

REVERSAL OF INTERLEG COUPLING IN BACKWARD LOCOMOTION IMPLIES A PRIME ROLE OF THE DIRECTION OF LOCOMOTION

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Summary

Conventional descriptions of interleg coupling relate to anatomical definitions such as fore- or hindlegs, right or left legs (i.e. the body is the frame of reference). This convention is obvious for forward walking, where forelegs (in anatomical terms) are also the leading legs (in terms of direction). In backward locomotion, however, the leading legs in terms of direction are the hindlegs in terms of anatomy. What effects do the anatomy and direction of movement have on the sequence of stepping? Our observations on the locomotion of mole rats in a transparent acrylic tunnel revealed that, as in nature, mole rats moved both forwards and backwards. They typically employed a diagonal sequence of steps in forward walking, whereas in backward walking they typically employed a lateral sequence. However, when stepping was described with movement direction as the frame of reference, both forward and backward walking were made up of the same sequence of steps. The same invariant trend was recorded during backward galloping, but to a lesser extent than during walking. We suggest that the backward sequence is simply a reversal of the forward sequence: a hindleg during backward locomotion acts like a foreleg in forward locomotion, while a foreleg acts like a hindleg in forward locomotion. Interleg coupling therefore remains invariant in relation to the direction of locomotion.

Introduction

Together with intraleg coordination, interleg coordination is an important aspect of the study of the neural control of locomotion. The mechanism controlling stepping is still unknown, and proposed models (e.g. a 'flip-flop' model for the work of the central pattern generator; Lundberg, 1980; Grillner, 1981) are still controversial (Loeb, 1989). However, there is no doubt that interleg coordination is an intrinsic and basic property of the spinal nerve cord (although the brain may take over the control of this property under some circumstances). This study investigates the role of movement direction in determining the order of stepping during forward and backward locomotion.

Key words: mole rat, neural control of locomotion, locomotor behavior, lateral sequence, diagonal sequence, stepping, footfall pattern, *Spalax leucodon*.

Sequences of steps are traditionally described by specifying the stepping leg according to its anatomical position: right and left forelegs and hindlegs. During forward progression, the forelegs are the anterior legs because the direction of locomotion and anatomy coincide. In contrast, during backward locomotion the hindlegs are at the anterior (leading) end, and anatomy and direction of locomotion are therefore contradictory. A comparison of forward and backward locomotion may therefore reveal the roles of the direction of locomotion (extrinsic factor) and of anatomy (intrinsic factor) in interleg coordination. If the intrinsic factor (anatomy) were to dominate interleg coupling, we would expect stepping sequence to be preserved, but if the extrinsic factor (direction of locomotion) were to dominate, stepping sequences should differ during forward and backward movement.

Most freely moving animals do not locomote backwards over distances greater than their body length unless they are forced to do so (e.g. by being tested on a treadmill). Mole rats (*Spalax leucodon ehrenbergi*) are an excellent natural model for studying unforced backward locomotion because they naturally locomote forwards and backwards in their tunnels.

Materials and methods

Animals

Four male and four female adult mole rats (*Spalax leucodon ehrenbergi*; mass 178 ± 35 g) were selected at random from a colony of wild animals held in captivity (under the supervision of the ethics committee of Tel-Aviv University). The mole rat is a blind rodent approximately the size of a small rat. It has an elongated and unarched trunk with relatively short legs, as is typical of fossorial animals. The mole rats were housed singly in small cages (35cm \times 25cm \times 20cm) under a 14h/10h light and dark regime. Food (carrots and standard rodent food) was provided *ad libitum*.

Apparatus

A transparent acrylic tube 83cm long and 6.3cm in inner diameter was employed. The dimensions of the tube allowed the animals to locomote freely forwards and backwards, with the trunk in contact with the tube walls, thus maintaining the tactile stimuli encountered in natural tunnels (Fig. 1). A barrier at each end of the tube prevented the animal from escaping, but allowed free air-flow and constant temperature and oxygen levels. The tube was placed above a mirror and the image of the bottom view of the

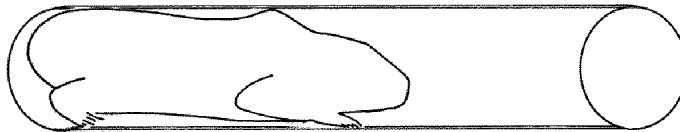


Fig. 1. A mole rat in the apparatus.

animal in the tube was filmed from the mirror. This arrangement allowed a simultaneous observation of all four legs.

Procedure

Mole rats were brought to the testing room to acclimate 30min prior to testing. Each mole rat was introduced into one end of the transparent acrylic tube in which it was able to move forwards and backwards without turning at either end. This behavior was recorded on a video cassette recorder for 10min per mole rat. Testing was conducted between 21:00 and 24:00h; each animal was tested once.

Behavioral analysis

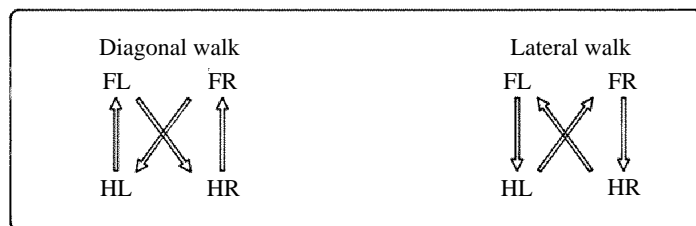
Synchronized binary and digital time codes were recorded on the videotapes together with the picture (Telcom T911 timecode processor). The digital time code allowed accurate identification of each frame on screen, whereas the binary code was read by a computer using a special interface card (Telcom PC600) and custom software 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 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 transferred to Minitab software for analysis of the sequence of steps (strides). Similarly, the computer system enabled us to record any additional information about the movement (such as the direction of progression, direction of a step and the length of a step).

Sequences of steps

In a first playback of the video tapes, periods of continuous forward and backward progression (regardless of the sequence of steps) were identified. For each mole rat we then selected the 10 longest periods each of forward and backward locomotion for analysis. Each selected period was then analysed frame by frame, with only one leg being analysed during each run through the sequence. This procedure guaranteed that the observer concentrated only on the scored leg and was not aware of the actual sequence of steps. The steps of all four legs were then sorted by time to yield the chronological sequence of stepping. Steps were arranged in sequences of four steps; one step per leg in each sequence (stride). Inspection of these four-step sequences revealed that mole rats frequently switched stepping sequences; thus, a period of locomotion consisted of strides of different stepping sequences. Analyses were performed at the level of the different stepping sequences (strides). These sequences were then divided into symmetrical sequences, in which each step of a foreleg was followed by a step of a hindleg and *vice versa*, and asymmetrical sequences, in which successive steps of both forelegs and both hindlegs were recorded. The sequences of steps in each group and the respective terminology (according to Gambaryan, 1974) are shown in Fig. 2.

Strides of mole rats moving backwards in the tube were analysed and compared with strides of forward locomotion of the same animals made during the same observation period. This procedure guaranteed an optimal control (forward progression) for the behavior under test (backward progression).

A Symmetrical sequences



B Asymmetrical sequences

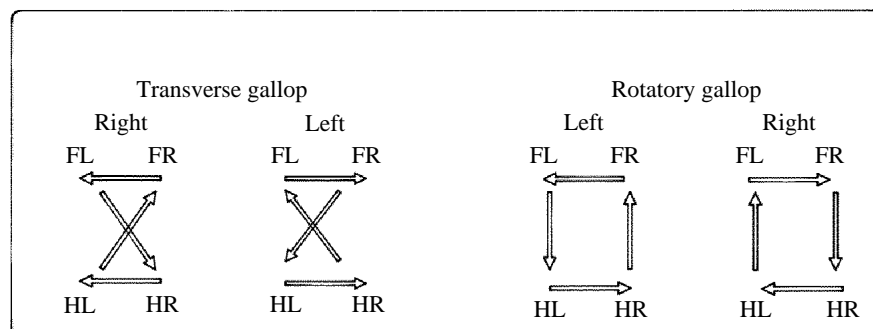


Fig. 2. Diagrams of symmetrical (A) and asymmetrical (B) sequences of steps. In symmetrical sequences each step of a foreleg is followed by a step of a hindleg and *vice versa*. When a foreleg step is followed by a step of the hindleg on the opposite side of the body, the sequence is termed diagonal (HL, FL, HR, FR). When a foreleg step is followed by a step of the hindleg on the same side of the body, the sequence is termed lateral (HL, FR, HR, FL). Diagonal and lateral sequences are performed during walking. Simultaneous stepping of diagonally opposing legs (HL+FR, HR+FL) is termed trotting (not presented in the figure). In asymmetrical sequences there are successive steps of the legs of each girdle. In transverse sequences, the successive steps of both forelegs and both hindlegs follow the same order (left to right in left transverse galloping or *vice versa* for right transverse galloping). In rotatory galloping, the stepping order of forelegs and hindlegs is opposite. Bound and half-bound are sequences with synchronized stepping of the forelegs or the hindlegs or both. Such sequences were not noted in our observations and are omitted from the discussion.

Results

Symmetrical gaits

Forward locomotion

When comparing the usage of diagonal *versus* lateral stepping sequences in the pooled data from all eight mole rats, we found that the eight tested mole rats had a total preference to use a symmetrical diagonal sequence of steps rather than a lateral sequence (Fig. 3A, top). Trotting was performed occasionally. Most of the lateral sequences (52 out of 69) were contributed by two mole rats. These two specimens (lateral mole rats) preferentially moved using a lateral sequence (Fig. 3C, top) while the other six mole rats (diagonal mole rats) generally used a diagonal sequence (Fig. 3B, top). The implications

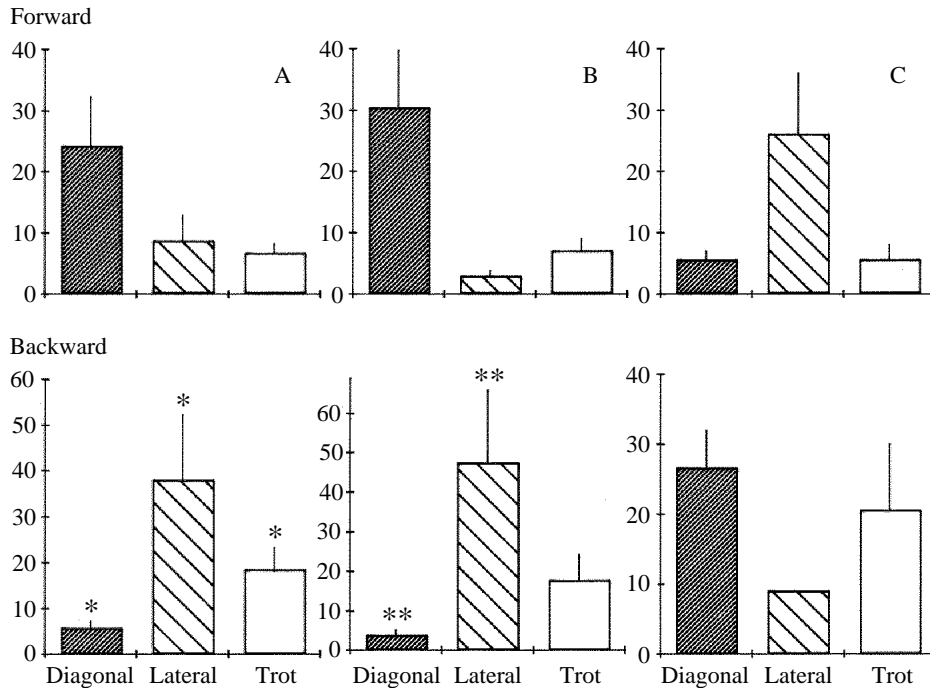


Fig. 3. Mean (+S.E.M.) occurrence of diagonal (shaded bar), lateral (hatched bar) and trotting (open bar) sequences of steps in forward (top) and backward (bottom) locomotion. (A) Data for all eight mole rats, where the general preference to use diagonal sequences during forward locomotion diminished during backward locomotion. (B) The data from mole rats which demonstrated a preference for diagonal sequences during forward locomotion ($N=6$). This preference was reversed during backward locomotion of these mole rats. Mole rats which preferred lateral sequences during forward walking (C) ($N=2$) also had a reversed preference during backward locomotion. Asterisks indicate a significant difference in the occurrence of the specified sequence between forward and backward locomotion (* $P<0.05$; ** $P<0.01$; Mann-Whitney U -test). No statistics were performed on the two lateral mole rats.

of these individual differences are discussed later in this article and, as will be shown below, were in accordance with the scope of the present study.

Backward locomotion

During backward locomotion the overall occurrence of each stepping sequence was reversed. The number of lateral sequences was significantly higher than the performance of diagonal sequences ($P=0.018$, Mann-Whitney U -test). In comparison to forward progression the number of lateral and trotting sequences increased, whereas the number of diagonal sequences decreased (Fig. 3A, bottom). Therefore, there seems to be an overall reversal in the occurrence of stepping sequences between forward and backward locomotion.

When the data from the diagonal and lateral mole rats were analysed separately, the reversed preference was apparent in both groups: mole rats that preferred diagonal

sequences during forward progression preferred lateral sequences during backward locomotion (Fig. 3B, bottom), and mole rats that used lateral sequences during forward locomotion preferred diagonal sequences during backward locomotion (Fig. 3C, bottom). Therefore, in the transition from forward to backward walking, the mole rats reversed their preference in any event: from diagonal to lateral or *vice versa*.

Asymmetrical gaits

The use of transverse galloping during forward locomotion was significantly biased in all mole rats towards an individual preferred direction. Each mole rat typically performed one type: right transverse galloping or left transverse galloping ($P=0.0011$; Mann–Whitney U -test). This preference was abolished during backward locomotion ($P=0.5636$; Mann–Whitney U -test). Fig. 4 describes the preference for one type of transverse galloping (left or right) in all mole rats (Fig. 4A), in mole rats which prefer left

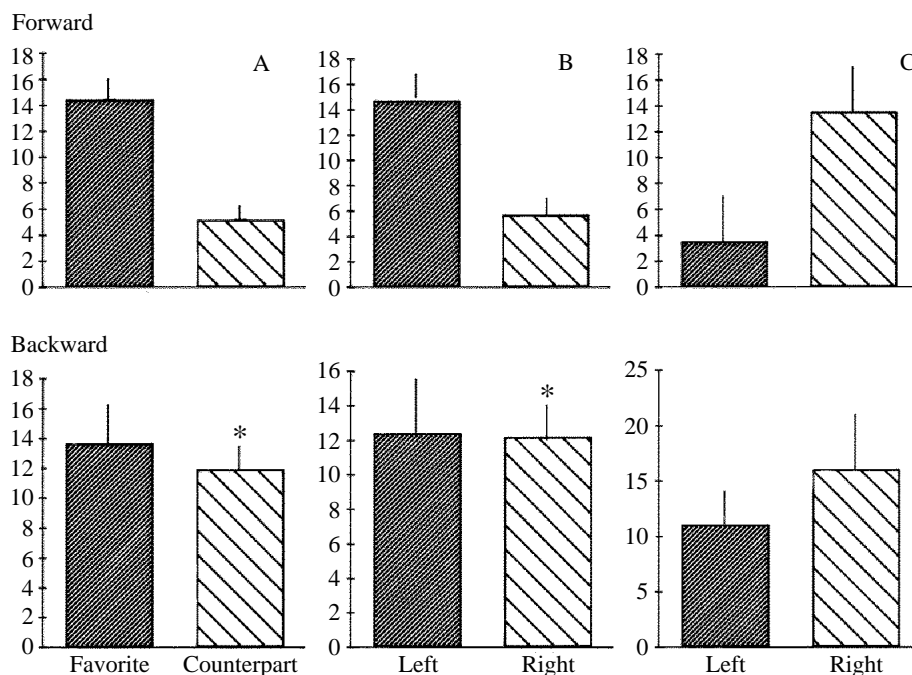


Fig. 4. Mean (+S.E.M.) occurrence of transverse galloping sequences of steps in forward (top) and backward (bottom) locomotion. (A) Data from all eight mole rats, where the general preference to use one type of gallop (shaded bar) during forward locomotion is abolished during backward locomotion by a significant increase in the performance of the non-preferred type of gallop (hatched bar). (B) The data for the six mole rats which preferred left transverse galloping (shaded bar). This preference was abolished during backward locomotion by an increase in the performance of right transverse galloping (hatched bar). Mole rats which preferred right transverse galloping (C) ($N=2$) had only a non-significant increase in the performance of left transverse galloping during backward locomotion. Asterisks indicate a significant difference in the occurrence of the specified sequence between forward and backward locomotion (* $P < 0.05$; Mann–Whitney U -test).

transverse galloping (Fig. 4B) and in mole rats which prefer right transverse galloping (Fig. 4C). In all groups there is a change from a preference for a specific type of galloping (left or right) during forward locomotion to no preference during backward locomotion.

The majority of asymmetrical sequences during both forward and backward locomotion were transverse galloping (156 out of 181 sequences in forward locomotion and 200 out of 219 in backward locomotion). We did not analyse the small number of rotatory galloping sequences. Galloping sequences did not include an aerial phase and the animal maintained at least one foreleg or hindleg in contact with the substratum throughout the stride. The application of the term galloping to these sequences was thus based on the stepping order, which included successive steps of forelegs and hindlegs. During both forward and backward locomotion, asymmetrical sequences made up 40 % of the total sequences (data not shown).

Discussion

The results demonstrate that, in switching from symmetrical forward to backward walking, mole rats also switch from diagonal to lateral sequences of steps or *vice versa*. In asymmetrical sequences, each animal prefers a specific type of transverse galloping during forward locomotion. This preference is abolished in backward locomotion. In the following discussion we propose that forward and backward locomotion are not independent in terms of interleg coupling, but are a similar sequence influenced by an extrinsic factor – the direction of progression.

Fig. 5 (top) illustrates the stepping sequences of a mole rat which locomotes forwards in a diagonal sequence and backwards in a lateral sequence. This definition of sequences is in terms of anatomy: left and right forelegs and hindlegs. However, ignoring the labels of the legs and looking only at the arrows which represent the stepping order reveals that the sequences are identical. In other words, interleg coupling is fixed with respect to the direction of progression, regardless of the anatomy.

Previous studies of backward locomotion have generally concentrated on intraleg changes in the step cycle and the corresponding muscle activity (Ayers and Davis, 1977; Perell *et al.* 1991). Other studies have dealt with Grillner's hypothesis (Grillner, 1981) concerning the neural control of forward and backward locomotion (Ayers and Davis, 1977; Buford and Smith, 1990; Buford *et al.* 1990). A reversal of the sequence of steps made by a cat walking on a treadmill was described by Buford *et al.* (1990). The sequence of steps made during backward locomotion (HR, FL, HL, FR) was accomplished by the cat with changes in posture as well as changes in hindleg kinematics. Our results, however, demonstrate a similar reversal in a naturally backward-walking animal, where backward and forward locomotion are performed using a similar posture. The uniform posture used during forward and backward locomotion observed in the present study could have been constrained by the testing procedure (transparent acrylic tube; see Fig. 1), but open field observations of mole rats show that forward and backward locomotion are also achieved using a similar body posture (D. Eilam and G. Shefer, in preparation). Although Buford *et al.* (1990) found the same stepping pattern in backward walking as was found for mole rats in this study, they did not interpret their results in

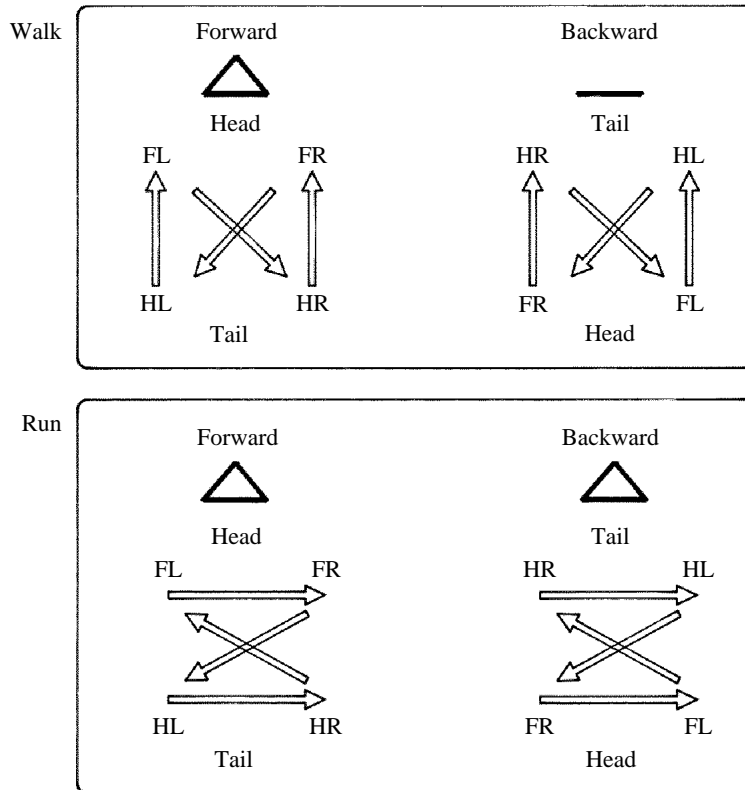


Fig. 5. Illustration of symmetrical stepping sequences used during walking (top) and running (bottom) in forward (left) and backward (right) locomotion. Arrows indicate the order of stepping; triangles indicate the direction of locomotion. When forward walking or running are compared to the respective backward locomotion, the order of stepping is invariant with respect to the direction of progression (arrows are fixed in relation to triangles), but is reversed with respect to anatomy.

terms of the direction of progression. Interleg coordination of insects is more irregular during backward locomotion than during forward locomotion (Graham and Epstein, 1985). Our results, however, do not agree with this observation, as we found that backward locomotion has the same characteristics as forward locomotion, but in a reversed order.

Although the preference for different stepping sequences is different during forward and backward locomotion, the overall repertoire of sequences remains the same. Indeed, mole rats trot and gallop backwards as well. The effect of the direction of locomotion on trotting cannot be evaluated since this sequence is based on alternation between synchronized stepping of diagonally opposing legs: HL+FR followed (or preceded) by HR+FL. Trotting is thus identical in forward and backward locomotion when considered with respect to either direction or anatomy.

If galloping had been affected by the direction of locomotion, like the diagonal and lateral sequences of walking, we would have expected that reversing the direction of

locomotion would result in a reversed preference for left and right gallops in relation to anatomy, but invariance in relation to the direction of movement (Fig. 5, bottom). However, such reversal was not consistent in our results: the preferred galloping sequence of forward locomotion was abolished rather than being reversed. Neither forward nor backward gallops contained an aerial phase, as seen in gallops of heavy-weight mammals, where an aerial phase is absent (Hildebrand, 1977).

By looking at a natural behavior, we have described the changes that occur during backward compared to forward locomotion. Although we cannot negate the interpretation that the sequence of steps is indeed changed from diagonal to lateral, our interpretation that the sequence is fixed in terms of locomotion direction is less complicated. The implication of our interpretation is that interleg coupling should be defined with respect to leading and trailing legs and not with respect to forelegs and hindlegs. In more general terms, this implies that the intrinsic neural interleg coupling is primarily affected by an extrinsic factor – the direction of progression. The role of movement direction in interleg coupling should thus be taken into consideration in models of neural control of locomotion, because it provides further evidence about the way in which the system works.

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