RESEARCH ARTICLE

Gait transitions and modular organization of mammal locomotion

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SUMMARY

Quadrupedal locomotion is the result of complex interactions between biomechanical and neural systems. During steady gaits, both systems are in stable states. When the animal changes its speed, transitions between gaits can occur in which the different coordination parameters are dissociated. Consequently, transitions are the periods where it is possible to detect and identify those parameters involved in the mechanical or neural control of locomotion. We studied interlimb coordination using a sequential method (antero-posterior sequence) to measure the footfall patterns of dogs when accelerating and decelerating from 1.5 m s^{-1} to more than 6 m s^{-1} and back. We obtained 383 transitions between all the symmetrical and asymmetrical gaits used by the dogs. Analysis of the interlimb coordination modifications and of each foot parameter showed that mechanics drive the stance phase whereas coordination is controlled during the swing phase. Furthermore, comparison of the transition patterns between all gaits reveals the modular organization of locomotion: a pectoral module coordinates the two forelimbs, a pelvic module coordinates the two hindlimbs and an axial module coordinates the two pairs of limbs and the trunk motion. The three modules cooperate to give rise to a template of stable interlimb coordination pattern, such as walk, trot or gallop.

INTRODUCTION

Locomotion is the result of the coordinated motion of the parts of an animal that change with speed. Some stable interlimb coordination patterns are typically used by tetrapods. These patterns are identified as gaits and include walk, trot and gallop. From a biomechanical point of view, the different gaits correspond to stable states around the body system's natural dynamic state (Diedrich and Warren, 1998). From a neurophysiological point of view, a gait is considered as a stable mode of coupling of the four limbs resulting from the coordination of the activity of the different limb pattern generators. These pattern generators are located in the spinal cord and are responsible for limb muscle activation and thus control limb movements and coordination (Grillner, 2009). Interlimb coordination pattern analysis is an integrated way to study locomotion given that it concerns the expression of the complex biomechanical and neural interactions. During steady locomotion, the system is in a stable state, and it is difficult to discriminate the mechanical from the neuronal control factors. However, the change from one stable dynamic state to another during gait transition must involve modifications where the different mechanical parameters are dissociated. A gait transition also involves a change in the chronology of limb movements, breaking the coordination controlled by the nervous system (Afelt et al., 1983; Vilensky, 1991) (Nauwelaerts et al., in press). Consequently, transitions are periods where it is possible to detect and identify the parameters involved in the mechanical or neural control of locomotion. If we are able to understand the role of mechanics, i.e. the part driven by the general laws of the physical environment, and the role of motor control, i.e.

the part driven by the structural organization of the body, we hope to be able to contribute to the understanding of the morpho-functional organization of mammalian locomotion.

The cyclic nature of locomotion has been highlighted in all studies on gaits, by studying the events inside one locomotor cycle beginning with an event and ending with the next same event. The chosen event is often the touch-down of a hindfoot, because the succession of the motion of the four feet can be expressed inside its cycle. However, it is not possible to follow the motion of the four feet inside the cycle of only one of them during unsteady locomotion (Abourachid et al., 2007) and another approach has been proposed: analyzing the interlimb coordination as the succession of the motion of the four feet, associating the motion of the two forefeet and the motion of the two hindfeet in an antero-posterior sequence of movements (Abourachid, 2003). In order to be able to make hypotheses on the functioning of mammal locomotion, we analyzed the limb coordination during dog locomotion using a quantification of the coordination patterns of the four limbs that was as exhaustive as possible. The interlimb coordination during steady speed was presented previously (Maes et al., 2008). Here, we analyzed the interlimb coordination during acceleration and deceleration over a large range of speeds, with a special focus on the transitions. We detail the patterns for each limb to better understand its participation to the global coordination. These data allow us to propose a new hypothesis on the modular organization of locomotion and to discuss the processes that may underlie the interplay between the mechanical and neural systems during locomotion in mammals.

MATERIALS AND METHODS

Fifteen Belgian shepherd dogs, *Canis lupus familiaris* L. (3.8 ± 2.2 years of age, 29.8 ± 2.6 kg, 0.56 ± 0.03 m hip height), were filmed at 250 Hz (BASLER A504K, Highland, IL, USA) while moving on a 16 m long trackway. First, dogs were walking slowly (1.5 m s^{-1}), and subsequently accelerated to an intermediate speed of around 3 m s^{-1}. Next, dogs started at an intermediate speed and accelerated up to 5–6 m s^{-1}. Each dog accelerated and decelerated at least five times at each speed. The trials were used when the transition was preceded and followed by at least three sequences of the same gait. All 14 dogs used lateral walk and trot; 13 of them used transverse gallop, 10 used rotary gallop and seven used pace.

For each trial, the position and timing of the footfalls of the four feet was noted. The trials were analyzed using the antero-posterior sequence (APS) method (Abourachid, 2003; Abourachid et al., 2007). Trials were divided in APSs that associate the motion of the two forefeet and the following motion of the two hindfeet. The APSs started with the touchdown of the trailing forefoot (f1) that first touches the ground during the gallop; the contra-lateral forefoot, leading in a gallop, was denoted f2. The h1 hindfoot was on the same side as f1 and touched the ground after the f1. The h2 is ipsilateral to f2 (Fig. 1A; supplementary material Figs S1, S2).

In order to quantify the coordination between the four limbs, we used three coordination parameters: the fore lag (FL), the lag between touchdown of the two forefeet divided by the cycle duration of the first forefoot (D_{f1}); the hind lag (HL), the lag between touchdown of the two hindfeet divided by the cycle duration of the first hindfoot (D_{h1}); and the pair lag (PL), the lag between the touchdown of the first foot of the two pairs divided by the D_{f1}. The HL is different from that defined for steady speeds (Abourachid, 2003) as the cycle duration may be different between forefeet and hindfeet when the speed is changing (Fig. 1B).

In order to get accurate information on the motion of each limb, the following spatio-temporal parameters were calculated for each foot (x): the swing duration (Sw, in s), the period of time when the foot has no with contact the ground; the stance duration (St, in s), the period when the foot touches the ground; the cycle duration (D, in s); the stride length (L, in m), the distance between two successive

placements of the foot; finally, speed (u) was a calculated as the product of the f1 stride length (L_{f1}) multiplied by its cycle duration ($u=L_{f1}/D_{f1}$, in m s^{-1}).

We first used the three lag parameters to identify the gait type. Next, we used the PL, a parameter that discriminates all the gaits (Maes et al., 2008) to identify the APS of transition. For each sequence, we calculated the absolute difference between the PL of a given sequence and the PL of the sequence just before |ΔPL|. For each trial, the sequence with the larger |ΔPL| was labeled APS 0. The subsequent APSs were labeled in increasing order (APS 1, APS 2, APS 3…) and the previous APSs were labeled in decreasing order (APS –1, APS –2, APS –3…) (supplementary material Figs S1, S2).

The mean values and standard deviation of the parameters for each APS across all trials including both accelerations and decelerations were calculated. To test for differences between the different APSs and the individual dogs, a multivariate (M)ANOVA was run in SPSS V.15 with lag, speed, stride length, stride duration, stance duration, swing duration and duty factor as dependent variables for the six APSs before and following the transition. Interaction effects were tested and Bonferroni *post hoc* tests were used to test differences between the different APSs for all types of transition. The results of the *post hoc* tests are illustrated in Figs 1–7.

RESULTS

The MANOVA showed significant effects of the APS (Wilks' lambda=0.006, F=13.3, $P<0.001$), individual (Wilks' lambda=0.018, F=12.1, $P<0.001$) and their interaction (Wilks' lambda=0.001, F=2.08, $P<0.001$). This indicates that gait parameters change depending on the APS and the individual. Moreover, the changes in gait characteristics from one APS to another are dependent on the individual. Below we describe the overall changes in gait characteristics observed at the population level relative to each APS and the transitions studied (Table 1).

Interlimb coordination

Coordination was stable before and after the transition, without significant differences between two successive APSs (Fig. 2). They correspond to the typical steady gaits of the dogs (lateral walk, trot and pace: FL=HL=50 and PL=75, PL=50, and PL=100, respectively;
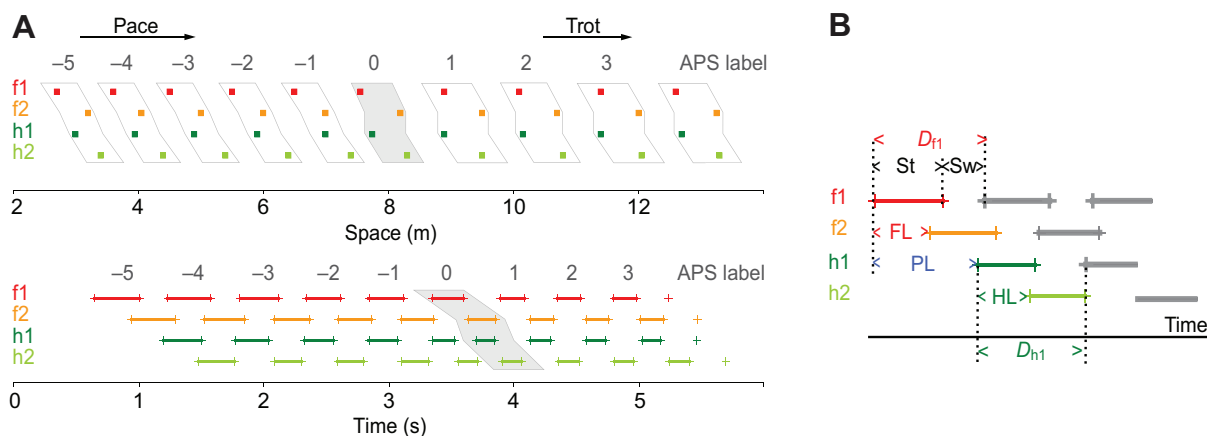

Fig. 1. (A) The position of the feet on the runway and the time at which this occurred were noted and plotted on graphs. The footfalls were associated with an antero-posterior sequence (APS) labeled in decreasing and increasing order before and after the transition (APS 0), respectively. (B) For each APS, the foreleg lag (FL), the hindleg lag (HL) and pair lag (PL) were calculated, as well as the stance phase (St) and the swing phase (Sw) for each foot. The FL was expressed as a fraction of the first forefoot cycle duration (D_{f1}), and the HL as a fraction of the first hindfoot cycle duration (D_{h1}).

Table 1. Summary table describing the distribution of the 383 transitions obtained

Start	End				
	Lateral walk	Pace	Trot	Transverse gallop	Rotary gallop
Lateral walk		**41**	**66**	**0**	**0**
Pace	18		**17**	**3**	**0**
Trot	73	0		**59**	**30**
Transverse gallop	0	1	54		
Rotary gallop	0	0	7		

Data are divided into transitions involving accelerations (bold) and decelerations.

gallop: FL<50, PL>50 and HL<50 for transverse gallop, and HL<0 for rotary gallop) (Abourachid, 2003).

During transition from one symmetrical gait to another, no change in either forelimb or hindlimb coordination was observed (FL and HL=50) except for a small difference for the HL in the pace to trot transition. In contrast, the transitions between trot (symmetrical) and gallop (asymmetrical) gaits involved intra-pair changes: HL and FL decreased, breaking the alternated coordination of symmetrical gaits. The HL decreased one APS before the FL, and it changed more radically to reach the rotary gallop. The transition from gallop to trot followed the inverse pattern except that FL increased at the same time as HL.

In all cases, the PL, measuring the interpair coordination change during the transitions, changed during one, two or three APSs around APS 0.

Thus, the combination of changes in the three parameters (HL, FL and PL) allows us to obtain the different patterns of coordination.

Speed

Dogs used a lateral walk or pace when moving at around $1.5\,\mathrm{m\,s^{-1}}$ (supplementary material Fig. S3). They used pace or trot at around $3\,\mathrm{m\,s^{-1}}$, and transverse gallop or rotary gallop at speeds over $4\,\mathrm{m\,s^{-1}}$. However, the change in coordination involved a more or less gradual change in speed: the speed may change significantly between APSs before the transition (trot to walk), during the transition only (trot to rotary gallop) or both before and during transition (transverse gallop to trot), or even not at all (walk to pace).

Thus, the use of one gait or another corresponds to different speeds but the speed itself is not constrained by the coordination.

Stance duration

The stance durations were longer at lower speeds than at higher speeds (Fig. 3). The stance duration of the forelimbs was usually longer than that of the hindlimbs, except in the walk after a deceleration. As for speed, the decreases and increases of the stance phases were rather gradual even if there were some significant differences between successive APSs during the transitions. There were no differences in the ranges of the changes between the feet, but there may be differences in the timing, with the hindlimb stance increasing one APS before in the trot to walk transition, for instance.

The changes in the stance phases followed the same pattern as the changes in speed.

Swing duration

The swing phase duration was not correlated to speed and there were no significant differences between the swing duration at the beginning and the end of the trials (Fig. 4). In contrast to the stance phase, swing phase duration was generally smaller for the forelimbs than for the hindlimbs. The transitions were marked by an abrupt and punctual change of the swing phases of the hindlimbs in symmetrical transitions to a trot, and a change in one hindlimb (h1) swing in symmetrical–asymmetrical transition. There was no marked change during the transition from walk to pace. There was never a marked change in the swing phase of the first forefoot, even if some small differences between the APSs may have been observed.

All transitions except the walk to pace corresponded to significant punctual changes of the swing phase.

Duty factor/suspension phase

Like the stance phase duration, the duty factor of the forelimbs is larger than that of the hindlimbs (supplementary material Fig. S4). During a lateral walk, both pairs of feet have duty factors greater than 0.5, whereas during a trot or gallop they are smaller than 0.5. During the pace, the fore limb duty factor is greater than 0.5 (pace to trot transition) or close to 0.5 (lateral walk to pace, and pace to lateral walk transition) and the hind limb duty factor is always smaller than 0.5 such that there is a suspension phase when no hind limb touches the ground. There is no suspension phase for the fore limbs. During a transition with a walk, the hind limb crosses the 0.5 limit during the transitions; during the transition to the trot, the fore limb crosses the 0.5 limit at APS−1. The crossing of the 0.5 duty factor border is a unique feature happening during the walk to pace transition.

DISCUSSION
Modular organization of the gaits

Our results show that the lag parameters (FL, HL and PL) that measure the coordination of the motion of the two forelimbs, of the two hindlimbs, and of the forelimb and hindlimb pairs are powerful tools not only to identify gaits but also to describe the transition between them (Fig. 2). Clear patterns were observed: at slow speed during symmetrical gaits the dogs kept strictly alternating movements of the limbs inside each pair, even during the transitions (Fig. 2). When dogs changed from symmetrical to asymmetrical gaits, the limbs of the pairs tended to be more in phase, with the hindlimbs being more engaged in the synchronization than were the forelimbs. To reach a rotary gallop, the coordination of the forelimbs was the same as in a transverse gallop, but the hindlimbs accentuated the change in coordination. As during asymmetrical gaits the forelimbs and hindlimbs do not move the same way, it is likely that each limb pair has its own pattern of coordination, expressed depending on the gait. The difference between the symmetrical gaits derives exclusively from the pattern of coordination between the pairs. Because the pair coordination is also involved in the differences in asymmetrical gaits, this suggests a different mode of coupling between the two
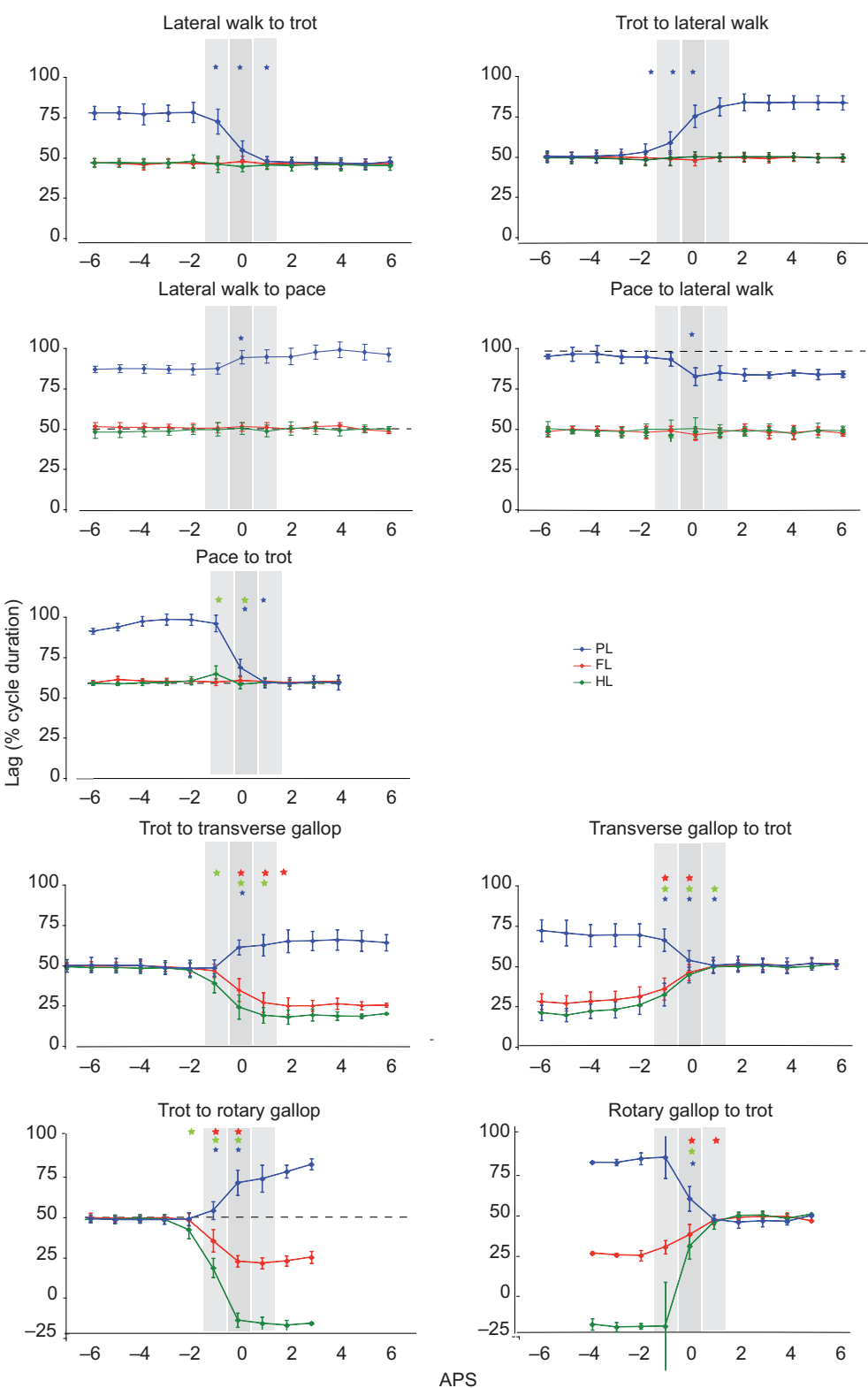
Fig. 2. Variation of the coordination parameters. The sequences were aligned using APS 0 when |ΔPL| was maximal. The transition APSs are indicated in gray. The asterisks indicate a significant difference between the marked APS and the previous APS for the same colored factor.

limb pairs. Thus, the interlimb coordination results from the interaction of the three patterns of coordination: between the two forelimbs, between the two hindlimbs, and between the limb pairs. These three patterns of coordination correspond to the basic morphological components of a dog involved in locomotion: the thoracic appendage, the pelvic appendage and the trunk (Fig. 5A).

The organization of interlimb coordination can be modeled using three structuro-functional modules (Gatesy and Dial, 1996) integrating the local musculoskeletal system and its control (Fig. 5B). The shoulder module integrates the two forelimbs, the pelvic module integrates the two hindlimbs, and the axial module integrates the axis and the axial musculature (Fig. 5A).
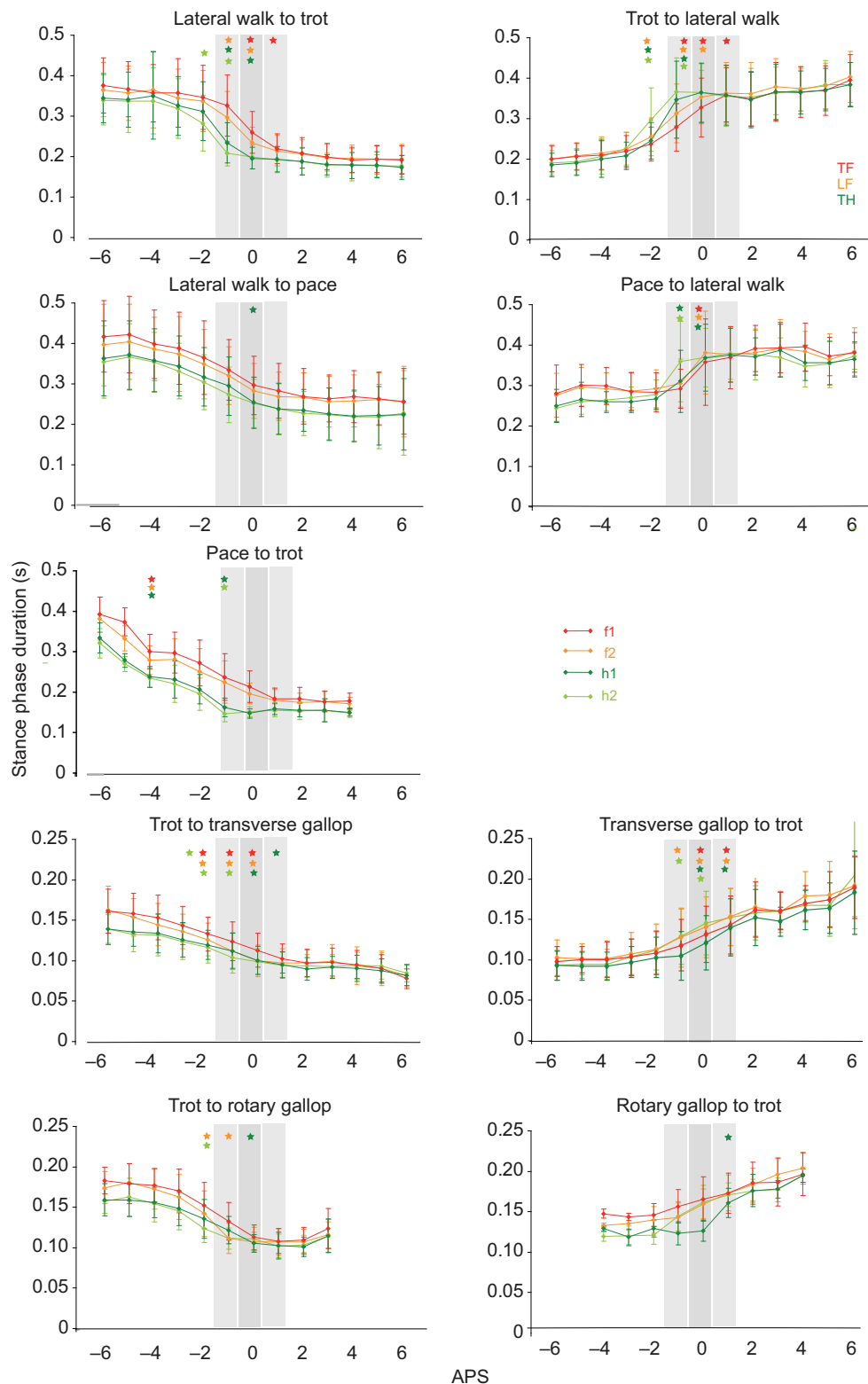
Fig. 3. Variation of the stance duration. The sequences were aligned using APS 0 when |ΔPL| was maximal. The transition APSs are in gray. The asterisks indicate a significant difference between the marked APS and the previous APS for the same colored factor.

The control of the appendage modules could be organized as proposed previously (Grillner, 2009), i.e. by reciprocal interactions between the limb central pattern generators (CPGs). During symmetrical gaits a reciprocal inhibition between the CPGs could coordinate the limbs of the same module and a mutual excitation between the CPGs leads to the synchronization of the two limbs during asymmetrical gaits. However, the synchronization of the limbs measured using neuronal preparations is not achieved during the gallop of a dog, and this may be linked to biomechanical feedback. Grillner proposed that each limb CPG is a part of a system of direct interactions between the four legs (Grillner, 2009). However, our results suggest that
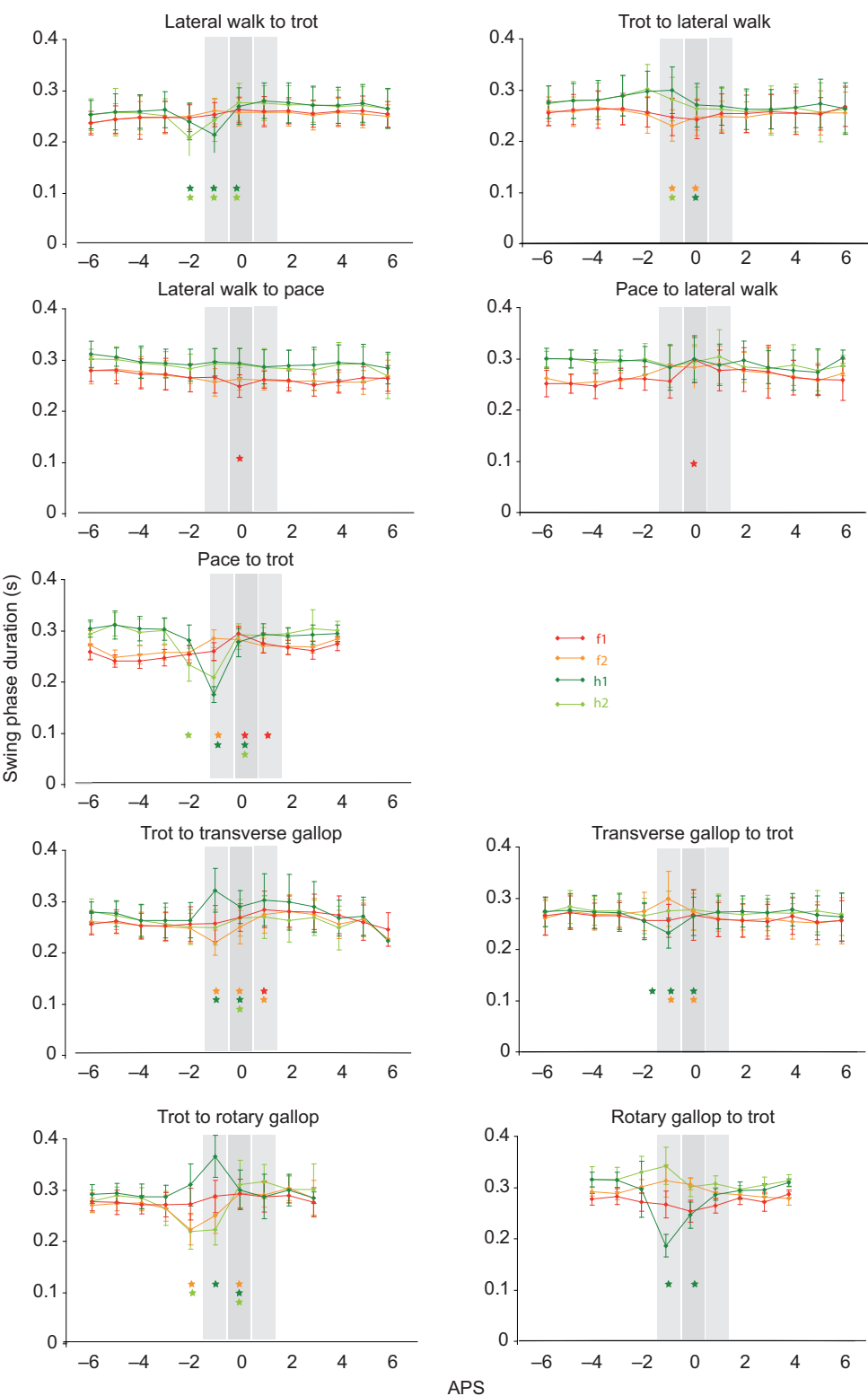
Fig. 4. Variation of the swing duration. The sequences were aligned using APS 0 when |ΔPL| was maximal. The transition APSs are in gray. The asterisks indicate a significant difference between the marked APS and the previous APS for the same colored factor.

the coordination between the forelimbs and hindlimbs is not direct but that the axial module may be implicated in the coordination between the two pairs of limbs. Although the pattern of coordination of the axial musculature in quadrupeds is far less well known than the interlimb coordination, Schilling and Carrier recorded different patterns of muscular activation for each gait: an asymmetrical activation of the muscles on both sides that gives rise to a traveling wave of lateral bending of the back during walking; a symmetrical activation of the muscles that generates a standing wave of lateral bending, as well as a stabilization of the dorso-ventral bending during trot; and a pattern of activation during gallop that is consistent with sagittal extension (Schilling and Carrier, 2010). Futhermore, a metachronal wave of activity of the axial muscles in humans, which is coordinated differently
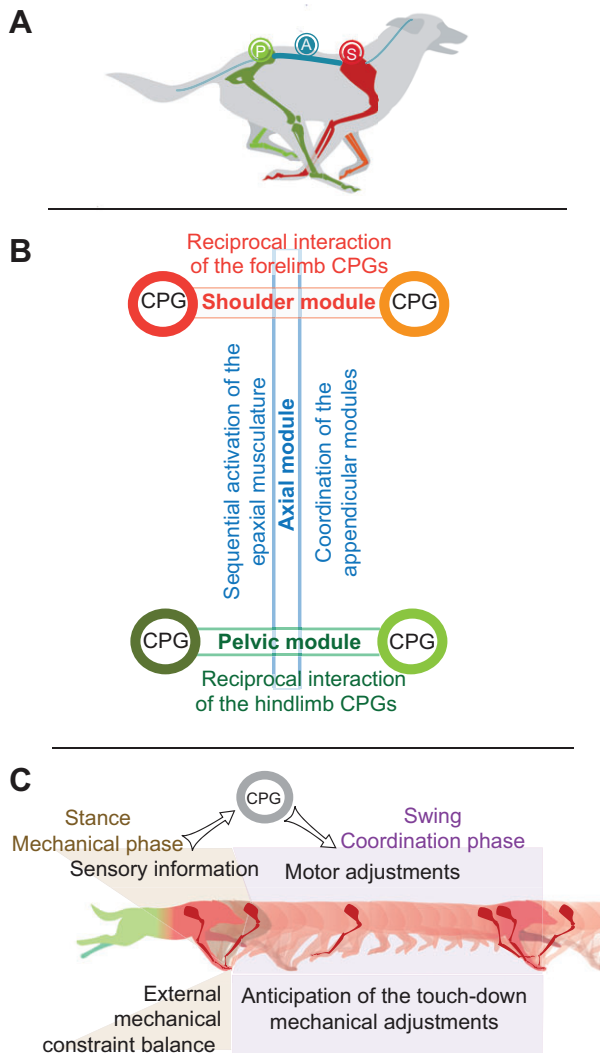
Fig. 5. The modular organization of the locomotor coordination in quadrupeds. (A) Three modules interact to coordinate the movements of the post-cranial musculoskeletal system. The shoulder module (S) coordinates the movements of the forelimbs, the pelvic module (P) coordinates the movements of the hindlimbs and the axial module (A) coordinates the movement of the trunk. **(B)** At the girdle modules, the reciprocal interaction between the central pattern generators (CPGs) coordinates the rhythms of the two limbs. The axial module coordinates the rhythms of the girdle modules. It also coordinates the sequential activation of the axial musculature by a metachronal coupling of the motor command along the spinal cord, generating a wave of muscular contraction. Depending on the coordination of the muscular activity, the command gives rise to lateral bending, sagittal bending and stabilization of the trunk (after Shilling, 2011; de Sèze et al., 2008). **(C)** Each limb CPG coordinates limb motion through the pattern of activation of the limb muscles. During swing, the limb is free of external mechanical constraints and the motor control can adjust the limb kinematics and dynamics (such as swing duration, protraction position and limb stiffness) at touch-down. During stance, mechanical constraints dominate. The limb mechanics have to balance the force exchanges with the ground and are, moreover constrained by the full body dynamics. Consequently, the limb's ability to respond is reduced. Sensory feedback informs the CPGs of the loading state and the position of the limb.

depending on the relative motions of the arms and legs, also suggests the presence of a spinal neuronal network implicated in the coordination between the pairs of limbs (Falgairolle and Cazalets, 2007).

The collaboration between the three modules gives rise to gait templates

During symmetrical gaits, the two girdle modules coordinate alternating rhythms of the limbs; the FL and HL are stable at 50 and the axial module coordinates the activity of the axial musculature. The activation of the axial module likely also corresponds to the coordination between the two girdle modules with a 0.75 phase delay during a lateral walk and a 0.5 out-of-phase delay during trotting. The diagonal walk used by primates corresponds to 0.25 phase delay between the two girdle modules.

True pacing (PL=100) is used by horses (Hildebrand, 1965), dogs (Maes et al., 2008), camelids (Pfau et al., 2011) and primates (Schmitt et al., 2006). Elephants also use a pacing gait with high PL (Hutchinson et al., 2006). In camelids and in elephants, lateral bending is not possible because of the morphology of the trunk (Gambaryan, 1974). Here, we propose that the axial module recruits the musculature for stabilization during pace as well as the in-phase activation of the thoracic and pelvic modules.

During steady gaits the interplay between the three modules does not change. However, the limb CPGs could adjust the motion of the limbs in order to cope with unpredictable evens, such that stability is ensured by limb joint control (Daley et al., 2007) and the plasticity of the system is maintained.

Each limb participates

During a transition (APS−1 to APS2) the stable interlimb coordination is broken and modifications arise in the swing of an individual limb, indicating an individualization of the motion of each limb. Grillner proposed that each limb CPG is subdivided into unit CPGs involved in the pattern of activation of the different limb joints (Grillner, 2009). Thus, the transition could be explained by modification of this intra-limb coordination. Our results show that all transitions occur according to the same pattern: in all cases speed modifications are correlated to stance duration modifications (supplementary material Fig. S3; Fig. 3), with punctual changes in swing duration driving the change in coordination (Figs 2, 4). Swing duration is not correlated with speed as was previously observed for steady speed locomotion (Maes et al., 2008). Different changes in swing duration (Fig. 4) between the anterior and posterior limb pairs (e.g. a decrease of the hindlimb but not the forelimb swing duration as observed in the lateral walk to trot transition) allow changes from one symmetrical gait to another; changes in the diagonal feet swing phases (e.g. an increase of the first hindfoot and a decrease of the second forefoot swing duration as observed in the trot to transverse gallop transition) result in changes from symmetrical to asymmetrical gaits. The same pattern was previously observed for cats, dogs, horses and vervet monkeys (Afelt et al., 1983; Vilensky et al., 1991), suggesting a common pattern of transition for mammals.

Is it possible to infer the mechanical and neuronal interplay from the transition?

During the swing phase when the coordination changes occur, the limb is free from mechanical external constraints and a transition could derive from the adjustment of the motor coordination of the individual limb joints (Fig. 5C). For example, during the lateral walk to trot transition, the successive punctual decrease of one and then the other hindlimb swing phase indicates that in each limb, the interjoint coordination changes. The different synergies between flexor and extensor muscles of the joints could modify

the limb kinematics and/or joint stiffness. This could in turn influence the duration of the swing, the latter inducing the modification of the interlimb coordination and the former a change in the limb configuration at the next touchdown. As the angle of attack at touch-down participates in the dynamic stability of the system (Seyfarth et al., 2003; Hackert et al., 2006, Segers et al., 2007) we speculate that its modification during the transition could also participate in a change toward a new stable state. The force exchanges between the animal and the environment occur when the foot is on the ground (i.e. during the stance phase). The stance phase is correlated with speed and not with the abrupt punctual changes occurring during the transition. Together with the coordination between the pairs, the stance duration enhances stability during slow gaits such as walking (Hildebrand, 1965; Cartmill et al., 2002) or the dynamics of the system during faster gaits allowing, for example, the emergence of a suspension phase. During this phase, the limbs thus have to balance the forces exchanged while being constrained by the whole-body dynamics. During the stance phase, sensory feedback can inform the limb CPGs that control the pattern of activity of the limbs joints about the loading state and the position of the limb (Pearson, 2000; Grillner, 2009). Modifications of the activity pattern during stance can change the forces exchanged and the dynamics of the system without inducing changes in the interlimb coordination. The transition from a lateral walk to a pace can be interpreted in that way. In this case, two stable coordination states are identified, with a significant difference between the PL before and after a transition (Fig. 3). However, no punctual changes are observed in the spatio-temporal gait parameters. Stride length, stance duration, swing duration and duty factor all gradually change with speed. However, the transition between the two gaits is marked by the change in the hindlimb duty factor from more than 0.5 to less than 0.5, which corresponds to the insertion of a suspension phase between the stance phases of the two hindlimbs. The occurrence of a suspension phase is not required (Biknevicius and Reilly, 2006) but can be indicative of a change in the behavior of the center of mass mechanics from vaulting to bouncing mechanics. Consequently, the transition between a walk and a pace can be interpreted as a change in the mechanical behavior of the hindlimbs that is sufficient to induce a transition from a stable locomotor state, the lateral walk, to another one, the pace. Such a mechanical transition could also be used when accelerating, without switching to a trot or a gallop, in the case of alternated symmetrical gaits (Robilliard et al., 2007; Anderson et al., 2012).

Concluding remarks

The very simple and global approach used in this study, the foot-fall pattern, is a powerful tool for studying locomotion in an integrative way. It does not give details that are as accurate as those obtained by more specific approaches, such as biomechanical studies incorporating kinematics and force recordings, or EMGs for studying the specific motor patterns, but it gives a quantification of the result arising from their interaction. This study reveals the basically modular nature of locomotion in mammals. In contrast to other studies on steady locomotion based on a cyclical organization of the interlimb coordination, the sequential APS analysis of the transition shows that the basic post-cranial 'bauplan' – the axis and two pairs of limbs – corresponds to the organization of the locomotor motion so that we can define three locomotor modules that cooperate to give rise to templates of stable patterns of interlimb coordination, the gaits. Inside each module, gradual changes can occur without modification of the overall pattern, as when an animal accelerates without changing its gait. Punctual abrupt changes in one or the other limb swing phase give rise to the change in coordination that could be associated with a new dynamical state. As the modular organization of locomotion allows an explanation of both steady gaits and the transitions in accordance with the organization of motor control and with biomechanics, and because it provides a very intuitive link between the basic morphological bauplan and its function, we are confident in its heuristic value.

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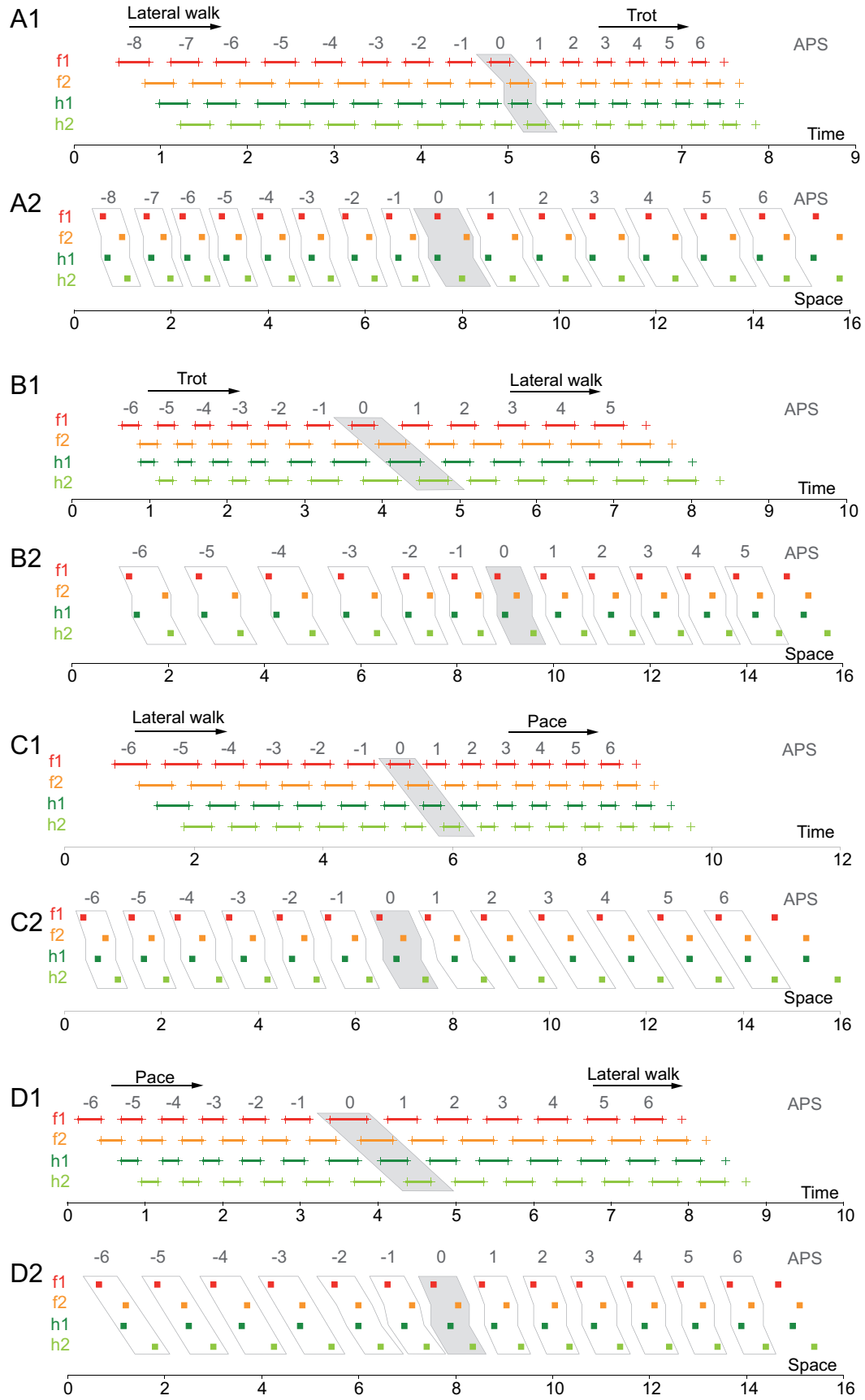
Fig. S1. Gait graphs of the transition between symmetrical gaits. (A) Typical lateral walk to trot trial. (B) Typical trot to lateral walk trial. (C) Typical lateral walk to pace trial. (D) Typical pace to lateral walk trial. 1, time of foot falls; 2, position of the feet; f1, first forefoot; f2, contralateral forefoot; h1, hindfoot on the same side as f1; h2, contralateral hindfoot.
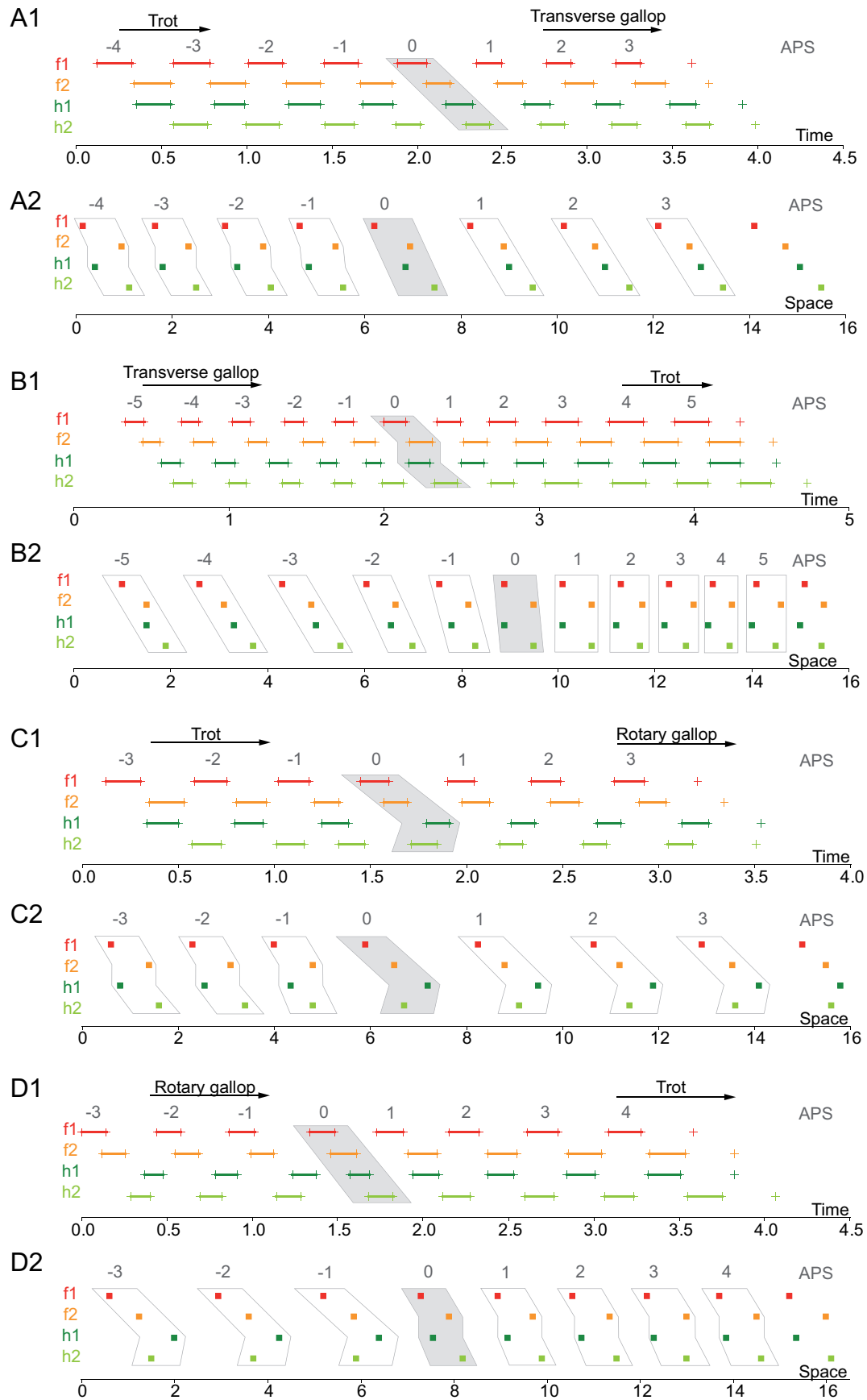
Fig. S2. Gait graphs of the transitions between symmetrical and asymmetrical gaits. (A) Typical trot to transverse gallop trial. (B) Typical transverse gallop to trot trial. (C) Typical trot to rotary gallop trial. (D) Typical rotary gallop to trot trial. 1, time of foot falls; 2, position of the feet; f1, first forefoot; f2, contralateral forefoot; h1, hindfoot on the same side as f1; h2, contralateral hindfoot.
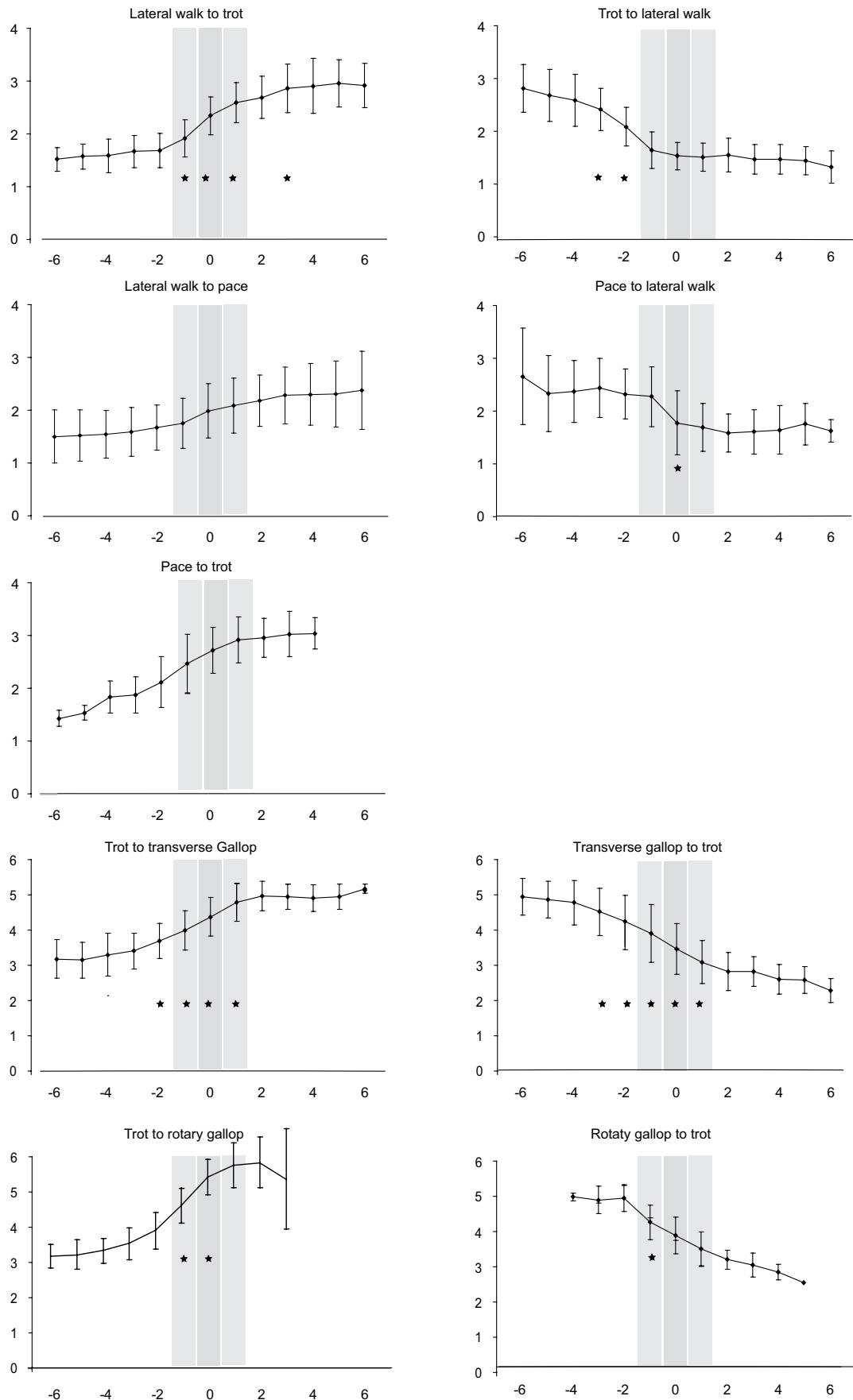
Speed (m/s)

Fig. S3. Variation of speed. The sequences are aligned using APS 0 when |ΔPL| is maximal. The transition APSs are in gray. The asterisks indicate a significant difference between the marked APS and the previous APS.
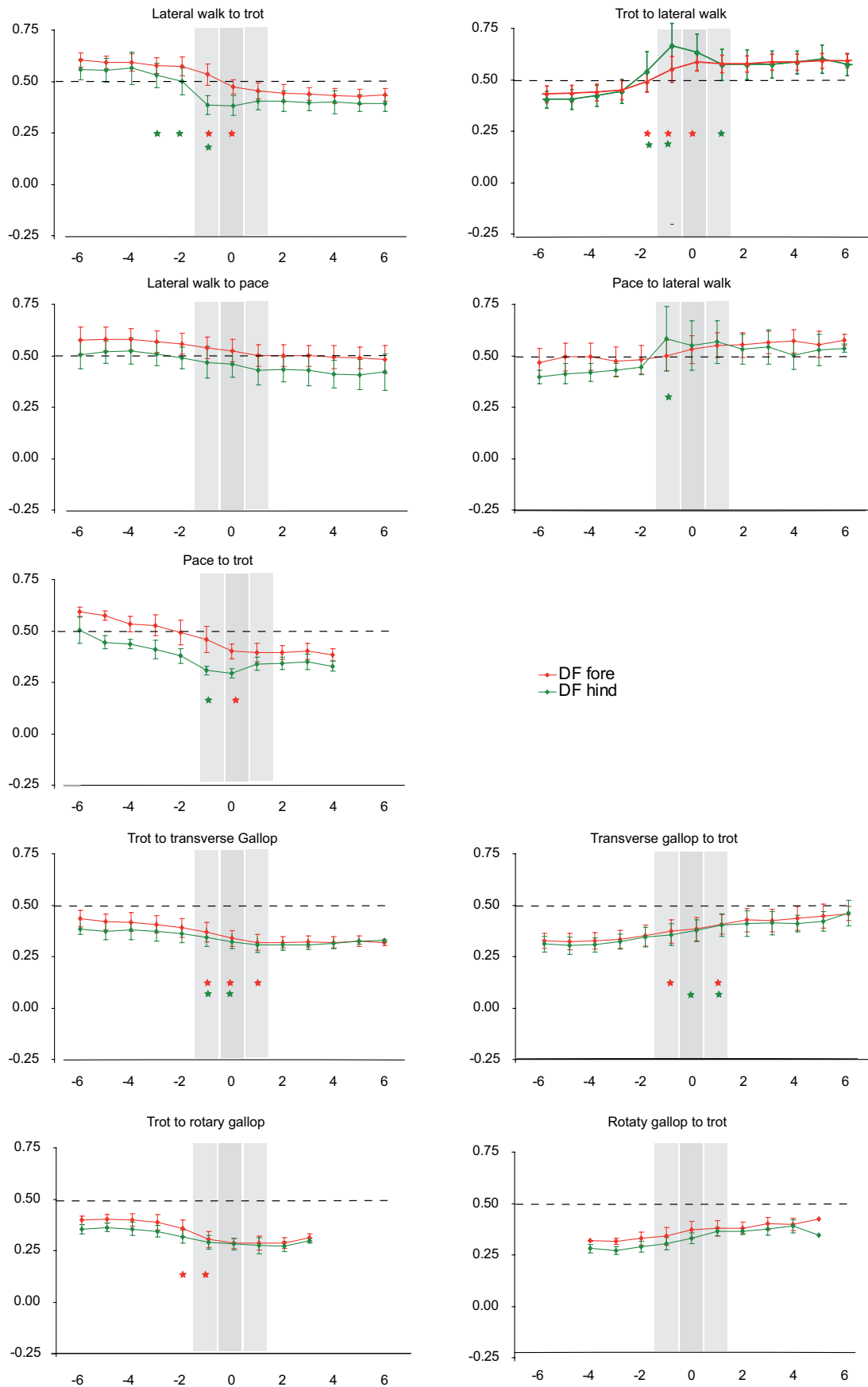
Fig. S4. Variation of duty factor. The sequences are aligned using APS 0 when the |ΔPL| is maximal. The transition APSs are in gray. The asterisks indicate a significant difference between the marked APS and the previous APS for the same colored factor.