger sample or selection of species according to phylogeny or convergence was impossible. The five reproductive species selected represent different morphologies and locomotor habits, or matching morphology but different body size and/or zoogeographic origin, as follows (based on Mendelsohn and Yom-Tov, 1987; D. Eilam, unpublished data). (1) Voles (*Microtus socialis*; Microtidae; voles,  $N=15$ ): burrow dwellers which feature a cylindrical trunk and forelegs and hindlegs of equal length. Adult voles tend to locomote by trotting and lateral stepping sequences; they rarely gallop. (2) Gerbils (*Gerbillus dasyurus*; Gerbillidae;  $N=15$ ): inhabitants of rocky mountains featuring a short arched trunk with hindlegs of about twice the foreleg length. Adult gerbils tend to locomote by bounding (Blumberg-Feldman and Eilam, 1995). (3) Jirds (*Meriones tristrami*; Gerbillidae;  $N=15$ ): featuring similar

morphology to the gerbil, but have a mass four times greater. (4) Dormice (*Eliomys melanurus*; Myoxidae;  $N=15$ ): featuring a wide short trunk with hindlegs less than twice the foreleg length. Adult dormice progress in an irregular sequence of leaps and are expert climbers easily able to climb up vertical smooth plywood. (5) Jerboas (*Jaculus orientalis*; Dipodidae;  $N=3$ ): bipedal rodents resembling kangaroo rats (*Dipodomys* sp.) and featuring a short wide trunk with hindlegs four times the foreleg length.

Five litters, comprising 15 pups (2–6 pups per litter), were observed for each species, except for the jerboa, for which only four litters (2–4 pups per litter) were bred and only one litter (three pups) survived throughout the entire observation period. Detailed data on this litter of the jerboa are available elsewhere (Eilam and Shefer, 1997) and, because of the unique development of the jerboa, this litter was used in the present study for comparison with the other four species in aspects not restricted to individual and litter variability.

### Apparatus

Locomotor behavior was studied on a 100 cm × 100 cm transparent glass table fenced with a 30 cm high wooden wall. A mirror was placed 5 cm below the glass, tilted at 4°, so that a camcorder placed diagonally (45° front/above) to the apparatus could capture both a bottom image and a top view of the experimental animal. This setting allowed an evaluation of the horizontal and vertical orientation of the trunk, and of the stepping of the limbs (in terms of releasing and establishing contact with the ground). Previous studies (Eilam and Golani, 1988; Blumberg-Feldman and Eilam, 1995) revealed that testing on a glass table does not affect the onset of the different types of behavior or their developmental order.

### Procedure

Filming was conducted between 10:00 and 14:00 h. Filming of each litter began during the first 24 h after birth (day 0), and continued on every alternate day until day 20, except for the jerboa, for which observations continued until day 50, after bipedal locomotion had emerged. Pups were brought to the filming room in a small box filled with their nesting materials. Each pup was isolated from its littermates, placed gently in the center of the apparatus, and its intact and undisturbed behavior was continuously recorded for 5 min on a video cassette recorder (50 fields s<sup>-1</sup>).

### Behavioral analysis

Digital time codes were recorded on the video tapes together with the picture (Telcom Research T-800 and T-5020 time code generators). These time codes allowed accurate identification of each frame on screen and were readable 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 to each behavioral 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 to calculate the incidence and duration of each behavioral category, as well as the order of stepping.

During initial viewing of the video tapes, periods of spontaneous forward progression were identified. For each pup, the four longest (in terms of distance) continuous bouts of forward locomotion were selected for analysis. Each selected bout underwent field-by-field analysis (Panasonic AG6200), 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 chronologically sequencing the data from each foot. 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 a stride.

#### *Footfall patterns*

A gait is traditionally described in terms of footfall patterns and/or phase relationships between legs (Gambaryan, 1974; Hildebrand, 1989; Collins and Stewart, 1994). In the present work, the classification of strides was based on the order in which the feet released contact with the ground. Swing phase (the duration for which a leg is off the ground) ranged from 4 to 8 fields (1 field=20 ms), with a maximum phase lag of four fields between the establishment of ground contact of the stepping foot and the release of contact of the successive stepping foot during walking and running. Simultaneous release of contact of feet with the ground in the same field, with establishment of contact in the same field or with a delay of one field, was considered as simultaneous stepping. Consequently, the selection of bouts of continuous walking and running resulted in the following phase relationships in the observed footfall sequences.

*Lateral walk* (left hindfoot, LH; left forefoot, LF; right hindfoot, RH; right forefoot, RF): in this sequence, legs stepped in succession, with not more than 50% of overlap of the swing phase of two successive steps.

*Trot* (LH+RF, RH+LF): simultaneous stepping of diagonal feet, which implies simultaneous release of ground contact and 75–100% overlap of the swing phase of diagonal feet.

*Bound* (LH+RH, LF+RF): simultaneous stepping of both hindlegs, followed by simultaneous stepping of both forelegs. This implies simultaneous release of ground contact and 85–100% overlap of the foreleg and of the hindleg steps.

*Half-bound* (LH+RH, LF, RF or LH+RH, RF, LF): simultaneous stepping of both hindlegs, followed by successive stepping of the forelegs. This implies simultaneous release of ground contact and 85–100% overlap of hindleg steps, and up to 50% overlap in the steps of the forelegs.

*Gallop* (LH, RH, LF, RF or RH, LH, RF, LF or LH, RH, RF, LF or RH, LH, LF, RF): successive stepping of both hindlegs, followed by successive stepping of the forelegs. This

implies a delay of at least one frame in lift-off or touch-down in each girdle (i.e. in both forelegs or in both hindlegs) and up to 50% overlap of the legs in each girdle. In a preliminary inspection of the data, it was evident that the main type of gallop in all species is transverse gallop, in which the order of successive stepping for both forelimbs and hindlimbs is the same (LH, RH, LF, RF or RH, LH, RF, LF). Rotary gallop strides, in which the order of successive stepping in the forelimbs is the opposite of the order in the hindlimbs (LH, RH, RF, LF or RH, LH, LF, RF), were rare and, rather than excluding these, they were added to the incidence of transverse gallop and termed together as 'gallop'.

The incidence of these types of strides was noted for each pup throughout the bouts selected in each daily observation. Only sequences that adhered firmly to the above definitions were counted. For instance, a delay of one frame in the release of contact in 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 regular speed of video-taping resulted in less than 10% of footfall sequences other than lateral walk, trot, gallop and bound. The other sequences mainly included the half-bound or one diagonal leg pair synchronized and typically preceded the emergence of common sequences (diagonal walk, trot or bound), indicating that these could be transitional sequences. Phase relationship was implicit in the above definition of strides. While locomoting freely at varying speeds, pups of the different species kept switching gaits within the same bout of locomotion. Consequently, successive strides of the same bout could comprise different footfall sequences. For this reason, the developmental process is presented only according to the incidence of footfall sequences as defined above and not in terms of phase relationships for locomotor bout or developmental day, as those comprised an amalgamation of different strides.

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

#### *Morphological measurements*

After each daily observation, the following measurements were taken for each pup: body mass (g); body length (mm, from the tip of the snout to the base of the tail), tail length (mm, from its base on the trunk to the tip of the end brush) and length of forelegs and hindlegs (mm, from the outer origin of the legs on the trunk to the tip of the toes). Body mass for jerboas was not recorded, to minimize the removal of these pups from the nest, as successful breeding in this species is rare. In addition, the days of pigmentation appearance, fur cover and opening of eyes were recorded for each pup.

Statistics

A two-way analysis of variance (ANOVA) was employed to establish whether a significant ( $P < 0.05$ ) change in the course of postnatal development occurred within/or across species.

Results

Distance traveled

The behavioral and morphological changes that pups underwent during postnatal development were reflected in their level of activity. Forward locomotion was hardly evident during the first postnatal week, except in the gerbil and to a lesser extent in the jird. Voles reached a peak distance traveled in the second postnatal week, whereas gerbils and jirds reached their highest levels by the end of the third postnatal week. Dormice displayed a moderate amount of locomotion in the third week, whereas the jerboa hardly locomoted at all during the first 4 weeks. For voles, jirds and bipedal locomotion in jerboas, the increase in distance traveled was abrupt, in contrast to the gradual increase shown by gerbils and dormice and for quadrupedal walking in jerboas (Fig. 1).

Emergence of stepping sequences across ontogeny and species

Fig. 2 depicts the number of strides displayed by each species in the course of postnatal development. All species first progressed by lateral walking and trotting strides, typically with a higher incidence of lateral strides in the early postnatal days. In voles, the incidence of both gaits increased significantly on postnatal day 10 ( $P < 0.05$ ), culminating in peak levels on day 10 for lateral walking and on day 16 for trotting. In gerbils, lateral walking and trotting were both observed on day 0, followed by the emergence of bounding on day 10, reaching a peak for

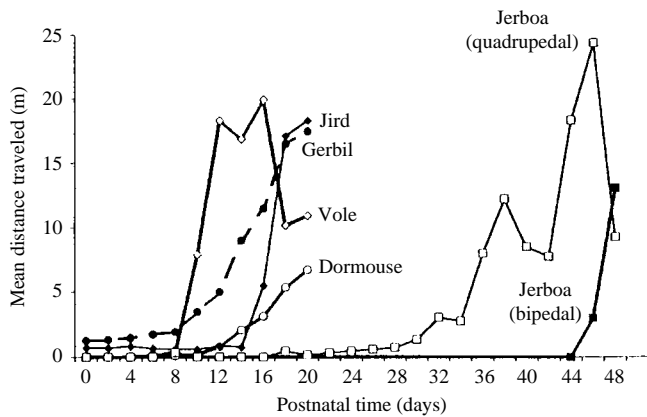


Fig. 1. Changes in the mean distance traveled (in meters) for the four quadrupedal species in the course of postnatal development (for clarity of presentation, error bars are not shown). For the bipedal species (jerboa), the mean values of distances traversed by quadruped and by bipedal locomotion are plotted separately. In each species, the increase in the distance traveled in the course of postnatal development was significant ( $P < 0.005$ ). The differences between species were also significant ( $P < 0.0001$ ) ( $N = 15$ , except for the jerboa where  $N = 3$ ).

trotting on day 12 and for bounding on day 20 ( $P < 0.05$  for the increase in the incidence of each stride). In the jird, lateral walking, trotting and galloping underwent only nonsignificant changes in the course of postnatal development. Bounding was recruited to jird locomotion on day 12, and its incidence increased by the end of the third postnatal week ( $P < 0.05$ ). In dormice, lateral walking was the main gait in the course of the second and third postnatal weeks, increasing significantly both across ontogeny and compared with other strides ( $P < 0.0001$ ). Episodes of quadrupedal stepping were observed in jerboa pups starting on day 22. These locomotor bouts were brief, and only on day 38 could they be analyzed in terms of strides. At this age, locomotion consisted entirely of lateral walking and trotting. Bipedal walking in jerboas, consisting of alternate stepping of the hindlegs, emerged as late as day 46.

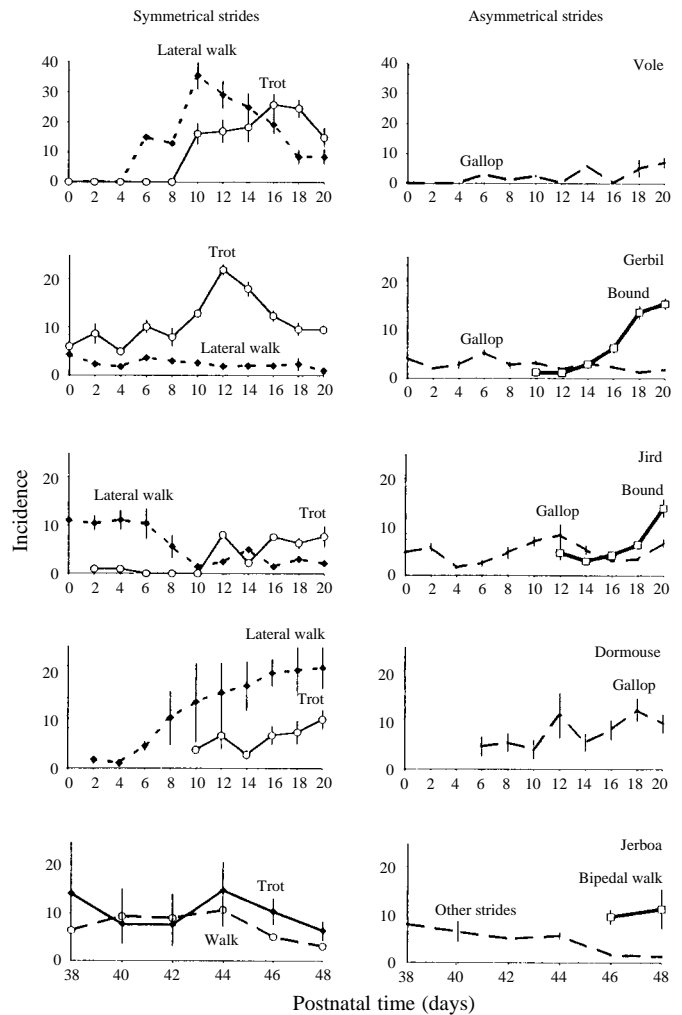


Fig. 2. The mean ( $\pm$ S.E.M.) incidence of footfall patterns in the five species tested as a function of postnatal development ( $N = 15$ , except for the jerboa where  $N = 3$ ). The left-hand graphs describe symmetrical strides and the right-hand graphs asymmetrical strides. Note the different scales for voles (top graphs) and the different developmental period for the jerboa (bottom graphs). In each graph, the incidence indicates the mean number of strides per pup per day of the gait specified. Postnatal time is indicated along the ordinate.

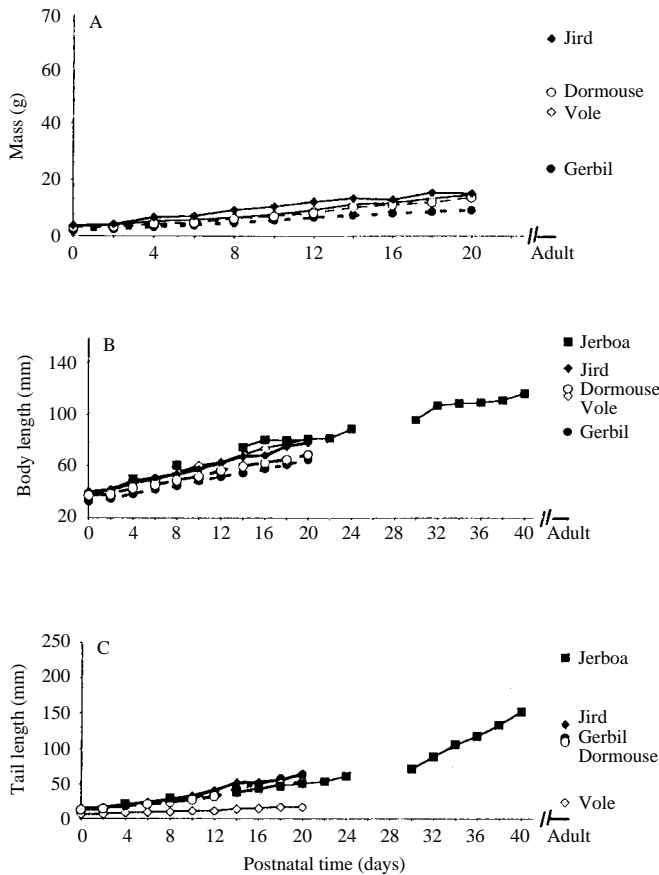


Fig. 3. Changes in the mean mass (A), body length (B) and tail length (C) during the course of postnatal development (ordinate) ( $N=15$ , except for the jerboa where  $N=3$ ). The right-hand values in each graph are the adult values (as described by Mendelsohn and Yom-Tov, 1987). For the clarity, error bars are not shown.

*Decreases in stride duration and duty factor*

Decreases in stride duration ( $P<0.001$ ) and duty factor (the proportion of a stride for which a foot is in contact with the ground) ( $P<0.01$ ) were evident, but their values were higher in dormice than in voles and jirds. Phase relationships of footfalls are not presented since each locomotor bout contained different strides. The average phase relationships for a bout thus comprised a mixture of strides and could not indicate a specific gait.

*Changes in body mass, body length and tail length*

The large differences in adult body mass, ranging from 23 g for the gerbil to 70 g for the jird, were not apparent in the early postnatal period. This was evident in the overlap of mass measurements for the four species throughout the first 3 weeks (Fig. 3A). The main change in body mass must have occurred after weaning, during the pre-adolescent period. Like body mass, differences in body length of the different species were minor in the first 3 weeks, despite the differences in the body length of adults (Fig. 3B). Differences in tail length, like differences in body mass and body length, of the different species were minor in the newborn. Tail length then diverged:

Table 1. Morphological variables for the five species

		% of adult value			
		Adult	Newborn	Weanling	Rate
Body mass (g)	Vole	44	5.6	26.7	4.8
	Dormouse	51	5.1	21.7	4.3
	Jird	70	7.4	37.7	5.1
	Gerbil	23	7.3	33.1	4.6
Body length (mm)	Vole	115	34.7	70.6	2.0
	Dormouse	120	30.8	56.9	1.9
	Jird	135	28.9	56.9	2.0
	Gerbil	87	37.6	74.3	2.0
	Jerboa	156	31.7	74.4	2.3
Tail length (mm)	Vole	24	25.5	71.3	2.8
	Dormouse	110	11.7	47.8	4.1
	Jird	135	10.9	48.1	4.4
	Gerbil	117	10.7	54.2	5.1
	Jerboa	228	9.4	66.5	7.0
Forelegs (mm)	Vole	40.2	30.8	65.6	2.1
	Dormouse	44.3	24.6	60.5	2.5
	Jird	39.8	31.2	76.0	2.4
	Gerbil	27.3	34.4	96.9	2.8
	Jerboa	38.5	48.1	93.5	1.9
Hindlegs (mm)	Vole	46.8	26.8	68.4	2.5
	Dormouse	52.3	20.6	65.3	3.2
	Jird	64	21.4	78.3	3.6
	Gerbil	59.3	21.9	78.9	3.6
	Jerboa	143.8	16.3	94.1	5.8

Morphology (body length, tail length, hindleg length, foreleg length) and body mass are presented in the vertical columns for newborns and weanlings as a percentage of these parameters in the adult (second column from left).

In the newborn pups of all species, the length of the body, tail, hindlegs and forelegs does not exceed 48% of the adult length. In contrast, the newborn mass is approximately 5% of the adult mass. The weanling values reach 48–94% of the adult values for morphology, but the mass does not exceed 38%.

The right-hand column provides the rate of growth between weanlings and newborns. The rates of growth of the length of the tail, the forelegs and the hindlegs, but not of the body mass and body length, differ substantially among the species tested.

in voles, it remained short throughout life, whereas in the jerboa it grew to 1.5 times body length (Fig. 3C).

*Growth in hindleg and foreleg length*

Fig. 4 depicts foreleg and hindleg length. In newborn individuals of all species, the length of the hindleg was very similar to that of the foreleg, but the length of the legs diverged as growth proceeded in the different species. In voles and dormice, the difference between foreleg and hindleg length was small throughout the postnatal period, whereas in 20-day-old gerbils, jirds and jerboas, hindleg length was double the foreleg length. Compared with the other species, the jerboa was an exception in that the hindleg

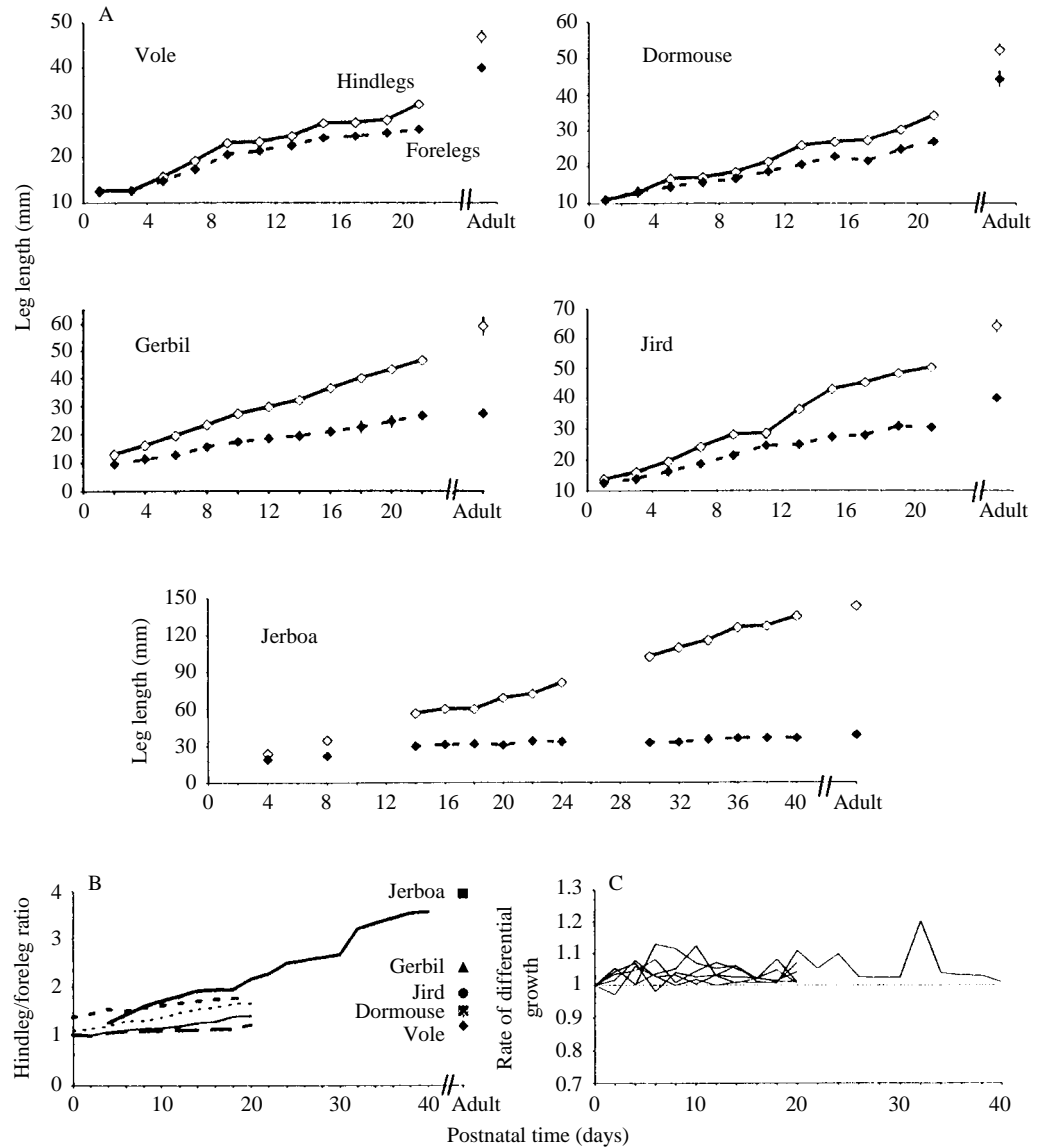


Fig. 4. Changes in the mean ( $N=15$ , except for the jerboa where  $N=3$ ) of foreleg length (broken line) and hindleg length (solid line) in the five species tested during the course of postnatal development (ordinate). The right-hand values in each graph are the adult values (as described by Mendelsohn and Yom-Tov, 1987). Two-way ANOVA for each species revealed a significant increase in the length of the hindlegs and forelegs in the course of postnatal development and a significant difference between foreleg and hindleg length in all species ( $P<0.005$ ). (B) The hindleg/foreleg length ratio in the course of ontogeny. The ratio was significantly different ( $P<0.01$ ) between species and in the course of postnatal development. (C) The differential change in this ratio (the rate of change between two successive measurements). Two-way ANOVA revealed no significant differences in this parameter.

length kept increasing until, in adults, the hindlegs are four times the foreleg length (Fig. 4B). However, there was an overlap in the differential rate of growth in all species, implying that the higher hindleg/foreleg ratio of the jerboa was due to a longer period of growth (Fig. 4C).

The differential rates of growth for body mass, body length and tail length also overlapped in all species (data not shown, but are implicit in the linearity of the changes in these parameters in Fig. 3). This implies that the divergence of body morphology is due less to a higher rate of growth than to different durations of growth.

#### Morphology and size

To compare the relative changes in body and leg length at delivery and weaning, data for each limb are presented in Table 1 as a percentage of the adult length of that limb. As shown, body length in the newborn was 29–38% of the adult length and increased to 57–74% in weanlings. Hindlegs in the

newborn were 16–27% of the adult length and grew to 65–94% in weanlings. Except for voles, which possess a short tail throughout life, tail length in the newborn was approximately 10% of the adult length, reaching 48–67% in weanlings.

In contrast to morphological characteristics, the body mass of the newborn was only 5–7% of the adult mass and increased to approximately 30% in weanlings. However, although weanlings (after pre- and postnatal periods) reach only 30% of the adult mass, they develop a greater species-specific adult morphology than newborn pups and, in fact, resemble miniature adults.

#### Weanlings: miniature adults

The divergence to the species-specific morphology in the course of postnatal development is presented in Fig. 5. Species are represented in rows, with each vertical column depicting a specific age. The morphological similarity in early postnatal

Table 2. A proposed scheme of the changes in the limb interrelation in stepping

Gait	Alternation		Synchronization		Succession	
	Between girdles	Within a girdle	Between girdles	Within a girdle	Between girdles	Within a girdle
Lateral walk	+	+	-	-	-	-
Trot	+	+	+	-	-	-
Bound	+	-	-	+	-	-
Gallop	-	-	-	-	+	+
Bipedal walk	-	-	-	-	-	+

Spinally controlled (?)
Supraspinally controlled (?)

The different gaits are arranged in the left-hand column in the order in which they emerge in ontogeny. The phase relationships of the legs are classified separately between girdles and within a girdle, according to the following definitions: *alternation*, when there is little (less than half the swing phase) or no overlap of the swing phase of two successive steps; *synchronization*, when two legs take off and touch down simultaneously (almost full overlap of the swing phase); and *succession*, when legs step in succession but swing phases overlap (more than half the swing-phase duration). A girdle is the pair of the forelegs or the pair of the hindlegs (e.g. the pelvic girdle).

+ indicates the presence and - the absence of a specific relationship.

As shown, the first gaits that emerge in ontogeny are based on alternation between and within girdles. Synchronous stepping then emerges, first between and then within girdles, and successive stepping then emerges within (and later also between) girdles. The bottom line divides these relationships according to their neural control, as proposed in the literature.

life and the acquisition of the adult morphology before postnatal day 20 are evident.

### Discussion

The relatively low degree of complexity of structure and function in early postnatal development in rodents is very attractive for experimental analyses (Spear and Barke, 1983). Newborn altricial pups are furless, have closed eyes, are mostly immobile and are poorly supported by their limbs. Within 2 weeks, fur covers the body, the eyes open and well-developed legs support the body. By the end of the third postnatal week, pups of many rodent species exhibit marked activity to a degree that is hardly matched later in life (Spear and Barke, 1983). The morphological, physiological and behavioral demands imposed by walking and running increase markedly as speed, endurance and body size increase (Hildebrand, 1989; Hildebrand *et al.* 1985). During this early postnatal period, body systems undergo dramatic changes: morphology is modified by allometric growth (Bertram and Biewener, 1992; Blumberg-Feldman and Eilam, 1995; Peters, 1983), specialized gaits are added to the basic ones (Blumberg-Feldman and Eilam, 1995; Peters, 1983), the neural control of locomotion is expanded to supraspinal centers (Viala *et al.* 1986) and muscle mass, muscle fiber physiology and metabolism all undergo change (Oron, 1990). This period of major change was employed in the present work to establish a comparison of developmental stages within and across species. The following discussion first describes postnatal development from several aspects and then examines the interconnection of form, function and time in the development of the different gaits in the different species. It should be noted, however, that despite the coherency between the present and previous results as presented in the following discussion, evidence from the ontogeny of additional species with these and other gaits is

required for the consolidation and generalization of this discussion.

#### *Uniformity in the development and control of interlimb coordination: specialized gaits develop after less-specialized gaits*

Animal movement sequences are hierarchically and multidimensionally organized (Fentress, 1992). Behavioral observations on the postnatal development of voles, dormice, gerbils, jirds and jerboas reveal that their first locomotion takes the form of lateral walking and trotting. Whereas in the vole no further changes occur, the other species undergo additional development. Jirds and gerbils incorporate bounding, the dormouse incorporates brief forward leaps (gallop) and the jerboa shifts to bipedal locomotion. In all, the development of locomotion follows similar stages: from a relatively slow lateral walk to the faster trotting sequence, and then from symmetrical (walking, trotting) to asymmetrical (bounding, galloping) sequences. A similar developmental pattern of gaits was previously described in kittens (Peters, 1983) and gerbils (Blumberg-Feldman and Eilam, 1995). In terms of interlimb coordination, alternate stepping (walk) is the first to be displayed, and synchronous stepping is observed first between diagonal legs (trot) and then between the two forelegs and between the two hindlegs (bound) (Blumberg-Feldman and Eilam, 1995).

Interlimb coordination has provided a tool to study the neural control of locomotion because of the repetitive and relatively rigid structure of the step cycle and stride structure (Grillner, 1981; Loeb, 1989) and the control of the nervous system over motor output (Peters, 1983; Nicolopoulos-Stournaras and Iles, 1984). Grillner and Wallén (1985) proposed that the transition from trot to bound could result from a change in the action of only two synapses. Viala *et al.* (1986) have shown that the development of synchronous stepping involves supraspinal mechanisms, since the transition

from alternate to synchronous stepping in rabbit pups was reversed following spinalization. Other studies have also proposed a considerable degree of supraspinal control of spinal pattern generators (Atsuta *et al.* 1988). If these assumptions are considered in the light of the behavioral descriptions provided in this and previous studies of the development of locomotion, it may be proposed that interlimb coordination undergoes a typical developmental order (Table 2). This developmental order of gaits may well reflect the developmental order of the neural controlling mechanisms.

*Is there a parallel between ontogeny and phylogeny in the development of gaits?*

Allometry and size have traditionally formed the core of the parallel between ontogeny and phylogeny (Gould, 1966). In a previous study, I proposed a parallel in the ontogeny and phylogeny of locomotion in vertebrates (Eilam, 1995). The present representation of the development of interlimb relationships (Table 2) supports the separation of symmetrical and asymmetrical gaits and the consideration of lateral walk and trot as more primitive than the more specialized bound, gallop and bipedal gaits (Dagg, 1973; Edwards, 1977; Hildebrand, 1980). These studies suggested that lateral walk and trot were the ancestral forms of quadrupedal terrestrial locomotion. Similarly, these gaits were the first gaits of newborn pups, whether locomoting immediately after birth (gerbils) or as late as postnatal day 38 (jerboas; see Fig. 2).

Thus, as far as information from ontogeny may be extrapolated to support hypotheses on phylogeny, the present results reconfirm unequivocally the concept that these two symmetrical gaits precede the development of the more specialized gaits of bound, gallop or bipedal locomotion (Peters, 1983; Hildebrand, 1989; Blumberg-Feldman and Eilam, 1995). Edwards (1977) proposed that trot (not lateral walk) was the ancestral gait in tetrapods, on the basis of studying locomotion in the most primitive recent tetrapods – the salamanders. Observations in the present study reveal that trotting is performed by pups 2–4 days after walking (voles, jerboas, dormice and jird) or emerges together with walking (gerbils); however, the incidence of walking in the newborns is higher than that of trotting. Nevertheless, the present results cannot demonstrate which of these forms of locomotion is the more reasonable candidate for the first tetrapod gait.

*Body size, morphology and gait*

Functional morphology and physiology have concentrated on the link between body size, morphology and gait (Hildebrand, 1968; Dagg, 1973; McMahon, 1975; Garland, 1985; Biewener, 1989; Losos, 1990; Garland and Janis, 1993). Large animals have a much better fuel economy than small ones, both at rest and when running (Langman *et al.* 1995; Taylor, 1994). For instance, the African elephant is able to carry 1 g of its tissue for 1 km at one-fortieth of the cost of this exercise for the mouse (Langman *et al.* 1995). Longer legs and

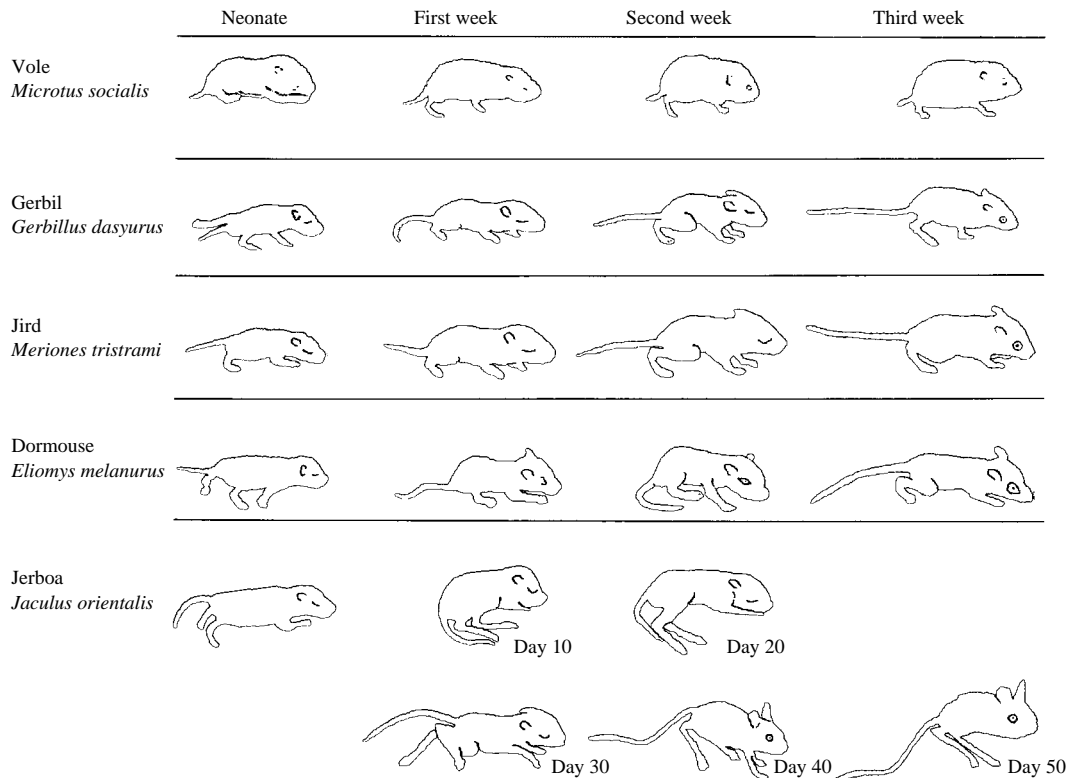


Fig. 5. Typical postures at four developmental stages: neonate, 1-week-old, 2-week-old and 3-week-old pups of the different species. Six stages are described for the jerboa to encompass its morphogenesis. Developmental stages are depicted vertically and species across the rows. The neonates show very similar morphologies which subsequently diverge. All plots were digitized from the video tapes.



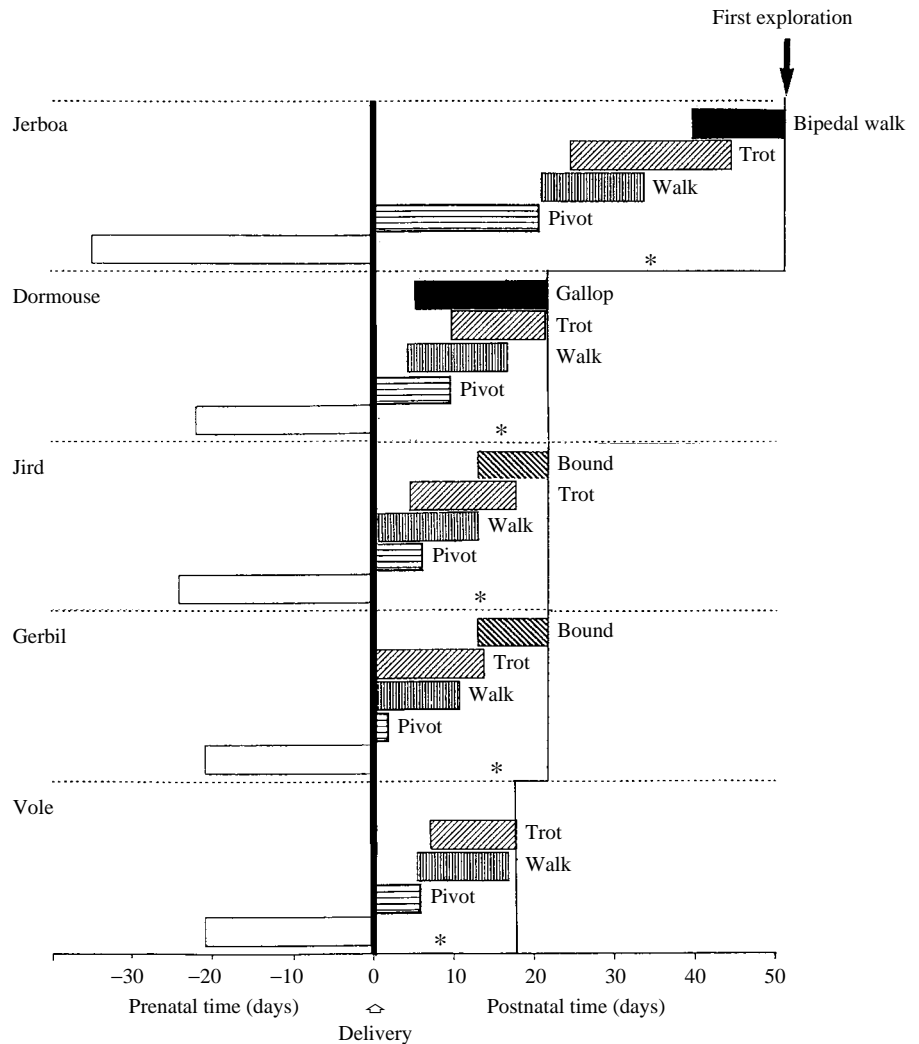


Fig. 6. A comparison of the development of the vole, gerbil, jird, dormouse and jerboa. The vertical black line represents birth, and the duration of pregnancy is depicted by white bars to the left of it (35 days in the jerboa; 21–22 days in the other species). Postnatal development is aligned to the right of the birth line. Pivoting (for a definition of pivoting, see Altman and Sudarshan, 1975) is the first quadruped activity to appear in three species, and it peaks on days 2, 7 and 20 in the gerbil, vole and jerboa, respectively. Walk and trot are present in the gerbil immediately after delivery, but appear in voles and jerboas on days 7 and 24 respectively. In the gerbil and the jerboa, the adult mode appears thereafter. Opening of the eyes is indicated by an asterisk. The figure illustrates the short period of development of the adult mode of locomotion in the vole, the condensed development (earlier onset) in the gerbil compared with the vole, and the extended pre- and postnatal periods in the jerboa (hypermorphosis) compared with the vole and gerbil.

longer steps allow slower rates of force application and the use of slower, more economical muscles (Taylor, 1994). Body architecture is designed to meet the stress imposed by the specific body size on the muscles and bones during locomotion (Gordon, 1989), and specific stepping sequences are employed by animals with a certain body size, enabling development of the force required for lift-off and preventing collapse upon touch-down (Hildebrand, 1968; Dagg, 1973; Biewener, 1989; Taylor, 1988).

Previous results (Carrier, 1983, 1996; Garland, 1985; Cabana *et al.* 1990; Carrier and Auriemma, 1992; Blumberg-Feldman and Eilam, 1995) demonstrated an allometric growth in early ontogeny in mammals. The present study reconfirms these results, but suggests that from weaning to adulthood the change in size occurs with less allometric and more geometric growth. Within a relatively short period, pups diverge from a similar developmental state to distinct morphologies and locomotor capabilities. Because they develop the adult morphology (e.g. hindleg length, foreleg length, tail length and body length), they seem to possess the same morphological constraints and adaptations of the adult in terms of locomotion, yet with a different body mass. Indeed, weanlings look like

miniature adults (Fig. 5; Table 1). The weaning mass in the tested rodents is in accordance with other taxonomic groups, where it was demonstrated that a neonate was weaned when it had grown to four times (range 3.2–4.9) its birth mass (Lee *et al.* 1991). Despite their smaller size, weanlings and juveniles already have the adult gait (present results), the same relative contractile strength in their muscles as adults and are capable of greater absolute rates of acceleration than the adults (Carrier, 1983). Indeed, Carrier (1983) has shown that young hares (20% of the adult mass) have estimated rates of acceleration that are more than twice those of adults, and roughly the same terminal velocity as adults in leaps initiated from zero velocity.

If weanling rodents possess the morphology of the adult but have a smaller body mass, then they may derive an advantage over the adult of this morphology during locomotion (Carrier, 1983, 1996), but suffer from the relatively higher cost of moving their lower mass. This implies that weanlings are less efficient in locomotion and that the cost of locomotion decreases concomitantly with increases in body mass. It is puzzling that, despite the higher cost of locomotion, weanlings locomote more than adults (Spear and Barke, 1983). Thermoregulation and the hypothesis that juvenile mammals

locomote more for 'locomotor training' (Bayers and Walker, 1995) may explain these high level of locomotion. It should be noted, however, that other studies suggest that morphological traits associated with cursoriality are effective only at large body size (Studel and Beattie, 1993) or that the energy cost of running does not depend on limb design (Taylor, 1994). According to this view, the correspondence between body morphology and gait is irrelevant to the cost of travel, which will decrease with the increase in size, mainly by restoring energy. Under the limitations of the small body mass of rodents, as well as other developmental factors which may affect locomotion in juveniles, it is proposed that the geometry in the morphology of weanlings and adults provides a better tool to assess the net effect of mass. Studying locomotion in pre-adolescence may, therefore, cast light on the role of mass in the cost of locomotion.

*Is matching morphology linked to matching forms of locomotion?*

A prominent feature of the rodent species tested is that their pups initially share very similar morphologies: they all feature an almost identical length of forelegs and hindlegs, and a horizontal and relatively elongated trunk. Accordingly, except for the jerboa, pups display walking and trotting gaits, regardless of their level of activity or the normal gait of the adult. Three weeks after birth, pups display different body morphologies and gaits (see Figs 2, 5), whether their development is fast, as in gerbils (Blumberg-Feldman and Eilam, 1995), or slow, as in dormice (Valentin and Baudoin, 1980). Therefore, when these species share similar morphologies, they also share similar forms of locomotion. While such a result could have indicated a prime role of form over function, the development of bipedal locomotion in jerboa pups demonstrates that function (locomotion) may be independent of form: newborn jerboas share the same body morphology as pups of the other species; however, they do not display the quadrupedal walk of the other pups, but rather crawl on their forelegs while the hindlegs are extended passively backwards. This pattern is preserved for 3–4 weeks, until the hindlegs reach three times the length of the foreleg. At this stage, the jerboa pups shift to fast quadrupedal walking and running (typically trotting), in which the hindlegs are folded like the hindlegs of the cricket and the trunk is kept horizontal during locomotion. In other words, the jerboa pups fulfill the morphological requirements of trotting (Dagg, 1973) by maintaining a similar functional (not anatomical) length of forelegs and hindlegs and a horizontal trunk (Peters, 1983). Bipedal walking develops as late as postnatal day 46. In the same vein, it can be argued that neonates of the different species, regardless of morphology, locomote with more stable gaits (lateral sequence and trot) because their support and control systems are immature. Form and function are obviously related since body form constrains the functioning of the organism (Taylor, 1988; Biewener, 1989; Losos, 1990; Carrier, 1996). However, animals with very different forms can have very similar functions (i.e. the two basic mechanisms for legged

locomotion are the pendulum and the spring; see Wingerson, 1983). Body form and function are both constrained, body form by the history of a lineage and function by factors such as mechanical and energetic constraints. The present results illustrate that form and function interact differently in different species and that neither form nor function should be considered as simply a result of its counterpart.

*Time is the key factor in divergence of body morphologies*

The nesting period of the quadruped altricial rodents examined in this study extended over almost similar time boundaries – 3 weeks. Within this period, some species (e.g. voles) must develop the basic gaits of walking and running (Clarke and Williams, 1994), while other species must develop more specialized locomotion (e.g. bounding in the gerbil and jird or climbing in the dormouse). There are two possible ways to diverge into the different gaits: (1) to develop each gait directly and independently of other gaits, making time an irrelevant variable; or (2) to develop the different gaits in the same sequential order so that time is a relevant variable since specialized gaits will develop only after the more basic ones. The present results illustrate that a similar developmental order characterizes the emergence of the different forms of quadrupedal locomotion. This gives rise to the question of how a more specialized gait (e.g. bounding) develops in the same period as a more basic gait (e.g. walking or trotting). A summary of the processes identified in the present study may resolve this question.

First, when locomotion comprises basic gaits and body morphology does not undergo considerable changes, the development of locomotion is short and starts relatively late. This pattern is shown by the voles, where walking emerged by the end of the first week and within a few days culminated in the gaits of the adult.

Second, when locomotion comprises more specialized gaits and body morphology undergoes considerable changes, the development of locomotion takes longer, but is condensed to the same developmental period as that of the voles by the relatively early onset of locomotion. This is represented by the gerbils and jirds, in which walking occurs immediately after birth (earlier onset; McKinney and McNamara, 1991) and the 3-week-old weanling possesses the body morphology and gait of the adult.

Third, when locomotion comprises a very specialized gait and body morphology undergoes extreme changes, the development of locomotion takes longer and may not be condensed to the same developmental period as that of the voles. In this case, the outcome is an extended development. This is represented by the jerboa, in which morphogenesis to the morphology and the gait of the adult is concluded after 6–7 weeks (hypermorphosis, or delayed offset; McKinney and McNamara, 1991).

To illustrate these developmental profiles, the timing of emergence of several markers in ontogeny is compared with the development of motor activity (Fig. 6), revealing the condensed development of the gerbil and the extended development of the jerboa compared with the vole. As evident in Fig. 6, different

gaits develop in the same sequence, with a terminal addition of more specialized gaits. However, the time scale varies greatly among the species, as does the incidence of specific gaits. For instance, pivoting (quadruped circling behavior; see Altman and Sudarshan, 1975) reached a peak in 2 days in gerbils, 7 days in voles and 20 days in jerboas. Nevertheless, despite the different time scales in the tested species, they all displayed a similar period of approximately 10 days between the emergence of the adult gait and the first exploration out of the nest (Fig. 6). Therefore, all the tested species appeared to have the same period of practicing, regardless of the specific adult gait or the duration of the postnatal nesting period.

The importance of time is corroborated by the linearity in the rate of growth which was evident in morphological parameters (Figs 3, 4, 5), revealing that the different body morphologies described in this study result from changes in the onset, offset and duration of changes and are not due to a differential rate of growth. This is not necessarily valid in other species, as shown by a non-linear elongation of the tail in the black rat (*Rattus rattus*; Ewer, 1971). However, the results for the species tested in this study reveal that even the extreme length of the hindlegs in the jerboa is not reached because of faster growth but because of a delayed offset of allometric growth (hypermorphosis; see McKinney and McNamara, 1991). Thus, starting with matching morphologies and gaits, time seems to be the key factor in the diversification of locomotion and body architecture during postnatal development of the rodent species studied.

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