

Experimental study of coordination patterns during unsteady locomotion in mammals

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Summary

A framework to study interlimb coordination, which allowed the analysis of all the symmetrical and asymmetrical gaits, was recently proposed. It suggests that gait depends on a common basic pattern controlling the coordination of the forelimbs (fore lag, FL), the coordination of the hindlimbs (hind lag, HL) and the relationship between these two pairs of limbs (pair lag, PL) in an anteroposterior sequence of movement (APS). These three time parameters are sufficient for identifying all steady gaits. We assumed in this work that this same framework could also be used to study non-steady locomotion, particularly the transitions between symmetrical and asymmetrical gaits. Moreover, as the limbs are coordinated in time and also in space during locomotion, we associated three analogous space parameters (fore gap, FG; hind gap, HG and pair gap, PG) to the three time parameters. We studied the interlimb coordination of dogs and cats moving on a runway with a symmetrical gait. In the middle of the runway, the gait was disturbed by an obstacle, and the animal had to change to an asymmetrical coordination to

get over it. The time (FL, HL, PL) and space (FG, HG, PG) parameters of each sequence of the trials were calculated. The results demonstrated that the APS method allows quantification of the interlimb coordination during the symmetrical and asymmetrical phases and during the transition between them, in both dogs and cats. The space and time parameters make it possible to link the timing and the spacing of the footfalls, and to quantify the spatiotemporal dimension of gaits in different mammals. The slight differences observed between dogs and cats could reflect their morphological differences. The APS method could thus be used to understand the implication of morphology in interlimb coordination. All these results are consistent with current knowledge in biomechanics and neurobiology, therefore the APS reflects the actual biological functioning of quadrupedal interlimb coordination.

Key words: gait, mammals, interlimb coordination, anteroposterior sequence.

Introduction

Quadrupedal vertebrate locomotion is basically carried out by the movements of two pairs of limbs, the fore pair and the hind pair. Each gait corresponds to a temporal coordination of the movements of the four limbs. Two kinds of gait can be distinguished: symmetrical gaits (walks, trots and paces), in which the two footfalls in each pair are evenly spaced in time (Howell, 1944), and asymmetrical gaits (gallops and bounds), in which the two footfalls are unevenly spaced in time in at least one pair. Hildebrand (Hildebrand, 1965; Hildebrand, 1977) proposed two distinct sets of parameters to classify either symmetrical or asymmetrical gaits. It was thus impossible to study the transition between the two kinds of gait using its methods, as the quantification of the gaits used different parameters. In Hildebrand's work, which became the framework

for most studies in quadrupedal locomotion, gait was classified by taking stride duration as the time reference. Stride duration is the time lag between two successive footfalls of the same limb during which the footfalls of the other three limbs need to happen. The succession of the four limbs' footfalls was examined within this time unit. Splitting a locomotor sequence into such strides was effective in the study of steady locomotion. However, as soon as gait transition or disturbed locomotion occurred, splitting a locomotor sequence into strides was not appropriate because the reference limb changed often and therefore the footfalls did not take place in the reference stride. Many aspects of interlimb coordination during tetrapod locomotion were thus not studied, such as the transition between symmetrical and asymmetrical gaits, or unsteady locomotion, although such occurrences are frequent in the daily life of animals.

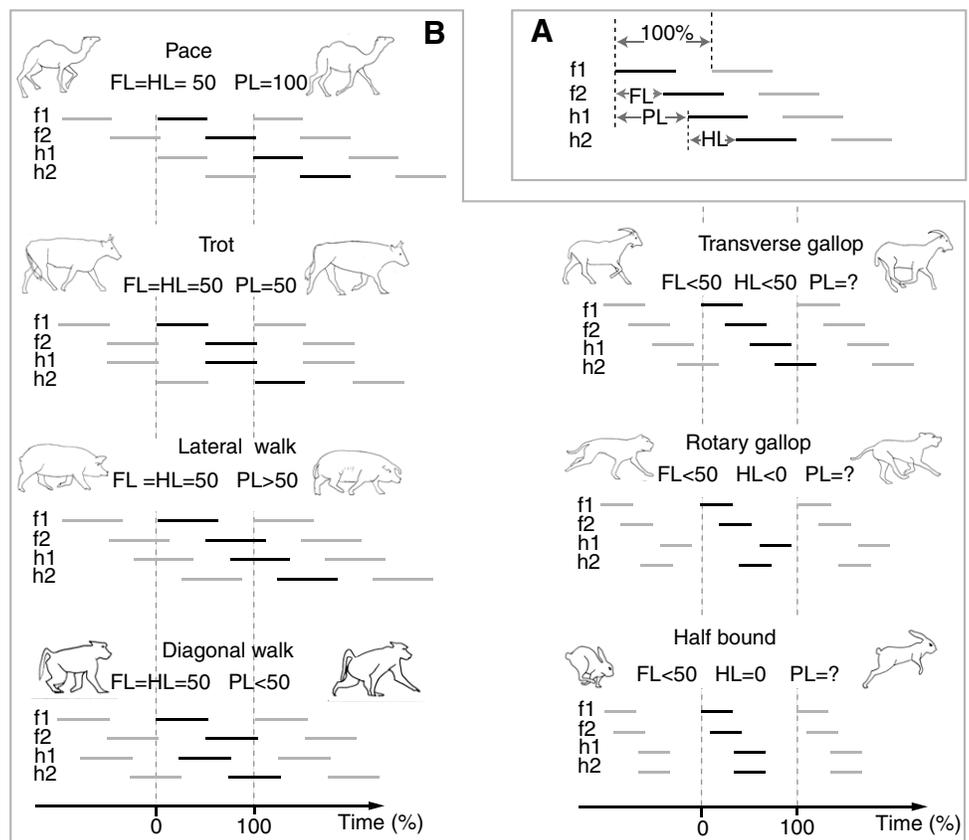
Recently another framework to classify gait was proposed, based not on a unit of time, but instead on a succession of definite actions in time and space (Abourachid, 2003). Abourachid's framework, called the anteroposterior sequence (APS), is defined as the association of the consecutive cycles of the two forelimbs followed by the consecutive cycles of the two hindlimbs. The APS is based on generally well-accepted assumptions: (1) two morphologically similar limbs, associated in the two pairs (fore and hind pairs), work together (Cartmill et al., 2002; Hildebrand, 1965) under the control of central pattern generators (CPG) (Grillner et al., 2000; Orsal et al., 1990; Pearson, 1976; Viala and Vidal, 1978) and (2) during forward locomotion, the forelimbs reach the obstacle first. CPG activation is initiated by an activity of the brainstem locomotor system. Thus, at least for locomotor initiation, there is a rostrocaudal activation of the spinal network (Grillner et al., 2000).

This framework suggests a common basic pattern of movement for all gaits: coordinated movements of forefeet, coordinated movements of hindfeet and a relationship between these two pairs. In contrast to stride-based analysis, the advantage of the APS approach is that one can characterize all limb coordination, irrespective of the steadiness of the locomotion, because the analysis is not constrained by stride duration. Three temporal parameters, which are slightly

different from those Hildebrand proposed for symmetrical gaits, are now sufficient to identify all quadruped gaits, symmetrical as well as asymmetrical (Fig. 1). These parameters are: (1) the fore lag (FL), defined as the time lag between the two forefeet footfalls, which measures temporal coordination within the fore pair, (2) the hind lag (HL), defined as the time lag between the hindfeet footfalls, which measures temporal coordination within the hind pair, and (3) the pair lag (PL), defined as the time lag between two ipsilateral feet footfalls, which measures temporal coordination within the two pairs. The symmetrical gaits have both footfalls in each pair evenly spaced in time, and therefore $FL=HL=50\%$. The distinctions between the symmetrical gaits (walks, trot and pace) arise from differences in coordination between the two limb pairs, which can be seen in different PL values. Asymmetrical gaits occur when FL and HL deviate from 50%, and each asymmetrical gait can be identified according to the nature and the magnitude of the deviation.

As the APS can identify all typical steady gaits using three time parameters, we assumed in this study that it could also be used to study non-steady locomotion, particularly to quantify the transition between symmetrical and asymmetrical gaits. Furthermore, during locomotion, movements are coordinated not only in time but also in space, so we assumed that the three time parameters could be associated with three analogous spatial

Fig. 1. Identification of the typical gaits (modified from Abourachid, 2003). (A) On gait diagrams, each line represents a foot: (f1, 1-fore; f2, 2-fore; h1, 1-hind; h2, 2-hind). The mark length represents the time the foot is on the ground. The anteroposterior sequence (APS) begins with the movements of the pair of forelimbs followed by the movements of the pair of hindlimbs. In the APS framework, three parameters, FL, HL and PL, are used to identify the gaits. Fore lag (FL) is the time lag between the touch-down of the forelimbs. Hind lag (HL) is the time lag between the touch-down of the hindlimbs. Pair lag (PL) is the time lag between the touch-down of the first forefoot (f1) and the ipsilateral hindfoot (h1). The time lags are expressed as a percentage of the duration of the first forefoot cycle (from one touch-down to the next). (B) Seven typical gaits are shown. In each gait diagram, three APSs are presented: the first and third in grey and the second in black. In symmetrical gaits, $FL=HL=50$, and the PL value is used to identify the different gaits. In asymmetrical gaits, it is the FL and HL values that are used to identify the gaits. The values shown are for typical gaits; actual values may vary. The animals shown are examples of species that naturally use the gait.



parameters. We tested whether or not these parameters are sufficient to quantify the spatiotemporal features of a transition between symmetrical and asymmetrical coordination. We examined variations in temporal and spatial parameters, and the relationships between these parameters in dogs and cats to test the validity of the APS method in different species.

Materials and methods

Animals

Five dogs (*Canis familiaris* L.) of similar size (withers height=0.50±0.05 m, body mass=25±5 kg): two Labrador retrievers, one boxer, one bearded collie and one German shepherd-like dog, and five domestic cats (*Felis catus* L.) (withers height=0.25±0.05 m; body mass=5±0.75 kg) were filmed.

White lines spaced 0.10 m apart were drawn perpendicular to the axis of a 10 m runway for dogs and an 8 m runway for cats. An obstacle was placed in the middle of the runway. Its height was adjusted in order to induce a break in interlimb coordination but not a powerful jump (30 cm high for dogs, 19 cm for cats). The dogs were led on a leash. They approached the obstacle using a slow gait, walking or trotting, did a small jump over the obstacle, breaking down the symmetrical coordination. Then they returned to a walk or a trot to leave. The cats moved freely and were encouraged with food to move on the runway. Each animal did 10 trials. The animals were filmed with a high-speed video recorder (Redlake® Motion scope1000sPCI, Tucson, AZ, USA) at 125 Hz during the whole progression. The camera was placed at obstacle level, 5 m perpendicular to the runway. Parallax deformations were corrected using the lines on the runway.

Data analysis

The records were analysed using Zoomplayer (Zoomplayer v4.03, 2000-2004 Inmatrix.com). We did not use the same terminology as Hildebrand (Hildebrand, 1965), in which the trailing forelimb is the forelimb that touches the ground first, and the leading forelimb is the one that touches the ground second but is the leader in space. This terminology may cause confusion between trailing or leading positions in space and time. Similarly, the right-left designation is not appropriate because of the lateralisation of asymmetrical gaits. Instead, we used a 1-2 designation for the sides of the animals. Thus, the 1-forelimb (f1), which is the reference limb, is defined as the first

to cross the obstacle and the 2-forelimb (f2) is the other one. Hindlimb designation, irrespective of footfall order, is dependent on forelimb designation. Therefore, the 1-hindlimb (h1) is ipsilateral to the 1-forelimb (f1) and the 2-hindlimb (h2) is ipsilateral to the 2-forelimb (f2). In this study, the jump is the only time in the trial when animals used an asymmetrical gait, so we used the jump sequence to find the reference limb. The times of footfall and of take-off of each limb were noted with a precision of 0.008 s. The distance between each footprint and the obstacle were noted with a precision of 0.05 m, with negative distances before the obstacle and positive distances after.

The data were shown graphically on classical gait diagrams (Marey, 1873; Vincent and Goiffon, 1779) and track diagrams (Fig. 2), with four superimposed lines representing the four limbs. In the APS framework, the gait diagram was modified so that two upper lines represent the forelimbs, and two bottom

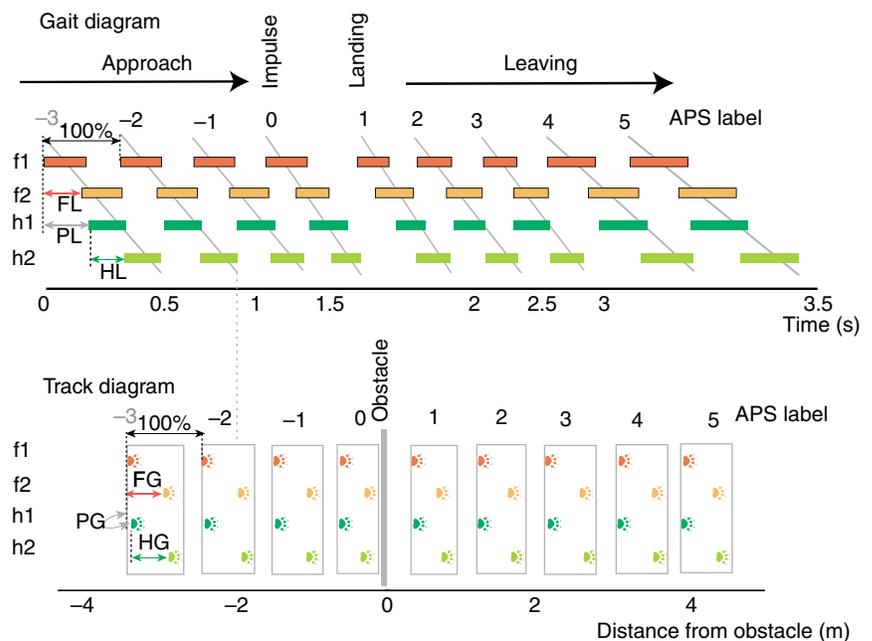


Fig. 2. Methods. Gait diagram: the x axis shows time in s. Horizontal bars (orange for fore pair and green for hind pair) represent the time each foot is on the ground (f1, 1-fore; f2, 2-fore; h1, 1-hind; h2, 2-hind). Each anteroposterior sequence (APS) is identified by a grey arrow, and is labelled from -3 to -1 for approach, 0 for impulse, 1 for landing and 2-5 for leaving. Track diagram: The x axis shows spatial position (m) and the dot paw prints represent the places where the feet were put down. Each APS is outlined in grey and labelled from -3 to 5, similar to the trial gait diagram. The places are measured as their distance to the obstacle (0), negatively before, and positively after the obstacle. For each APS of the trial, as was shown for the first APS, the time lag between touch-down of the two forefeet (fore lag, FL), the time lag between touch-down of the two hindfeet (hind lag, HL) and the time lag between the touch-down of the two trailing feet (pair lag, PL) were noted and expressed as a percentage of the time lag between two successive touch-downs of the 1-forefoot. Similarly, as shown on the track diagram, the distance between the positions of the two forefeet (fore gap, FG), between the positions of the two hindfeet (hind gap, HG), and between the places of the two 1-feet (pair gap, PG) were noted, and expressed as a percentage of the distance between two successive positions of the 1-forefoot. When a 2-hindfoot was placed before the 1-forefoot, the distance was noted as a negative value.

lines represent the hindlimbs. For both forelimbs and hindlimbs, the upper line represents the 1-limb. This is not the usual order, which is, from top to bottom, left hindlimb, left forelimb, right forelimb, and right hindlimb (Hildebrand, 1966). On the gait diagram, the x axis is time and the stance phase, when the foot is on the ground, is marked. On the track diagram, the x axis is distance and the place where the foot was put down is marked. Therefore, each trial was analysed using both its gait diagram (temporal aspects of the movement) and its track diagram (spatial aspects of the movement). After the identification of anteroposterior sequences (APSs) from the diagrams, the APSs were labelled. The APS just before the obstacle was labelled 0. The APSs were labelled in decreasing order from the obstacle to the beginning of the trial (from 0 to -4), whereas the APSs after the obstacle were labelled in increasing order (from 1 to 5). In each APS, the following time and space parameters were calculated. The time parameters, as previously defined, were: (1) the fore lag (FL), (2) the hind lag (HL) and (3) the pair lag (PL). By analogy with time parameters, the space parameters were: (1) the fore gap (FG), defined as the gap between the placement of the two forefeet, which measures spatial coordination within the fore pair (2) the hind gap (HG), defined as the gap between the placement of the two hindfeet, which measures spatial coordination within the hind pair, and (3) the pair gap (PG), defined as the gap between the placement of the two trailing feet, which measures spatial coordination between the two pairs. To normalise the measurements in all trials, each parameter was expressed as a percentage of the 1-forelimb cycle duration for the lags and stride length for the gaps. The mean values of these parameters were calculated from all trials and plotted vs APS number. All data were analysed with SAS software. The significant threshold of tests was fixed at 0.05. Variance equality of data was estimated using the F -test and if variance was equal, data were analysed using Student's t -test.

Results

We first observed the temporal and spatial parameters during the whole exercise to identify phases in the locomotion that were consistently observed in each trial (see below, 'Gait and track diagrams'). Then, we quantified the movements for each phase using the time parameters, and we observed a relationship between time and space coordination using the space parameters.

Trials with the same pattern of locomotion were used for statistical analysis (27 trials for dogs, 16 trials for cats). Other trials showed atypical patterns, with additional or fewer footfalls. These trials were rare (four trials for dogs and two for cats) and were not used for APS statistical treatment, but could be analysed qualitatively. The shortest trials, with fewer than six APSs, were discarded.

Gait and track diagrams

In each species, four phases were identified: approach, impulse, landing and leaving. During the approach, from APS

-4 until -1, the animal moved toward the obstacle. The impulse was APS 0, just before the obstacle, during which the animals began the jump. The landing was APS1, just after the obstacle. The leaving phase was APS2 and up, when the animal moved away. Cat trials (6 APSs) were shorter than dog trials (10 APSs).

In three dog trials, the trailing hindfoot was not put down during the landing phase (APS1), but was put down early in the first leaving APS (APS2). The other footfalls were not affected. In one dog and in one cat trial, the impulse (APS0) was similar to an approach but the trailing hindfoot was put down one time more at the end of the stance of the leading hindfoot, close to the obstacle. The other footfalls and the other APSs were not affected. In one dog and two cat trials, the animal changed its trailing feet during the jump, while no other differences were observed during the trial. These trials were not used for statistical calculations.

Time parameters

Fore lag (FL) and hind lag (HL)

Fig. 3 shows that during the approach phase, FL and HL for dogs and cats remained constant (FL=51±3% and HL=49±6% for dogs, and FL=50±4% and HL=52±7% for cats; means ± s.e.m., $P>0.05$). Thus, the movements of the paired limbs alternated and the animals used a symmetrical gait.

During the impulse phase, FL and HL were less than 50% ($P<0.05$). This meant that the footfalls of the limbs within each pair tended to synchronise, and therefore the APS was asymmetric. The HL was less than the FL in both dogs and cats (HL=25±10% for dogs and 26±11% for cats; FL=34±5% for dogs and 35±5% for cats; $P\leq 0.05$), meaning that hindlimbs were more synchronous than forelimbs.

During the landing phase, FL was the same as during impulse, whereas HL increased, resulting in fore and hind limbs with the same coordination (FL=31±11% for dogs and 31±11% for cats; HL=35±12% for dogs and 33±14% for cats).

During the leaving phase, FL and HL returned to the values of symmetrical gaits (50%). For dogs, the APS was symmetrical from APS2 onward (FL=49±4% and HL=50±6%), whereas for cats in APS2, FL was less than 50% (44±5%) and HL was more than 50% (59±11%). For cats, the first symmetrical APS after the obstacle was APS3 (50±2% and 54±5%).

Pair lag (PL)

During the approach phase, PL remained constant in both dogs and cats (PL=63±12% for dogs and PL=66±10% for cats). However, the large variability (STD) reflected the diversity of the symmetrical gait (from lateral walk to trot) used by the animals, depending on the initial gait. There was no change from one gait to another during the approach phase.

During the impulse phase, PL decreased to 50±7% for dogs and 51±7% for cats ($P<0.05$), indicating that the movements of the two pairs became closer in time. The variability was less than during the approach phase.

During the landing phase, PL increased (64±9% for dogs and 62±10% for cats) and the variability made it impossible to distinguish it from the next sequence PL.

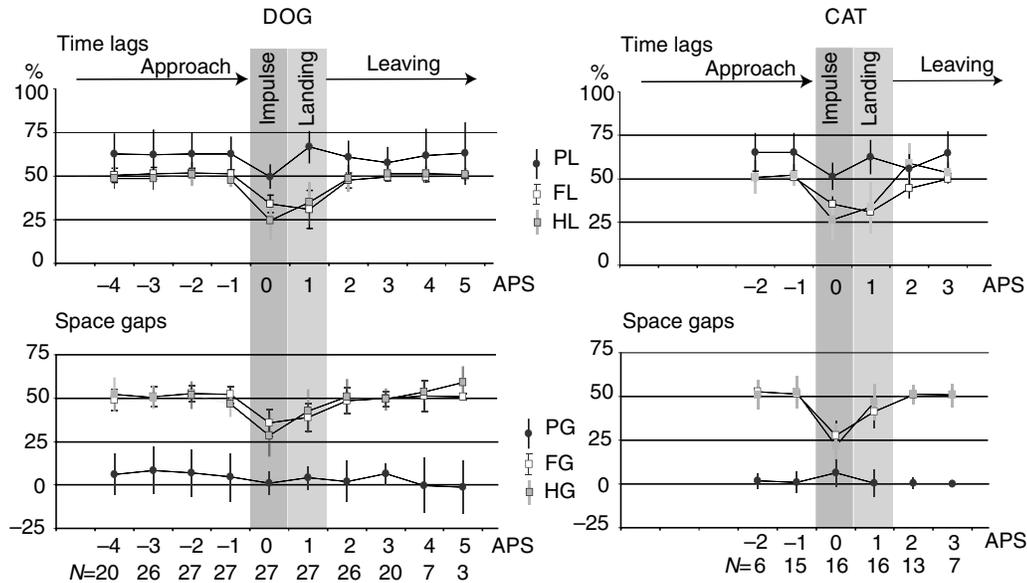


Fig. 3. Time lags and space gaps in dogs and cats. The vertical (y) axis represents percentage of the 1-forefoot cycle duration (Time) or stride length (Space). The horizontal (x) axis represents successive sequences of the series: from -4 to -1: approach phase, 0: impulse phase; 1: landing phase; from 2 to 5, leaving phase. The symbols represent the mean value of the parameters pair lag (PL), fore lag (FL) and hind lag (HL) for time, and pair gap (PG), fore gap (FG) and hind gap (HG) for space. Values are means \pm s.e.m., N =number of trials for each sequence.

During the leaving phase, PL ($60\pm 10\%$ for dogs and cats) was similar to that during the approach phase, indicating a return to a walk or a trot.

Space parameters

Fore gap (FG) and hind gap (HG)

Fig. 3 also shows that during the approach phase, FG and HG remained constant and did not differ from 50%, meaning that within each pair, one foot was put down in the middle of the other foot's stride (FG= $51\pm 5\%$ and HG= $50\pm 8\%$ for dogs; FG= $52\pm 6\%$ and HG= $52\pm 8\%$ for cats; $P>0.05$).

During the impulse phase, FG and HG decreased, indicating that for each pair, the feet were put down closer to each other (FG= $34\pm 8\%$ and HG= $28\pm 12\%$ for dogs; FG= $28\pm 8\%$ and HG= $22\pm 12\%$ for cats). In dogs, FG was greater than HG, indicating that the hindfeet were closer to each other than the forefeet. The difference between the pairs was not significant in cats.

During the landing phase, in dogs FG did not increase significantly ($37\pm 8\%$) compared to the impulse, whereas in cats it increased ($41\pm 9\%$). HG increased significantly ($41\pm 12\%$ for dogs and $47\pm 10\%$ for cats) so that for landing, both FG and HG were not different in each species.

During the leaving phase, FG and HG values indicated that the feet were regularly spaced within each pair (FG= $49\pm 5\%$ and HG= $51\pm 8\%$ for dogs, FG= $52\pm 7\%$ and HG= $52\pm 6\%$ for cats).

The lags and gaps within the pairs (FL-FG and HL-HG) were similar for all the APSs for dog data ($P<0.01$). For cats, the pattern of increases and decreases was the same, but the values were different during the landing phase, the gaps being larger than the lags.

Pair gap (PG)

During all trials, the mean PG remained stable near 0% ($2.7\pm 10.8\%$ for dogs and $1.9\pm 5.9\%$ for cats), meaning that the

ipsilateral feet were placed at almost the same place. However, for dogs, the variability was larger during the approach and the leaving phases than for impulse and landing phases, meaning that during the impulse and landing phases, the feet positions were more precise. For cats, the variability was lower than for dogs.

Discussion

The APS method allowed us to quantify interlimb coordination during the symmetrical and asymmetrical phases and the transition between them in both dogs and cats. It showed that space and time parameters reflected similar coordination patterns in different species. Are these results in agreement with previous data on biomechanics or the motor control of interlimb coordination?

Methodological considerations

Normalisation of measurements

We needed to normalise the measurements to compare the motions of the four feet and to compare the APSs. We chose to normalise our measurements to the distance and time corresponding to the cycle of one foot. Another possibility would have been to normalise using the cycle of one forelimb as the reference for the forelimbs, and using the cycle of one hindlimb as the reference for the hindlimbs. However, we then would have had the unsatisfactory situation of having different references in time and space for two parts of one animal. The choice of one limb cycle as a unit event, irrespective of the limb, has repercussions for calculations, particularly during transition phases when the cycle duration and cycle length of the four feet are not identical. If the cycle duration (length) of the chosen limb is larger this will minimise the time lags (gaps), and *vice versa*.

Unlike conventional analyses in which stride duration is the time reference, and the locomotor sequence is split into strides,

the choice of one limb cycle as a unit event for the purposes of normalisation only does not mean that the movements of the other feet have to happen during this cycle.

Coherence of results obtained using the APS method

Symmetrical sequences

The approach phase and leaving phase presented the same coordination patterns and can be discussed together. The three time parameters of FL, HL and PL allowed us to identify the gaits (Abourachid, 2003). When FL and HL equalled 50%, this was a measure of strictly alternating movements of paired limbs, typical of symmetrical gait (Hildebrand, 1965). This is in accordance with the strict alternation of the CPG that occurs during slow locomotion (Grillner et al., 2000). The pair lag quantifies the coordination between the two pair movements and indicates the type of symmetrical gait (Fig. 1). Dogs and cats used a lateral walk, identified by a mean PL around 60%. PL variability is high (10%), higher than the variability of FL and HL. No specific symmetrical gait was imposed during the experiment, and dogs and cats used either a trot (PL=50%) or a lateral walk (PL>55%), which explains the variability of PL. In both species, FG and HG indicate that during symmetrical gaits the distance between the positions of the two forefeet and the distance between the positions of the two hindfeet are the same, and equal half the distance between the two successive positions of one forefoot. In symmetrical gaits, the FL, FG, HL and HG were the same, showing that these parameters reflected the link between the temporal and spatial inter-limb coordination.

Dogs and cats put their hindfeet close to the place where their ipsilateral forefeet were placed (PG=5% for dogs, PG=0.5% for cats). Dogs put down their hindfeet in front of their forefeet, bypassing the forefeet. We also observed a concomitant slight lateral bending of the back. Cats put down their hindfeet and forefeet at almost the same place without observable lateral bending of the back. This result suggests that PG could be related to the back's role during locomotion.

Asymmetrical impulse sequence

During the impulse phase, FL, FG, HL and HG were less than 50%, showing that the movements in the pair were no longer strictly alternating and were more synchronised than during the approach phase. The footfalls of the hind pair occurred closer, more in-phase than the footfalls of the forelimbs, and the hindfeet were positioned closer than the forefeet. The same pattern was reported in dogs (Alexander, 1974) and in horses (Leach et al., 1984). The decrease in PL arose from an increase in the swing phase during the 'parabolic' jump, which increased the cycle duration (100%). The PG remained constant because the stride length (100%) was measured on the ground and did not take into account the parabolic trajectory of the animal. Consequently, the jump APS is characterised by an increase in the impulse in the vertical direction only.

Asymmetrical landing sequence

During the landing phase, HL increased compared to

impulse phase HL, so that the landing phase HL value became very slightly larger than the FL value. FL remained constant between the impulse and landing phases. The same variations were observed for HG and FG, indicating a coherent relationship between time and space measurements. The same kind of timing pattern can be seen in horses, where the hindlimbs are less in-phase than during the impulse phase (Schamhardt et al., 1993).

Transition phases are quantifiable only using the APS method

The transition between symmetrical and asymmetrical sequences was observed when the animal changed from the symmetrical approach to the asymmetrical impulse, and from the asymmetrical landing to the symmetrical leaving. The symmetrical–asymmetrical transition (approach–impulse) was achieved by a decrease in FL and HL, indicating a change from the strictly alternating pattern of limb pairs characteristic of symmetrical gait to a more in-phase coordination within each pair. This pattern has already been described in the general control strategy for vertebrate locomotion (Grillner et al., 2000). Increasing stimulation of the brainstem locomotor centre induced a change in the pattern of coordination between strict alternating within each pair, as in symmetrical gaits, to an approximate in-phase coordination of the pairs, as in asymmetrical gaits. The transition between asymmetrical and symmetrical sequences (landing–leaving) was also achieved in one sequence (sometimes two in cats) by an increase in FL and HL values to 50%, and by a return to an alternating motor pattern. The change in FL and HL is coordinated with similar changes in FG and HG. We found no relationship between the change in PL and the PG, which did not exhibit any special patterns during the transition between asymmetrical and symmetrical sequences. Conventional stride based methods did not permit us to assess the problem of transition between symmetrical and asymmetrical gait. From a methodological point of view, the stride-based method cut the locomotor sequence into strides, defined by the cycle of one reference limb. The four footfalls had to happen during one stride of that limb. It was typically a hind limb (Hildebrand, 1966; Hildebrand, 1977), but sometimes a forelimb (Herbin et al., 2004; Renous et al., 2002). However, in our experiments, with conventional stride-based analysis, the same foot could not be used as a reference for all trials. If a hindlimb (h1 or h2) cycle was chosen as the reference, one footfall was missing when the animal changed from a walk to a trot. If the trailing forelimb (f1) was chosen, there were two leading hind (h2) footfalls during the stride before the obstacle. If the leading forelimb (f2) cycle was chosen, it was more often possible to follow the four footfalls in all strides. The main problems arose then from the interpretation: during the stride containing the jump, the leading forefoot (f2) and the two hindfeet were placed before the obstacle whereas the trailing forefoot (f1) was placed after the obstacle. This meant that the movements grouped together in the stride provided the impulse over the obstacle for three limbs whereas the movement of one limb was in a landing phase. There is no coherent biomechanical interpretation for

this situation. Furthermore, the fore lag was about 75%, highlighting a fore pair that is out of phase, which is not consistent with the motor pattern of interlimb coordination (Grillner et al., 2000).

Particular cases

In a few trials, different patterns occurred during the impulse or the landing sequences, and these were always observed for the hind pair. Either the 1-hindfoot was put down once more before the obstacle or the 1-hindfoot was not put down during the landing sequence. These observations highlight the importance of studying each pair separately.

Methodological terminology

If we take a forelimb cycle as the time reference, or forelimb stride duration as the space reference, instead of the hindlimb reference used by Hildebrand, this makes the definition of either lateral or diagonal walks less intuitive. According to the APS method, a lateral-sequence walk occurs when a forelimb footfall is followed by the contralateral hindlimb footfall, whereas a diagonal walk occurs when the ipsilateral hindlimb follows the reference forelimb. The definitions used for different walks are dependent on the framework, either stride-based or APS. Walks can, however, be easily analysed in the APS context.

Conclusion

The APS framework allowed us to quantify perturbed locomotion. The results obtained with APS were consistent with actual motor patterns and biomechanical interpretations. We showed that the parameters allowed us to link the timing and the spacing of the footfalls, and to quantify the spatiotemporal dimensions of gait in different mammals, such as dogs and cats, and that the results were in accordance with what is known in horses. However, the small differences we observed between dogs and cats can reflect morphological differences. The APS could thus be used to understand the implication of the morphology in interlimb coordination. We confirm that diagonality is not needed for gait description (Abourachid, 2003). The tendency to synchronise diagonal feet during symmetrical gaits is a secondary effect of the inter-pair coordination, i.e. from the interference between two periodic oscillators. Even if diagonality were important for animal stability (Cartmill et al., 2002; Sukhanov, 1966), diagonality is

not the basic coordination pattern of quadrupedal locomotion. The use of diagonal supports during slow motion corresponded to an increase in animal stability. APS seems to reflect the biological functioning of quadrupedal interlimb coordination and it provides a new heuristic framework for the study of tetrapod locomotion.

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