SPEED CONTROL IN ANIMAL LOCOMOTION: TRANSITIONS BETWEEN SYMMETRICAL AND NONSYMMETRICAL GAITS IN THE DOG

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Abstract. Transitions between symmetrical and nonsymmetrical gaits as a speed control mechanism in dog locomotion were investigated. The external locomotion parameters such as swing and stance durations as well as stride length were measured in freely moving animals and were used to determine the spatial and temporal phase shifts between limb movements. The typical transition from trot to gallop and two kinds of gallop-trot transitions are described in detail. Such transitions occur usually in one or two steps and are linked with step length momentary changes within one diagonal pair of limbs. An example of walk to trot transition is also shown. This transition also occurred abruptly in one step and rapid leaps of the phase shift during walk — trot transitions were caused by a momentary decrease of the hindlimb step lengths. Finally, correlation between the external parameters of locomotion and the speed is discussed.

INTRODUCTION

The main goal of most research in the field of animal locomotion is the search for the neural control mechanisms. These investigations fall into several general trends. One of these emphasizes studies in the

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activity of locomotion structures at different levels of the nervous system, frequently using lesion and pharmacological techniques. Results thus obtained are correlated with the activity of single muscles or the whole limb. Another trend involves the investigation of external movement parameters of animal locomotion, for example step cycles with their components, joint angles, forces exerted on the ground etc. Such research is limited to normal animals and covers a broad range of locomotion in various conditions.

Since steady locomotion has already been quite adequately described (e.g., 2, 3, 5), current tendencies involve the study of the influences of what is widely understood as being a disturbance of locomotion and an unstable state, such as that observed during the states of transitions between gaits. This work prefers the latter tendency. Transition between symmetrical gaits, especially walk-trot has been already described in some detail (2, 3, 10). According to most authors, there are smooth phase shifts between movements of the four limbs from at least slow walking through fast trotting (3, 7, 9) and this smoothness renders the transition point from walking to trotting somewhat arbitrary. Little information, however, has appeared about the transition between symmetrical and nonsymmetrical gaits. Roberts (9) maintains that the transition from trotting to galloping concerns legs of a single diagonal pair. A similar view has been advanced by Shik and Orlovsky (10) in their analysis of treadmill locomotion in dogs. Miller et al. (6) have found that in cats the transition is completed within one or two steps. However, such examination did not analyze in detail the temporal and spatial phase shifts between limbs during the transition period. Because this transition is associated with radical changes in the coordination of all limbs without disturbing the rhythm of locomotion, a detailed investigation is called for to account for this phenomena.

METHOD

The experiments, carried out in two phases, were performed on 10 male mongrel dogs of different sizes weighing between 9 and 18 kg. The first phase involved a preliminary training in which the animal was habituated to the experimental situation (especially to the electrode fixation) and was taught to run along the experimental platform. After two weeks of such training the dog was tested in experimental sessions twice a week for three weeks. Each session consisted of 50-150 trials per animal, during which the subjects were required to run along the stationary platform. Each run (trial) was reinforced with food at the ends of the platform. The inter-trial intervals were equal to the duration
of food intake. The pattern of locomotion, the velocity as well as the number of trials were not forced by the experimentators but depended solely on the animal.

The platform, fixed to the floor, consisted of soft wire-netting one meter in width and eight meters in length. The ends of the net were connected to direct current voltage source, so that a linear increasing voltage potential was obtained along the platform.

The electrodes were made of soft copper wires. Four identical electrodes were fixed precisely to the pad of the third digit. The arrangement and dimension of the electrodes were chosen in such a way that they did not disturb the locomotion. The electrodes were coupled to a connector fixed to a neck collar and via wires to the recording system. Signals from the electrodes were recorded on eight-channel tape and ink recorders.

The swing and stance durations, as well as the actual position of the supporting limb with respect to the end of the platform, were recorded for all four limbs. These parameters were used to determine the temporal and spatial phase shifts and other locomotion parameters. In our work, we described the pattern of locomotion by using phase shifts. A temporal phase shift was defined as the time interval between the middle of the stance phases of particular limbs divided by the step cycle. A spatial phase shift was defined as the distance between the support positions of the limbs divided by the stride length of one of the limbs. This method has been described in detail in our previous paper (1).

RESULTS

All ten dogs studied moved with typical walk, trot and transverse gallop patterns (except for three dogs which also used rotatory gallop from time to time). The type of gait used by the animal was not forced by the experimentator, but depended on the temperament and tiredness of the animal as well as the attractiveness of the food and the level of alimentary satiation. It was noted that two anxious, more reactive dogs generally moved slower preferring walk or trot — gallop being rarely used.

During each experimental session it was possible to record 50–150 trials (i.e., 300–1000 steps) at various velocities. The dogs usually preferred gallop at the beginning of the experimental session (the first 10–30 trials), while trot dominated during the last part of the session. In many instances, gallop was observed from the very beginning of the run, i.e., the animal was able to start with gallop. We limited the
Fig. 1. Trot. A: coordination of limb movements (redrawn from an original record, dog No. 3). The first trace is the one-second marker. Other traces show the sequence of swing (low level) and stance (high level) phases of individual limb; RF, right forelimb; LF, left forelimb; LH, left hindlimb; RH, right hindlimb. The amplitude of high level signals corresponds to the distance between support point of the limb and the grounded end of the platform. The calibration mark shows the amplitude of 8 m distance. B: changes of the step length (l) and swing-stance durations with velocity (v) in the forelimb of dog No. 10. C: dependency of stride length (L) and stepping frequency (f) on the size of the animal for the velocity of 2.8 m/s. The values given alongside are the mean limb lengths measured from ground to the hip joint for seven different dogs.
analysis to trot and gallop and the transition between them. These patterns are described using, as the main parameters, the temporal phase shifts between limb movements and the stride length.

Trot. All the dogs trotted at a speed range between 1.2 m/s and 3.0 m/s. An example of a typical record is given in Fig. 1A. An increase in speed caused an increase in the stepping frequency, while the step length changed within a limited range. This increased stepping frequency was connected mainly with the shortening of stance duration. The swing phase decreased slower and in a narrower range. For the fast trot, swing phase duration could even increase, which was caused by a lengthening of the step. The changes of step length influencing stepping frequency caused that the changes of frequency in the velocity were not monotonous, but occurred in the local extremum for the speed required for moderate trot (Fig. 1B). The same character of changes in the locomotive parameters was observed in all examined dogs; for example, in dog No. 10 (Table I) changes in velocity from 1.55 m/s to 2.8 m/s resulted in changes which differed between the fore and hind limbs. Below are the parameters for the fore limbs, while the corresponding changes for the hind limbs are given in brackets:

1. Stance duration from 209 to 161 ms, (177–120);
2. Swing duration from 244 to 220 ms, (279–250);
3. Stepping frequency from 2.21 to 2.60 Hz, (2.2–2.6);
4. Stride length from 0.7 to 1.04 m, (0.68–1.03);
5. Step length (amplitude of limb movement) from 0.32 to 0.44 m, (0.24–0.34).

For the same speed of locomotion, the stance phase depended on step length, which was correlated with limb length and was longer for the longer-limbed animals (Fig. 1C). It should be mentioned that the duration of stance for the hind limb was on an average about 10–20% shorter than that for the fore limbs in the whole range of speed. This is a consequence of the smaller amplitude of the hind limb movements in comparison with that of the fore limbs.

The temporal and spatial phase shifts between limbs within the same girdle were approximately equal to 0.5 of a cycle (Table I), which is obvious in symmetrical gaits. Temporal phase shifts between diagonal limbs in all dogs were almost zero and never exceeded the value of 0.1 of a cycle, while the spatial phase shifts for these limbs were 0.5 for velocities in which did not appear the unsupported phase. The presence of the flight phase caused a slight decrease of the spatial phase shifts in diagonal limbs with speed.

Gallop. The dogs in our experiments usually galloped at a speed from 2.1 m/s to 5.0 m/s. An example of a typical transverse gallop is
<table>
<thead>
<tr>
<th>Limbs</th>
<th>Fore</th>
<th>Hind</th>
<th>RF/LH</th>
<th>RH/LF</th>
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<th>Left</th>
<th>Stride length (m)</th>
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shown in Fig. 2. This pattern is similar to the gallop of a horse, i.e., after the unsupported phase, the animal’s limbs were placed on the ground in the following sequence: the hind limb, the pair of the diagonal limbs, and then the fore limb. In most cases, the animals galloped with a preference for one of the fore limbs as the leading limb, although sometimes a change of the leading limb from trial to trial was observed.

![Diagram of limb movements coordination](image)

**Fig. 2. Transverse gallop. Example of limb movements coordination redrawn from the original record, dog No. 2. All denotations as in Fig. 1.**

The chosen parameters of the transverse gallop are shown in Table II. For comparison, the changes of velocity from 2.1 to 3.5 m/s in the galloping dog (No. 10, Table II) caused changes in the following parameters (the parameters for the fore limbs are given first, while the corresponding changes for the hind limbs are given in brackets):

1. Stance duration from 160 to 120 ms, (124–102);
2. Swing duration from 249 to 213 ms, (293–235);
3. Stepping frequency from 245 to 3.0 Hz, (2.4–3.0);
4. Stride length from 0.86 to 1.15 m, (0.85–1.14);
5. Step length from 0.34 to 0.41 m, (0.24–0.34).

Changes of velocity were caused by changes of the propulsive force (as in trot) and the bounding angle preceding the unsupported phase. The above changes influenced primarily the lengthening of the stride. Changes of stance durations during an increase of speed in gallop were relatively smaller than in trot because of a further lengthening of step. The velocities of trot and gallop overlapped in a broad range and here the swing and stance durations were almost identical. In the galloping dogs the temporal phase shift between limbs of one diagonal pair was below 0.1 of a cycle, and did not depend on velocity for a broad range
## Table II

Phase parameters of transverse gallop

<table>
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<tr>
<th>Limb</th>
<th>Fore</th>
<th>Hind</th>
<th>RF/LH</th>
<th>RH/LF</th>
<th>Right</th>
<th>Left</th>
<th>Stride length (m)</th>
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of speed, but for the highest speed of gallop, this phase shift could increase even to the value of 0.25. In this case, the phase shift in the hind limbs was approximately zero (half bound gallop). For the second diagonal pair of limbs, the phase shift was within the range of \(-0.30\) to \(-0.45\) of a cycle and could be related to the speed. The sign "\(-\)" means that the fore limb of this pair was placed earlier on the ground than the hind limb.

**Transition from trot to gallop.** The animals were able to change their gait from trot to gallop irrespective of the actual speed of motion. Nevertheless, in most cases the transition was observed at a speed between \(1.5\) m/s and \(2.5\) m/s. In all cases, the transition occurred in one step and the pattern of changes in the limb coordinations was always the same (Fig. 3). The transition began during the diagonal support phase and consisted of changes in the swing duration of the limbs which were unsupported at that time. The swing of the fore limb was shortened, while simultaneously for the hind limb it was elongated. The successive stance durations of these limbs were also changed in the same direction, i.e., the lengthening of the swing phase caused the lengthening of the successive stance phase. After one step, the animal gained in all four limbs, the coordination typical for gallop. The changes of the swing phase duration were equivalent to the step length changes (the length of the fore limb step was shortened and the length of the hind limb step was elongated in comparison with the last step of trot). These changes evoked simultaneously changes of phase shifts between limb movements. Changes of phase shifts during the transition period are shown in Fig. 3. The phase shift between the limbs of only one of the diagonal pairs was changed during trot to gallop transition by a leap from 0 to \(-0.36\) of a cycle. For the second pair of diagonal limbs, slight changes of phase shift were also sometimes observed (to 0.15 of a cycle) during the transition period and in the next steps of the gallop the phase shift decreased below 0.1.

**Transition from gallop to trot.** Transition from gallop to trot was in most cases connected with a decrease of speed. The transition occurred in the opposite way to that in the trot-gallop transition, i.e., the step (swing phase) of fore limb was lengthened, while the step length (swing phase) of hind limb was shortened (Fig. 4). These changes occurred within one or two steps during double supports on the diagonal limbs working synchronously. It is interesting to note that the same diagonal pair of limbs was generally involved during both trot-gallop and gallop-trot transition periods. As a result of these changes, the second pair of diagonal limbs began to move synchronously. The eventual small phase shift was corrected during the next step.
Fig. 3. Trot to gallop transition. Upper part: typical limb movements coordination redrawn from the original record, dog No. 9. Lower part: phase shift changes $\Phi$ from step to step. Indices of $\Phi$ correspond to: one-girdle, (g): diagonal, (d) and lateral, (l) limbs. Other denotations as in Fig. 1.

Two of the dogs also used another manner of gallop to trot transition (Fig. 5). After the diagonal support in gallop, there was a phase of one (fore) limb support followed again by the diagonal support phase. This means that one step of the hind limb was left out and the whole
transition period was performed in two or three steps. This kind of transition was rather rare in transitions from transverse gallop to trot, but dominated in the rotatory gallop to trot transitions.

Fig. 4. Gallop to trot transition. Upper part: example of limb movements coordination, redrawn from the original record, dog No. 7. Lower part: phase shift changes during transition shown above. All denotations as in Fig. 1 and 3.
Fig. 5. Transverse gallop — rotatory gallop — trot transition. Example of limb movements coordination redrawn from the original record, dog No. 2. All denotations as in Fig. 1. This pattern of transition also appeared in the transverse gallop to trot transitions.

**Transitions between walk and trot.** During the last part of each experimental session, the tired dog usually trotted or walked. Walk is the symmetrical gait with a mean phase shift equal to 0.3 for the ipsilateral limbs and −0.2 for the diagonal limbs, while the girdle phase shifts are 0.5 of a cycle. All these phase shifts were independent on the speed changes. Transitions between walk and trot described in the temporal phase shifts were not “smooth”, but occurred also abruptly within one step (Fig. 6). Rapid leaps of the phase shift during walk-trot transitions were caused by a momentary decrease of the stance phase durations in the hind limbs in comparison to the last steps of walk. Such shortening of the stance phase duration was affected by the changes in step length. During transition from walking to trotting the step length was shortened beginning from the hind limbs. It should also be mentioned that there was no observed overlapping of walk and trot velocity ranges.

**DISCUSSION**

Locomotion movements result from the activity of neural mechanisms which allow both the coordination of muscles within one limb as well as between limbs. In the latter case, one can differentiate two basic forms of locomotion, symmetrical and nonsymmetrical. It is assumed that different forms of locomotion in symmetrical gait are the result of one mechanism.
Fig. 6. Gallop — trot — walk transition. All denotations as in Fig. 1 and 3. Note that lateral phase shifts in the transverse gallop are similar to the lateral phase shifts during walk. Trot to walk transition occurs abruptly — in one step, but the range of phase shift changes is smaller in comparison with that in the trot gallop transition.

It appeared interesting to do research on the mechanism responsible for changes during transition between symmetrical and nonsymmetrical forms of locomotion. These studies are confined mainly to the transition from trot to gallop and vice versa. These transitions always begin from the moment of support on one pair of diagonal limbs. The transition mechanism simultaneously acts on the second diagonal pair of limbs which are at this moment in the swing phase. Changes in the coordination of limb movements through the influence on the limbs being in the swing phase are optimal, because, on the one hand, such changes
do not disturb the current support and the equilibrium of the animal, while on the other hand, they do not disrupt the general rhythm of locomotion. Changes in the swing durations are in this case caused by changes in the step length of these limbs as compared with the previous steps. The phase shift changes within a girdle and between girdles are the result of the changes mentioned above.

The structure of changes occurring in the limb movements during the trot-gallop transition, especially in the remaining trot synchronization of one diagonal pair, leads to the conclusion that such a transition in this instance does not disturb the connections influencing trot coordination and partly retaining its mechanisms. The question remains, in what manner do changes in coordination occur in the second pair of limbs. It is known that reciprocal relationships between the limbs of one girdle (intragirdle) are very tight, and that the phase shift between these limbs during symmetrical gaits are exactly half a cycle and have little deviation. The intergirdle coordinations can be controlled by the diagonal and/or lateral programs. These two influences, intragirdle and intergirdle interact with each other and they have a functional character. Miller at al. (6) suggested a dominant influence of homolateral couplings in locomotion. However, in support of out results, it seems reasonable to postulate a dominance of the diagonal connections interacting with a lateral “spatial program”.

The next problem is how to explain changes in the second diagonal pair occurring during the transition period. Changes in the swing durations of these limbs are in opposite directions in comparison with the previous step. Accepting a common diagonal mechanism which influences the intergirdle coordinations and assuming exclusively a temporal control of locomotion, it is difficult to find a straightforward substantiation for these changes. Undoubtedly, there exists a possibility of an independent influence of an extra command on each limb. An additional mechanism activated during the transition period could act on the limbs in the opposite direction and simultaneously disturb the intragirdle interactions. However, respecting the necessity for a rapid change of limb coordination without disturbing the rhythm of locomotion, the command of particular limbs of the diagonal pair must be linked. It appears that changes in limb coordination taking place during the transition between symmetrical and nonsymmetrical forms of locomotion are the result of changes in the step lengths of appropriate limbs (spatial control against a background of unchanged locomotion rhythm (temporal control)). Here, the changes in swing and stance durations are secondary. In this case, changes in the limb coordination would be the result of action from common commands for the diagonal limbs whose influence on the
locomotion structures of the spinal cord could by differentiated depending on the girdle, e.g., (4) and (8). Changes in the limb movements resulting from the above could be controlled by afferent information.

One may also ask why the animal has to change its pattern of locomotion in such a way. This seems to be connected with the speed control mechanisms. The animal's velocity depends on the value and duration of the propulsive forces exerted by its limbs on the ground. During trot, the increase in velocity is caused by the increase of these forces, while the stance durations with their subcomponents decrease. The animal can have an influence on the stance duration by changing its step length, however, the range of these changes is limited during trot. This limitation results from the temporal phase shifts for homolateral limbs which is equal to 0.5 of a cycle which corresponds to the nil spatial phase shift. In other words, the fore position of the hind limb is limited by the hind extremal position of the ipsilateral fore limb. Transition from trot to gallop as well as from trot to walk eliminates this limitation and hence, such transitions are connected with the lengthening of the step. Moreover, transitions from trot to gallop improved the angle of bound in the unsupported phase enabling also the lengthening of the stride.

In conclusion, one can claim that: (i) locomotion is controlled by two programs, temporal and spatial, interacting with each other, (ii) the transition from symmetrical to nonsymmetrical forms of locomotion does not depend upon a complete change of the control program, but is linked with the functional reorganization of those programs affecting trot, (iii) the changes in limb coordination and velocity could be independent, which would attest to the existence of different commands causing such changes.

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