

Coordination of the legs of a slow-walking cat

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Summary. On the basis of behavioural studies the influences that coordinate the movement of the legs of a slowly walking cat have been investigated. The recording method applied here allows for the measurement of forward and backward movement of the legs which are called swing and stance movements, respectively. Influences between contralateral legs, i.e. both front legs or both hind legs, are stronger than those occurring between ipsilateral legs, i.e. front and hind leg of the same side. Influences which coordinate the front legs seem to be of the same kind as those for the hind legs. These influences are symmetrical, which means that the same type of influence acts from right to left leg and in the reverse direction. Two types of influences are described for contralateral legs: 1. When the influencing leg performs a swing movement, the influenced leg is prevented from starting a swing movement. 2. When the influencing leg performs a stance movement, the probability that the influenced leg starts a swing movement increases as the influencing leg moves backwards during its stance movement. In contrast to contralateral coupling, the ipsilateral influences are asymmetric, i.e. a different influence acts from front to hind leg than does in the reverse direction. The front leg is influenced to start a swing when both legs have approached each other to a given value. The hind leg is influenced to start a stance movement after the front leg has begun its swing.

Key words: Walking – Interlimb coordination – Cat

Introduction

The coordination of leg movements is a basic prerequisite for many different behaviours of a legged animal. Two main approaches are used to investigate the mechanisms which coordinate leg movements: observation of the behaviour of the animal and electrophysiological record-

ings. In investigations of interlimb coordination of walking cats many detailed results have been obtained by using the last method (e.g. Lloyd and McIntyre 1948; Miller et al. 1973; Schomburg et al. 1978, 1986; review Miller and Schomburg 1985).

However, although this approach allows the evaluation of particular reflex pathways at the neuronal level the complexity of the whole system makes it difficult to interpret these results in a functional context. Neither is a unique conclusion possible concerning the actual role of a pathway that is being measured in a walking animal, nor can one be sure about the relative contribution of this pathway in the framework of an unknown number of other pathways. By contrast, an investigation of the behaviour can provide information on a more functional level. With this information, the relative role of particular pathways can be better estimated. Several analyses of leg coordination are available (Miller et al. 1975a, b; Miller and van der Meche 1975; review Wetzel and Stuart 1976; Halbertsma 1983) that have used this behavioural approach. These investigations give detailed descriptions of the movement of legs in different situations. From these results it has been concluded that two types of coordination mechanisms exist: influences that produce an alternating phase (180° out of phase) and influences that produce an in-phase relation between two legs. However, no information is available about how these principles might actually be realized.

The present experiment investigated the influences which coordinate the movement of the four legs of a forward walking cat. Trotting and galloping were not investigated. There is general agreement that each leg is controlled by a separate step pattern generator which can produce the rhythmic movement of a walking leg (Shik and Orlovskii 1965; Grillner 1981; Kato et al. 1984). A step pattern generator is defined here so as to include all central and peripheral connections which are necessary to control the cyclic movement of a leg. This cyclic movement can be divided into two parts, the stance movement when the leg moves backwards, and the swing movement when the leg moves forward and returns to

start the following stance movement. The question concerns how these "oscillators" are coupled in order to produce the normally coordinated gait. Information on these coordinating influences can be obtained by evaluating the results by means of phase response curves (Pavlidis 1973). This method was successfully applied in the investigation of the movement of the swimmerets, which are appendages of the abdomen of the crayfish (Stein 1976), of the leg movement in turtle swimming (Lennard 1985), and of leg coordination mechanisms for different arthropods (Cruse and Müller 1986; Cruse and Schwarze 1988; Cruse and Knauth 1989; Müller and Cruse 1991). The phase response curve can show whether a given value, e.g. the stance duration, depends upon the phase of an event, e.g. the beginning of this stance, during the step cycle of a reference leg. If such dependencies exist, they enable conclusions about the underlying mechanism by which one leg influences the movement of the other leg. Interpretation of a phase response curve can be straightforward when the influence between two oscillators is known to act in only one direction. If, however, mutual influences between the oscillators can occur, the interpretation of the phase response curve is more difficult.

Material and methods

The experiments were performed with two female cats and one male cat aged 4 months. The cats weighed between 1.2 and 1.5 kg. The animals were familiarized with walking on motor-driven belts, and different belts for front and hind legs were used. The belt speed was varied between 30 and 46 cm/s. Scatter concerning the phase values was smaller for the higher belt speeds. This agrees with the results of Halbertsma (1983) who reported a considerable increase in the variability of all measured intervals for walking speeds below 40 cm/s. Most of the results shown here were obtained using a belt speed of 30 cm/s because the phase response curve provides more information when the range of phase values is greater. The cat was made to walk on the belts and to adopt the speed of the belt in the following way. During the walk the cat was continuously provided with food at the front end of the walking belt. As the cat was free to choose its position on the belt, this position could not always be held constant. Steps were only evaluated when the cat showed no recognizable movement in the anterior – posterior direction.

The movement of the four legs was registered using a video system as proposed by Godden and Graham (1983). The cat was viewed from above by a video camera (Fig. 1A). By means of two mirrors the side view of the legs was also visible. The system detects the intersection of the legs with a horizontal line in a parasagittal plane. For this purpose the contrast between the leg and the background had sometimes to be increased by affixing a piece of white adhesive tape to the leg. The position of the horizontal detector line was about two cm above the ground (Fig. 1A, broken line). Thus, this method does not measure movement in the form of flexion and extension but rather as forward – backward movement of the leg which is defined here as swing and stance. Data of walks lasting about 30 s and corresponding to about 40 continuous steps were stored and later plotted, as shown in the example of Fig. 1B. From these walks different parameters were evaluated by means of a graphic tablet (Apple II). These were either temporal values such as the duration of the whole step (step period) and time intervals between particular events in the movement cycle (d_1 , d_2 , see Fig. 1C and below), or geometrical values such as the stance or swing amplitude (a_1 , a_2 , see Fig. 1C). The temporal values could be directly measured with a resolution of ± 20 ms. The geo-

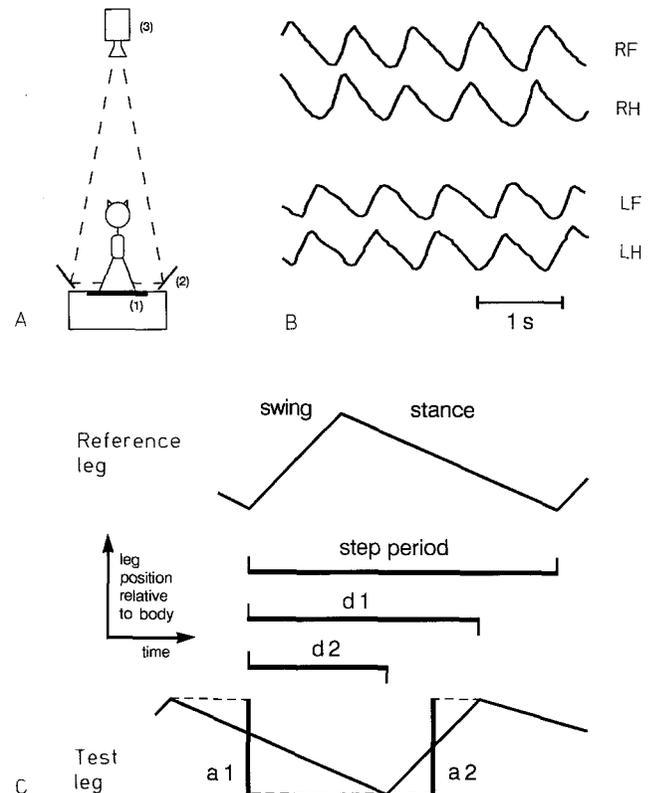


Fig. 1. A Schematic drawing of the experimental device. The cat walks on a motor driven belt (1) in a direction perpendicular to the drawing plane. By means of two mirrors (2) the videocamera (3) views the legs from the side. B One example of a section of a recorded walk. Abscissa is time, ordinate is relative position as measured by the video system. C The temporal and geometrical values measured. The step period is the sum of the duration of swing and stance movements. The phase of the end of the swing of the test leg in the step period of the reference leg is obtained by dividing the time d_1 by the step period of the reference leg. Correspondingly, the phase of the end of the stance is obtained by dividing d_2 by the reference period. a_1 and a_2 , respectively, show how the amplitudes of stance and swing movements are measured

metrical values are only given in relative units because the absolute value in this case depended on the adjustment of the height of the detector line which, due to technical reasons, was not the same for all sessions and all animals. This, however, does not influence the measurement of the temporal values.

The results are either shown in the form of phase histograms (Figs. 3, 7), or in the form of the phase response curve (Figs. 4, 8). The phase histogram shows the frequency of occurrence of an event in the activity of the test leg (e.g. end of swing movement) during the cycle of the reference leg (Fig. 1C). The phase response curve shows the duration of a time interval measured for the test leg (e.g. duration of swing) plotted against its phase within the cycle of the reference leg. With one exception (Fig. 4E) the phase value of the end of the time interval is used. In general, the step of the reference leg runs from the beginning of swing movement to the end of the stance movement. In Fig. 8C, D the reference cycle starts at the end of the swing movement. The time intervals plotted on the ordinate of the phase response curves (Figs. 4, 8) are not shown in ms, but in relative units as all values are normalized by division with the duration of the step (step period) of the reference leg. To calculate mean values and deviations in the phase histograms the methods of circular statistics have to be applied (Batschelet 1983). Instead of standard deviation the concentration parameter is shown. This takes a value of 1 for a zero deviation and a value of 0 in the case

of an equal distribution. Calculation of the slope of the phase response curves is a problem because the abscissa shows a circular variable. Nevertheless, for selected cases the correlation coefficient r and the slope b of the regression line which shows the minimum of the sum of the squared distances were calculated, but no statistical significances are given. The data presented are from two animals "T" and "M" in the case of the phase histograms and from one animal (T) for the phase response curves because the latter shows a larger scatter. All data presented refer to animals walking on the belt run at the same speed for all legs, with two exceptions (Figs. 5, 6) where front and hind legs walk at a different speed. An inspection of the other experiments (a total of 30 000 steps were evaluated including those of the third cat) showed essentially similar results.

Results

The characteristics of the movement of each leg have to be examined before turning to interlimb coordination. Figure 2 shows the absolute duration of swing and of stance movements plotted against the duration of the whole step for each of the four legs of one animal (T). The stance duration shows a clear dependency on the step duration. For the swing duration this dependency is much weaker and not significant in all cases. The mean values (\pm S.D.) of the duration of swing and stance movements at a belt speed of 30 cm/s are 207 (\pm 57) ms and 506 (\pm 121) ms for animal T and 233 (\pm 73) ms and 577 (\pm 76) ms for animal M, respectively ($n=200$ steps for each animal).

Figure 3A and B show the phase histograms of the occurrence of the end of the hind leg stance movement within the cycle of the front leg (Fig. 3A) and of the front leg in the cycle of the hind leg (Fig. 3B). The results show that the hind leg always starts the swing movement be-

fore the front leg starts its swing movement. Figure 3C, D shows the corresponding phase histograms for the end of the swing movement for the hind (Fig. 3C) and front legs (Fig. 3D). This shows that, in most cases ($>85\%$), the swing movement of the front leg starts before the swing of the hind leg is finished which means that the swing movements of both legs normally overlap to some extent. For the front legs the circular standard deviation is larger for the phase values of the end of swing than for those of the end of the stance movement (not shown). For the hind legs no clear results were found.

As it is not clear initially how the legs influence each other, the phase response curves of different values have to be investigated. For this purpose the duration of stance movement (Fig. 4A, B) and of swing movement (Fig. 4C, D, E) will be shown here. Except for Fig. 4E, the end of the measured time interval is used as corresponding phase value in all cases.

Figure 4A shows the duration of the stance movement of the hind leg relative to its phase in the step cycle of the front leg. The phase value is determined by the end of the stance of the hind leg. In general, in a phase response curve all phase values are calculated to appear in the range between 0 and 1. However, to make this figure clearer, those dots which have a relative stance duration of >1 are shown in the second reference cycle. As can be seen in Fig. 4A, the stance duration of the hind leg becomes longer when it ends later in the cycle of the reference leg. The slope of the line showing the minimum of the sum of the squared distances is $b=0.88$ (correlation coefficient $r=0.90$, $n=199$) for the values shown in Fig. 4A, and $b=1.26$ ($r=0.74$, $n=171$) for the values forming the left group only (abscissa <1.1).

Figure 4B shows the reverse case, the dependency of

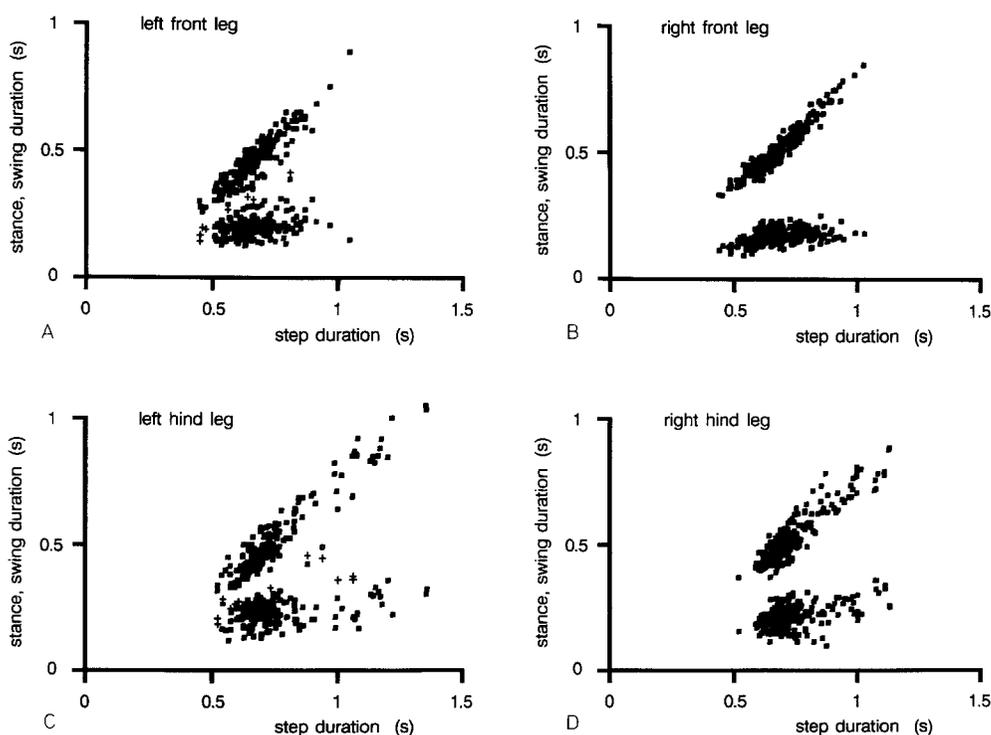


Fig. 2. The absolute duration of the swing movements (lower values) and stance movements (upper values) of the four legs versus the duration of step periods. Those values of the swing movements which cannot be uniquely attributed to this group are shown as crosses. Data cover 200 steps of animal T

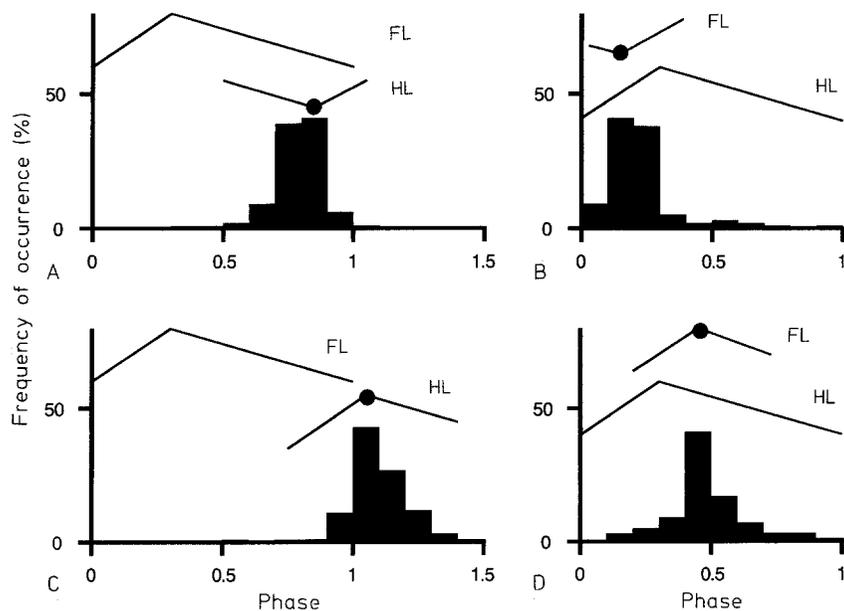


Fig. 3A-D. Ipsilateral coordination, phase histograms from 800 steps of two animals, T and M. **A, C** Use the front leg as reference, **B** and **D** use the hind leg as reference. **A, B** Show the phase of the end of the stance of the test leg, **C, D** Show the phase of the end of the swing of the test leg. The insets show the step period of the reference leg and, schematically, the event in the movement of the test leg whose phase is measured. Upper trace is front leg (FL), lower trace is hind leg (HL)

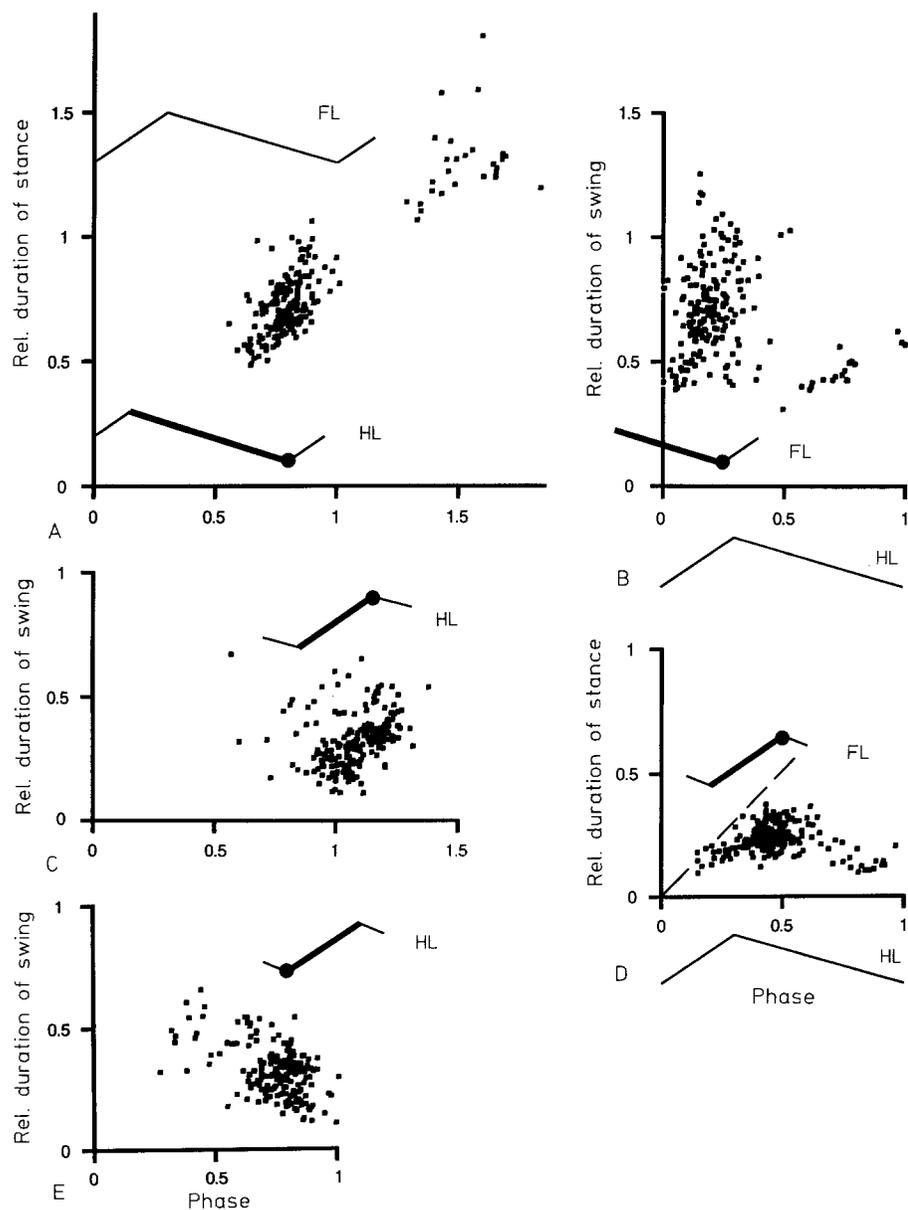


Fig. 4A-E. Ipsilateral coordination, phase response curves of 200 steps of the right legs of animal T. In **A-D** the test and reference legs are used as in Fig 4. **A-D**. In **A, C** the front leg is the reference leg as indicated by the upper inset in **A**. In **B, D** the reference leg is the hind leg as indicated by the insets below the abscissa. In **A, B** the ordinate shows the relative duration of the stance, in **C-E** the relative duration of the swing of the test leg as indicated by the thick lines of the inset figures. The dots represent the event whose phase value is measured

the stance duration of the front leg on the step cycle of the hind leg. The stance movement of the front leg depends much less on the phase within the hind leg cycle (Fig. 4B). Although the stance duration of the front legs shows a large scatter, most phase values are concentrated within a comparably small range. Only a small group of very short steps end in the phase range between 0.6 and 1.

Considering the swing movement of the hind leg, the phase response curves are shown in Fig. 4C, E. In Fig. 4C, as in all other presentations, the phase value of the end of the measured interval, here the swing, is used as abscissa. All values are shown to appear in the period between 0.5 and 1.5 in this case ($b = 1.4$, $r = 0.22$, $n = 198$). When those steps which finish the stance in the cycle that followed the reference cycle (see Fig. 4A, right group) are omitted, r is 0.28 and b is 1.69 ($n = 186$). By contrast, in Fig. 4E the beginning of the hind leg swing is applied. Here all values are shown to appear between 0 and 1 ($b = -0.64$, $r = -0.49$, $n = 197$). Whereas Fig. 4E shows a negative correlation, only a weak correlation is found in Fig. 4C. In Fig. 4D the swing of the front leg is represented in the same way as shown in Fig. 4C for the hind leg. This shows that the swing duration increases up to a phase value of about 0.5 and that it seems to decrease again for higher phase values.

The results given in Fig. 4B show that for the front leg the standard deviation of the relative stance duration seems to be higher than the standard deviation of the corresponding phase values (a quantitative comparison is difficult because the values on the abscissa are cyclic ones). Thus, stance movements of the front leg start in a broad phase range but end in a smaller phase range. This shows that the end of the stance movement of the front leg is influenced by signals from the hind leg. This agrees with the result that the standard deviation of the phase values of the end of the swing in the front leg is larger than that of the end of the stance.

Comparison of Fig. 4A and B shows that there is a clear difference in the behaviour of front and hind legs. The phase response curve, showing the duration of the stance of the hind leg (Fig. 4A), follows a line with a slope of about 1. This result is to be expected if the stance of the hind leg begins in a small phase range but there are no coordinating influences from the reference leg which determine the end of the stance. The corresponding phase response curve, showing the swing duration of the hind leg (Fig. 4C), yields a smaller correlation coefficient. When looking at the duration of the hind leg swing versus the phase value of the start of the swing (Fig. 4E), a negative correlation was found. Both results show that the end of the hind leg swing is less correlated with the movement of the front leg than its beginning. This indicates that the end of the swing movement of the hind leg is influenced by signals from the front leg.

All these experiments and evaluations have been repeated with walks where the front and hind legs walk on two belts at different speeds. The two belts were arranged one directly behind the other. The animal could still be made to walk freely. The results are the same as those described for constant speed of all legs with the exception of a higher standard deviation. However, one interesting

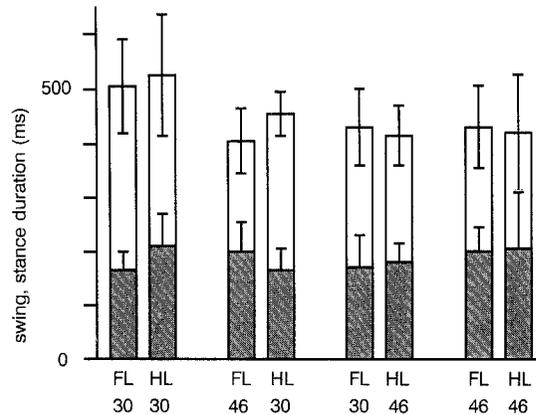


Fig. 5. Mean duration (\pm S.D.) of swing (hatched columns) and stance (open columns) of animal T in different walking situations. Each mean value is calculated from 200 steps. FL stands for front legs, HL for hind legs. The values below the columns give the belt speed for the corresponding leg pairs in cm/s. Differences between both left values and all other values are significant ($p < 0.1\%$)

result could not be obtained when using the same belt speed for front and hind legs. This is shown here for the most extreme speed difference used in our experiments. Figure 5 shows the mean duration of swing and stance movement for front and hind legs in four situations: two controls, when all legs walk with the same speed, either 30 cm/s or 46 cm/s, and two experiments where the front and hind legs walk at different speeds. The results show that there were no significant changes in swing durations. When all legs walk at a higher speed, the duration of the stance movement decreases as was shown by earlier authors (e.g. Halbertsma 1983). When only one leg pair walks at a higher speed, all legs adopt the short stance independent of which leg pair, front or hind legs walks faster. Only in the case when the hind leg walks slower was there a tendency for the hind leg stance to be somewhat longer, but it was still clearly shorter than in the controls where all legs walk slowly.

In addition to the duration of the step parts, the step amplitudes also have to be studied. A review of the original recordings indicated that the step amplitudes of front and hind legs are inversely related: when the front leg makes a longer stride during stance, the hind leg shows a shorter amplitude of swing. A quantitative evaluation of walks at the same speed for front and hind legs showed a clear negative correlation. This was particularly obvious when different speeds of 30 cm/s were used for the front legs and 46 cm/s for the hind legs (Fig. 6, $b = 1.35$, $r = -0.63$, $n = 200$, $p < 0.001$). An inspection of the walks revealed that the end of the front leg swing and the end of the hind leg stance occupy an approximately constant position relative to a body fixed coordinate system. Thus, an increase in front leg stance amplitude produces a backward shift of the end of the front leg stance. Because of the correlation shown in Fig. 6 this corresponds to a backward shift of the end of the hind leg swing. Thus, when the slope is about 1, both legs approach each other until the distance between front and hind leg at the end of the front leg swing reaches an approximately constant value. The fact that the slope is

somewhat larger than 1 ($b = 1.35$) could mean that the front leg contributes in general more to this compensation than does the hind leg. Another explanation might be that the hind leg swing may not become shorter than a given value (about 0.5), even when the front leg stance is very long. Therefore no normal distribution of the data occurs in this range which increases the slope of the linear regression line.

Comparison of phase histograms and phase response curves of contralateral legs, i.e., of both front legs or both hind legs, shows three general results. First, there seems to be no general difference for coupling between front legs and for coupling between hind legs. Therefore, the results presented here concern mainly the front legs.

Second, coordination is stronger between contralateral legs than between ipsilateral legs. Each part of Fig. 7 summarizes the phase values for the front and hind legs of the two animals. Figure 7A, B shows the histograms of the phase values of the end of the swing movement. Correspondingly, in Fig. 7C, D the phases of the end of the stance movement are shown. In Fig. 7A, C the

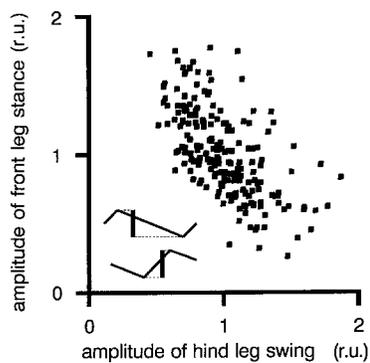
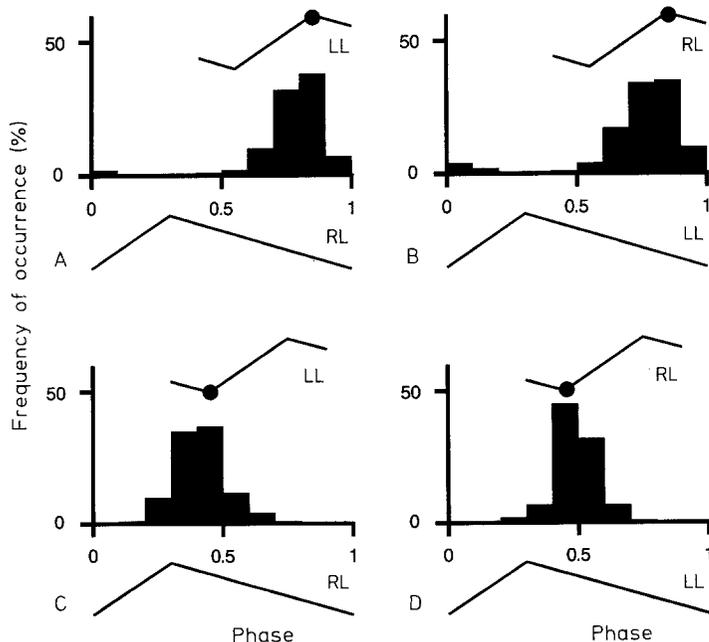


Fig. 6. Amplitude of stance movement of front leg (ordinate) versus amplitude of swing movement of ipsilateral hind leg (abscissa) in relative units (r.u.). 200 steps of animal T



reference leg is the right leg, while in Fig. 7B, D it is the left leg. The comparison between contralateral and ipsilateral concentration parameters (not shown) reveals that for animal T all ipsilateral concentration parameter values are smaller than the smallest contralateral parameter. For animal M there is some overlap but, although this animal shows very high concentration parameter values, the tendency is the same.

Third, coordination between two contralateral legs is nearly symmetrical in contrast to ipsilateral legs. This means that very similar figures appear, irrespective of which of the two legs is used as reference leg. However, a detailed study of the results reveals some differences. This becomes clearer when we look at the phase response curve. Fig. 8A, B show the duration of the swing movement of the test leg as a function of the phase value of the end of this swing movement (comparable to Fig. 7A, B). As in the earlier figures, the reference cycle starts and ends with the beginning of the swing movement, as shown by the inset figures. In Fig. 8A the left front leg is the test leg, and the right front leg is the reference leg. In Fig. 8B test and reference legs are reversed. Whereas the end of the left leg swing does not overlap with the swing of the right leg (Fig. 8A), there are many steps for which the right leg swing continues after the left leg swing has begun. Figure 8C, D show the duration of the stance movement of the test leg over the phase of the end of this stance movement. In Fig. 8C, D, in contrast to the earlier figures, it is not the end of the stance (= beginning of swing), but rather the end of the swing (= beginning of stance) that is used to mark the beginning and end of the reference cycle. The reference leg in both Fig. 8C and Fig. 8A is the right leg, whereas in Fig. 8D and Fig. 8B, it is the left leg. The results show that stance movements that end directly after the end of the reference swing can be very long, and that the maximum duration decreases with increasing phase value. The fact that the minimum duration also increases is due to the fact that no stance

Fig. 7A–D. Contralateral coordination, phase histograms of 800 steps of the front and hind legs of two animals, T and M. **A, C** Use the right leg as reference, **B, D** use the left leg. The movement of the reference leg is indicated below the abscissa. **A, B** Show the phase of the end of swing of the test leg, **C** and **D** the phase of the end of the stance of the test leg, as indicated by the dots marked on the inset figures

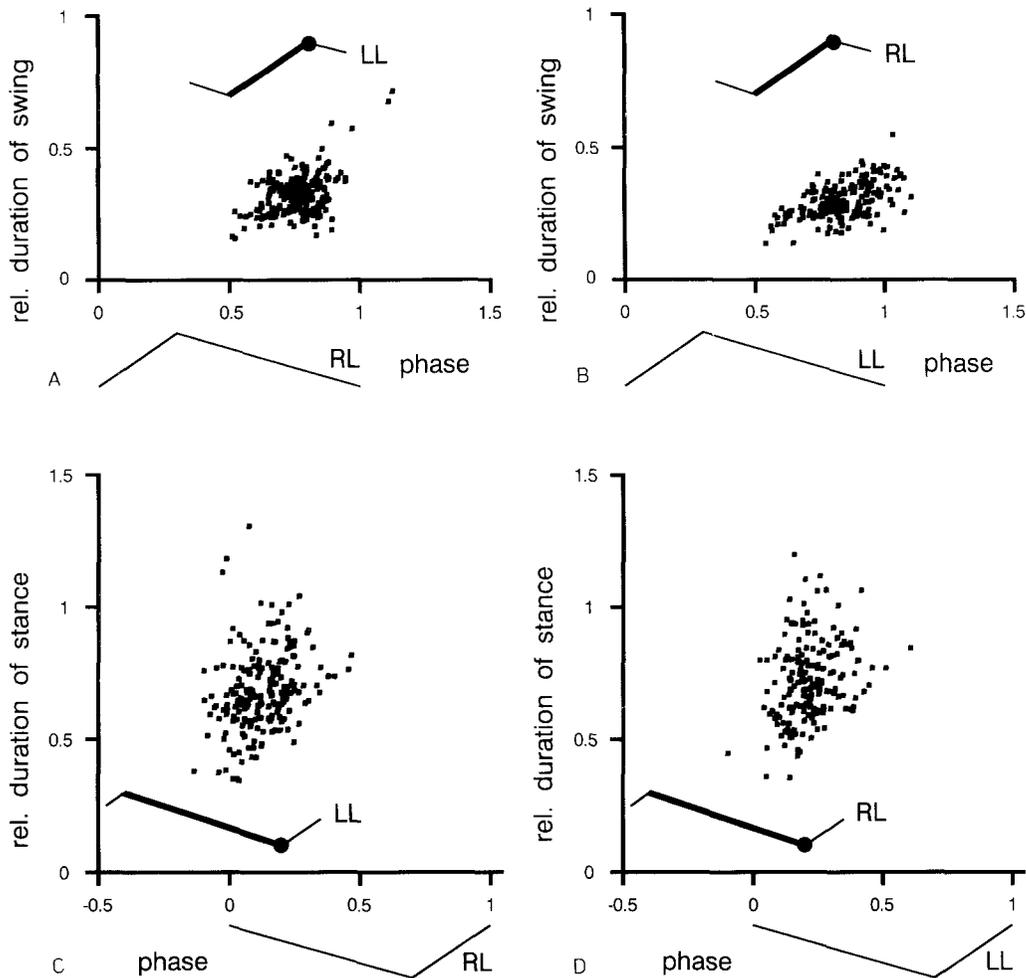


Fig. 8A–D. Contralateral coordination, phase response curves of 200 steps of front legs of animal T. In **A, C** the reference leg is the right front leg, in **B, D** it is the left front leg. In **A** and **B** the reference cycle runs from the beginning of the swing to the end of the stance movement as in all earlier figures, whereas in **C, D** the reference cycle begins with the stance movement and ends after the swing as indicated by the inset figures below the abscissa. In **A, B** the ordinates show the relative duration of swing. **C, D** Refer to the stance movement of the test leg as indicated by the thick lines in the inset figures. The dots indicate the event whose phase is measured

movement starts within the swing of the reference leg. In agreement with the differences illustrated in Fig. 8A and B, Fig. 8C shows that some steps can be seen to end their stance before the reference leg swing is finished.

Discussion

Concerning the phase values the present results agree with those of earlier authors. Contralateral legs were found to be coordinated in an alternating fashion with a mean phase value of about 0.5 for a wide range of walking speeds (Miller et al. 1975b; English 1979), whereas the phase shift is much smaller for ipsilateral legs (Miller et al. 1975a). This was also found by Halbertsma (1983), who moreover, concluded that coupling between ipsilateral legs is weaker than between contralateral legs because “after disturbance of the movement of a limb, the restoration of the appropriate coordination seems to be faster” between contralateral than between ipsilateral legs.

What can be concluded from these findings about the underlying coordinating mechanisms? When the output values of four oscillators are coordinated, this does not necessarily mean that each pair of oscillators is directly coupled. A measurable coordination between two os-

cillators A and B can also be observed when no direct coupling mechanisms exist between A and B, but both oscillators are directly coupled with a third oscillator C. In this case, however, a weaker coordination between A and B has to be expected than between the directly coupled oscillators A and C and between B and C (see Müller and Cruse (1991) for an extensive discussion of this problem). The figures shown here only reflect results concerning the coordination between ipsi- and contralaterally neighbouring legs. Coordination between diagonally neighbouring legs, e.g. the left front and right hind legs, were also investigated but showed much smaller concentration parameter values than directly neighbouring legs. Therefore we assume that in the walking animal no strong direct coupling exists between diagonally neighbouring leg pairs and we will concentrate on the coordination between ipsi- and contralateral leg pairs.

Ipsilateral legs

The results (Figs. 3 and 4) have shown that the end of the swing movement of the hind leg is influenced by signals from the front leg. Is it possible to describe the timing of this signal in more detail? The results shown in Fig. 6

indicate that the stance of the front leg finishes when the hind leg has approached the front leg to within a given value. The results show that this happens in a broad range of leg positions measured in a body fixed coordinate system. Therefore, it is not the position of the legs in the body fixed coordinate system, but rather the position of both legs relative to each other that constitutes the decisive criterion leading to the end of the front leg's stance movement. The signal for the hind leg to finish swing movement may either be calculated from the position relative to the front leg, or alternatively, it may be that the start of the front leg swing as such serves as a signal for the hind leg to finish swing movement. In any case, the switch in the hind leg follows after a certain delay, thereby producing the "understepping" of the hind legs. This is schematically shown in Fig. 9A. When the front and hind legs walk on two belts at different speeds, the faster legs determine the duration of the stance of the legs on the slower belt (Fig. 5). This can occur in either direction. Thus, excitatory influences run from the front to the hind legs and also in the opposite direction in agreement with the earlier conclusions.

Contralateral legs

The results show that the influences which coordinate contralateral legs are different to those which act between ipsilateral legs. When comparing the concentration parameters for the different leg pairs of each animal, in seven of eight cases, the concentration parameter of the phase of the stance end is smaller than that of the end of the swing. In one case they were both equal. This suggests that the end of the stance is under stronger control from contralateral coordinating influences than the end of the swing. This is supported by the finding that the scatter of stance duration is higher than that of swing duration (compare Fig. 8A, B with Fig. 8C, D). What is the nature of these coordinating influences? Results shown in Fig. 8C, D show that the maximum duration of stance movement decreases with increasing phase value. This points to a coordinating influence also described for insects (Cruse and Knauth 1989). This influence excites one leg to start a swing movement earlier when the position of the influencing leg has moved backwards a long way. According to this influence the stance duration of the test leg should be long when it ends at the beginning of the stance, but should become shorter when the reference leg has moved backwards a long way during the stance, as our findings have shown.

Halbertsma (1983) was able to run right and left legs on different belts. Whenever the speed difference exceeded a given value, the legs on the faster belt performed two steps while the legs on the other belt performed only one step. In these experiments the stance movement of the fast step, which includes the swing of the contralateral slow leg, showed a greater duration and amplitude compared to a step in 1:1 coordination. By contrast, the second fast step which is performed during the stance of the slow leg was shorter than a normal step. Although only a small number of steps was quantitatively eval-

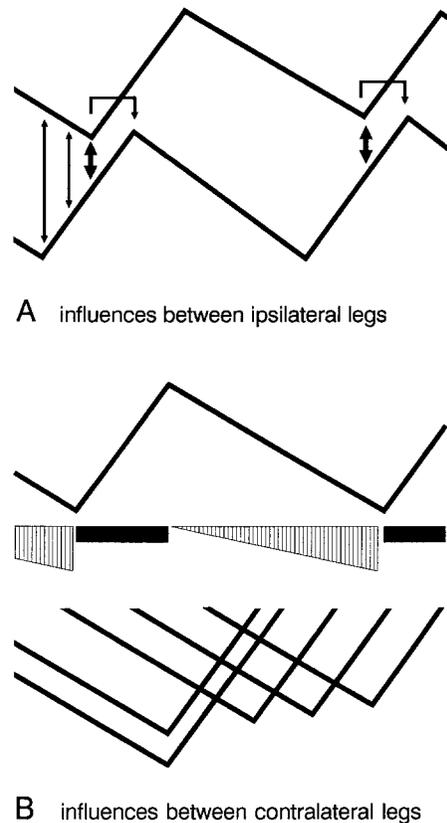


Fig. 9A, B. Schematic representation of the coordinating influences between **A** ipsilateral legs and **B** contralateral legs. **A** The coordinating influences between the front (upper trace) and ipsilateral hind leg (lower trace). The distance between both legs (two-way arrows) has to be smaller than a given threshold to start the swing movement of the front leg. After a certain delay the hind leg finishes the swing and starts stance movement (bent arrow). **B** The coordinating influences assumed to exist between contralateral legs are shown as if they acted only in one direction, from the leg shown in the upper trace to that shown in the lower trace. Several traces are shown for the influenced, lower leg to illustrate the effects resulting from the coordinating influences. During the swing movement of the influencing leg (black bar) the stance of the influenced leg may be prolonged because the start of the swing is inhibited. During the stance movement of the influencing leg the influenced leg is excited to start the swing movement. The farther the position of the influencing leg has moved backwards, the earlier will be the start of the swing (wedge)

uated, the shortening was particularly obvious and supports our assumption of the existence of an influence that excites the start of a swing movement.

However, this influence is in itself not sufficient to explain all our results: according to this influence, the start of a swing should also occur during the swing of the reference leg, something that, at least when the left leg is the reference leg, is almost never the case (in only 2 out of 200 steps). One might therefore speculate that an additional influence exists such that during the swing of the left leg the start of the swing of the right leg is inhibited. This is schematically shown in Fig. 9B. Moreover, the results shown in Fig. 8A, B strongly suggest that the swing of one leg is finished when the other leg starts its swing movement. Thus the "inhibitory" influence shown in Fig. 9 inhibits not only the start, but also the

continuation of an ongoing swing movement thereby "exciting" the start of a stance movement. But this assumption raises the question of why in some cases overlapping swings still occur. Two causes might be responsible. One possible cause could be an asymmetry of coupling. The inhibitory influence might be stronger from left to right than in the other direction. A second cause might be the following: as one front leg receives coordinating influences not only from its contralateral front leg but also from its ipsilateral hind leg, these "irregular" steps might be elicited by influences from the hind leg which are strong enough to override the contralateral inhibitory effects, and these effects might be stronger on the right than on the left side. This asymmetry was also found in animal M for both the front and hind legs, but in this case they were in the opposite direction.

Comparison with other results

As mentioned in the Introduction, the only investigation that has addressed the nature of the coupling mechanisms is the work of Halbertsma (1983). Halbertsma (1983, p 62,63) claims, on the basis of his data, that coordinating mechanisms influence the timing of the end of the swing movement. In our experiments this was only found for the influence from front to hind legs, but in two other cases (hind to front and contralateral legs) the end of stance was influenced.

The results summarized in Fig. 9 agree with the observations of Carter and Smith (1986) who disturbed normal walking by eliciting a paw shake response during the swing movement of a hind leg. This increased the duration of the swing of the hind leg concerned. As a consequence, the swing of the ipsilateral front leg was also increased, and the steps in both legs were followed by a shorter "recovery" step. Concurrently, stance duration of the contralateral hind leg (and the contralateral front leg) was increased, and exactly this should result from the coupling mechanisms presented in Fig. 9. Similarly Shik and Orlovskii (1965) found that in dogs coordinating influences between contralateral legs are symmetrical whereas those between ipsilateral legs are asymmetrical and less strong. No direct information on the nature of these influences is available from their results, but in a model calculation they discuss the possibility that in all legs the end of stance is modified according to the position of the controlling leg.

Only general statements are possible when we try to associate these functional principles with known results from electrophysiological investigations. A general problem related to methodological differences is the following. It is in the nature of the application of electrophysiological methods that the temporal parameters are at the center of interest. This might be the reason why these authors (e.g. Miller et al. 1975a) only discuss the importance of temporal relationships when considering the coordinating mechanisms. Our experiments suggest that the geometrical relationships may be even more important. What is known about the morphological basis of

these coordinating mechanisms? It has long been assumed that the ipsilateral connections are mediated by the long propriospinal pathways (Lloyd and McIntyre 1948; Miller et al. 1973; Schomburg et al. 1978) where both ascending and descending connections have been found. Descending pathways from front to hind legs have been found to have a stronger effect on the extensors than on the flexors (Schomburg et al. 1978) which, in the context of walking, might correspond to a signal to end swing movement. Contralateral coupling most probably occurs within the lumbosacral and cervicothoracic centers of the spinal cord (Miller et al. 1975a; see Miller and Schomburg 1985 for a concise review), but pathways including higher centers (Shimamura et al. 1985) are also possible.

A qualitative difference to the coupling mechanisms found in arthropods (see review Cruse 1990) is that in the cat, contralateral coupling is stronger than ipsilateral coupling. This might result from the fact that in the cat the coordination between ipsilateral legs allows both legs to perform overlapping swing movements, something that has been rarely observed in arthropods. What might be the reason for this difference? Simultaneous lifting of two ipsilateral neighbouring legs, in principle, causes instability of the body, particularly in a four-legged animal. Therefore one should assume that this situation is avoided by the system controlling leg movement. Nevertheless, the instability is much less of a problem for mammals, such as cats, than for an arthropod, such as the crayfish or the stick insect. In mammals, the right and left legs are generally arranged below the centre of body mass, in complete contrast to arthropods. Thus, in the cat, the horizontal projection of the lever arm, by which gravity rotates the body, is much shorter, and the body is, to a larger extent, also supported by the legs of the other side of the body. Thus, the cat can afford coordinating mechanisms that result in ipsilaterally overlapping swing movements.

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