Stride to stride variability in joint angle profiles during transitions from trot to canter in horses

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ABSTRACT

Spontaneous transitions from anti-phase to in-phase manual coordination are explained in the Haken-Kelso-Bunz (HKB) model that describes the two preferred states as stable regions that act as attractors in a stability landscape. Switching between states coincides with a temporary loss of stability. Coordination variability is believed to be indicative of such a loss of stability. In this study, the hypothesis was tested that an increase in variability in the angle profiles of the joints responsible for the transition will precede the transition. A full gait analysis of four miniature horses transitioning from trot to canter was performed. Joint angle profiles were determined for the joints of all four limbs and were time-normalised to stride duration. Per horse and per stride, the coefficient of variance was calculated as the mean standard deviation of the joint profile over all trials divided by the mean joint angle × 100. As hypothesised, the most proximal limb joints (hip, scapulothoracic, shoulder) followed the predictions to a large extent. The variability of the hip joint angle of the trailing hind limb showed a peak of variability at stride 0; this was quickly reduced after the transition was completed. The detection of this brief perturbation in the hip joint indicates the importance of this joint in the transition process. The hip joint is related to the movements of the limb, pelvis and back, which is one of the main differences between symmetrical and asymmetrical gaits.

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Introduction

It has been a long tradition within the field of animal biomechanics to study different types of gaits, defined as a sequence of limb oscillations with a specific interlimb coordination pattern. Historically, research has shifted from the classification of gaits (Hildebrand, 1965, 1968; Biknevicius and Reilly, 2006; Robilliard et al., 2007; Starke et al., 2009), through the explanation of why gaits exist (Hoyt and Taylor, 1981; Farley and Taylor, 1991; Minetti et al., 1994) to how transitions between gaits occur (Vilensky et al., 1991; Maes, 2009; Nauwelaerts et al., 2013). One approach to the study of transitions is the dynamic systems perspective based on an interpretation of the Haken–Kelso–Bunz (HKB) model (Haken et al., 1985), where changes in coordination patterns are explained by self-organisation principles (Peper and Beek, 1998). The HKB model predicates that spontaneous transitions from anti-phase to in-phase manual coordination occur because the two preferred states (anti-phase and in-phase) can be seen as stable regions that work as attractors in a stability landscape. A phase transition occurs spontaneously when a control parameter is varied, prompting a response from the system. When applied to quadrupedal locomotion, each gait (defined by its rhythmic interlimb coordination) can be considered to be a stable region. Stability of coordination is lost when switching between gaits and behaviour is attracted towards a second stable region. This means that a transition coincides with a temporary loss of stability that is recovered after the transition. The control variable that prompts the response from the system is the forward velocity of the centre of mass. Schöner et al. (1990) used this approach in an theoretical analysis of interlimb coordination patterns in quadrupedal locomotion by using relative phasing on which symmetry requirements were imposed. Based on their findings, they made the claim that understanding gait transitions as resulting from a loss of stability is a key step towards the recognition of an organisational coordination model. In this study, we use the prediction of instabilities around a transition as a starting point to search for the location of pattern instability with the underlying assumption that the joint in which the instability occurs will also be the controlling joint that will respond dynamically to this instability to restore stability in the entire system.

Coordination variability is believed to be indicative of loss of stability (Winter, 1989; Holt et al., 1995). In most studies, variability of coordination between limbs or between joints is studied by looking at the variability in angle–angle plots or phase relation-
ships (Hamill et al., 2000). We expand this approach to intra-subject joint angle profile variability. If joint angle variability is a measure of stability, then according to the model an increase in variability prior to the transition would occur and this variability would decrease again after the transition is fully completed.

Horses are the classic example of quadrupedal animals that move using different gaits when changing speed. When trotting, diagonal pairs of limbs (forelimb and the hind limb on the opposite side) move alternately and a suspension phase follows each stance phase. At the canter, one diagonal pair continues to move in a trot-like manner while the other diagonal pair becomes dissociated; the leading forelimb contacts the ground before its diagonal hind limb. A transition between trot and canter therefore necessitates a shift in the timing between forelimb and hind limb of one pair of limbs. Distal joints are considered to be driven passively in the horse because they are spanned mostly by tendons, even though they are connected to small muscles proximally (Biewener, 1998; McGigan and Wilson, 2003; Payne et al., 2005; Dutto et al., 2006). In addition, from the carpus distally in the forelimb and from the fetlock distally in the hind limb, swing phase movements of the joints are driven inertially and are controlled by eccentric muscle–tendon activity. Small changes higher up in the limb can result in large changes at the endpoint of a long limb; we hypothesise that the largest changes will occur at the proximal joints.

In this study, we investigated the changes in limb joint kinematics during a transition from trot to canter in a horse. We also determined the joint angle variability during an accelerative sequence of strides, including a transition, to test the hypothesis that variability in the joint profiles of the joints responsible for the transition will peak at the transition. If the model is correct and transitions occur due to self-organising mechanisms; this will enable us to pinpoint which joints are involved in this process. We hypothesise that it will be the proximal, driven, joints of the limb that control protraction and retraction of the entire limb (shoulder, elbow, and hip) that are responsible for initiating changes in inter-limb coordination patterns.

Materials and methods

Experiments

Four miniature horses (mean mass ± standard deviation, SD, 105 ± 32 kg) were used in this study. Thirty-four reflective markers of 6 mm diameter were attached to the skin over anatomical landmarks on the body and limbs of each animal using adhesive tape (Fig. 1). Eight Eagle infrared cameras (MotionAnalysis Company) operating at 120 Hz were used to cover a capture volume of 1 m × 1 m × 8 m. The capture volume was calibrated using a wand technique that yielded an error in linear measurement of 1 mm. We chose to work with Miniature horses in order to obtain a larger number of strides within the restrictions of a capture volume using eight cameras. A runner led the horses in hand in a straight line through the capture volume using a loose lead rope while accelerating with a transition from trot to canter. The runner aimed for a constant acceleration within each trial, but acceleration was not constant between trials. No cues to change gaits were given, so the transitions were initiated by the horses. Data collection continued until a minimum of 15 trials had been recorded. After quality check of the trials to ensure that all markers were present throughout a minimal of four strides and that acceleration of the centre of mass of the horse was constant throughout each trial including the transition stride, 30 trials were retained for further analysis.

Calculations

The strides were numbered according to the footfalls of the trot. Dissociation of the diagonal pair was detected based on the difference between the vertical coordinates of the hoof markers of the diagonal pair through time (Fig. 1). The first stride for which the diagonal pair of footfalls deviated from an in-phase pattern was assigned the stride zero number. In this stride, touchdown of the dissociating forelimb was designated as the start of stride zero. The strides preceding and following stride zero were designated negative and positive, respectively, and were numbered from the transition onwards. Joint angles of the head, neck and limb joints, and the trunk segment angle (Fig. 2), were calculated from the positions of the markers in every frame. Joint angle profiles were split into strides based on the start of contact of the leading forelimb and were time-normalised to stride duration and resampled in steps of 15 ms.

Range of motion (ROM) of each joint was calculated by subtracting the minimal joint angle from the maximal joint angle during each stride. Coefficients of variance (CVs) were calculated on a stride-by-stride basis as the mean ± SD of the joint angle profile over all trials of that animal divided by the mean joint angle multiplied by 100. Since not every sequence contained all six strides that were included in the final analysis, the data were corrected for differences in sample size by dividing the CVs by the square root of the sample size. This approach yielded one number (CV) for each joint for each stride number for each horse.

Statistical analysis

ROM variables were compared between strides in a multivariate analysis of variance (MANOVA) with stride number as a fixed effect and horse as a random effect (Hamill et al., 2000). We expand this approach to intra-subject joint angle profile variability. If joint angle variability is a measure for variability, increased prior to the transition and decreased again afterwards, a MANOVA repeated design test was performed to test for differences in CVs and CVs corrected for sample size between the strides. Univariate tests were used as post hoc evaluations for individual joints. By comparing the CVs in a repeated design, the variability for each joint angle of one stride number is compared with the variability of the other stride numbers within each horse.

Results

Coefficients of variance in a dynamics systems perspective

Differences between strides were found for the scapulothoracic and shoulder angles of the leading forelimb, and for the hip and fetlock angles of the trailing hind limb (Fig. 3). While the variability decreased after the transition, on the transition, the only hip joint angle of the trailing hind limb showed a clear maximum at 8% in the transition stride that decreased to 1% in the canter strides. When corrected for sample size differences, the same results were obtained.

![Fig. 1. Example trial of stride zero definition based on the vertical coordinates of the lateral hoof markers of one diagonal pair. Permanent dissociation (1) of the diagonal pair was detected. Stride zero started with the start of the stance phase (2) of the forelimb of the diagonal pair that dissociated.](image-url)
but the $P$ value of the trend towards significance of the fetlock joint angle of the leading forelimb went below the threshold value of 0.05, with a peak coefficient based on a standard error of 16% in stride zero, and followed the predicted pattern significantly. 

**Changes in kinematics over the transition**

The range of motion of the left and right stifle joints, both tarsi and the fetlocks differed significantly between strides. The changes in ROM followed a typical pattern; a steady increase of the range of motion was observed, followed by a sudden significant decrease in stride +1. For the tarsus of the trailing hind and the stifle joint of the leading hind limb, the decrease was not significant. In the stifle joint, the range of motion was largest in stride 1 and was significantly larger in this stride than during the strides prior to the transition.

**Discussion**

The transition from trot to canter involves a change in interlimb coordination of one diagonal limb pair from an in-phase coordina-
tion pattern to an out-of-phase coordination pattern. This change in coordination involves, after correcting for changes due to differences in locomotor speed, a change in footfall pattern consisting of brief decreases in stride durations and stride lengths of the forelimbs, while the hind limbs increase their stride length over two strides (Nauwelaerts et al., 2013).

In the dynamics systems perspective, instability is expected prior to a switch of states (Kelso et al., 1986). We chose to use variability as a measure for instability and, therefore, we expect the coefficient of variance to peak at or just before the transition. Variability within the states that are not unstable should be low. The goal in using this approach is to pinpoint which joint becomes unstable and is, therefore, responsible for triggering the transition.

The hypothesis that the two gaits, trot and canter, can be regarded as two stable states, and that switching between states requires going through a region of heightened instability, is supported by the finding that the variability in the scapulothoracic angle of the leading forelimb, the fetlock angle of the trailing forelimb, the hip, tarsal and fetlock angles of the trailing hind limb and the tarsus of the leading hind limb increased prior to and decreased after the transition. This is in contrast with the studies of Kao et al. (2003) and Seay et al. (2006), who looked at walk-to-run and run-to-walk transitions in human beings and did not find an increase in variability prior to, nor a decrease after, transition in coordination. However, this experiment was performed on an accelerative treadmill rather than over ground; this set-up could cause an artificially reduced variability (Nelson et al., 1972; Dingwell et al., 2001). If this effect is larger than the increased variability due to the transition, it is possible that the peak in variability could not be detected.

In addition, a walk-to-run transition might not have the same underlying mechanism as a transition from a symmetrical to an asymmetrical gait. It might be expected that the latter transition would occur more abruptly and would therefore coincide with a higher peak in dynamic instability. Our results did confirm the results of an earlier study (Diedrich and Warren, 1995) that found an increase in variability, despite using steady state situations in a series at different speeds, again on a treadmill, which may be inherently less variable, in addition to the decreased variability due to treadmill use. This conflict in results led Kao et al. (2003) to hypothesise that the predictions of the HKB model of an increase in variability before a transition to a different coordination pattern, followed by a decrease, can only be used in tasks during which postural stability is not a critical factor. This might indeed be the case for an accelerating quadrupedal animal, such as the horse.

A benefit of performing experiments on a treadmill could be that acceleration can be kept the same between trials. This was not the case for our experiments over ground, even though we kept the same handler for each horse. Such differences in acceleration could introduce additional variability in the joint angle profiles compared to having a fixed, imposed acceleration. However, we used trials of at least four strides and this problem is not restricted to particular joints. We therefore feel confident that the variability in acceleration did not create a bias on the patterns found in the joint angle variability. Furthermore, treadmill locomotion differs kinematically from over ground locomotion (Buchner et al., 1994), so we preferred to evaluate kinematics over ground.

Using the dynamics systems perspective to pinpoint the joints that are best correlated with the timing of the transition results in the selection of the hip joint of the trailing hind limb as the one joint that follows the theory exactly within the number of successive strides we were able to compare. The retention of the hip joint of the trailing limb is interesting. In fact, the hip joint is not entirely the most proximal joint of the hind limbs. The pelvis can be considered to be an additional body segment that connects the two hind limbs together and connects both hind limbs to the spine through the relatively immobile sacroiliac joints. The entire sacropelvic segment rotates in a sagittal plane at the lumbosacral joint, which is the most mobile joint in the thoracolumbosacral spine. Flexion-extension of the lumbosacral joint occurs in asymmetrical gaits (canter, gallop) and its range of motion increases with speed in these gaits (Johnson and Moore-Colyer, 2009). It is possible that these joints that can be considered even more proximal joints of the hind limbs would show a similar or even earlier variability effect than the hip joint.

Even though the hip of the trailing limb was the only joint that followed the theoretical predictions exactly, with peak variability in stride zero, we also found an increase and subsequent decrease in variability in several other joints (scapulothoracic angle of the leading forelimb, fetlock angle of the trailing forelimb, hip, tarsal and fetlock angles of the trailing hind limb and the tarsus of the leading hind limb) but decreased variability seemed to be delayed to stride +1 or +2. Dingwell et al. (2001) showed that, for walking human beings, local perturbations continued to affect the kinematics even 10 strides after the initial perturbation. It is therefore possible that, even though the transition visually seems to have been achieved, the joints involved in the process are still recovering from the perturbation in stride +1 and +2. For the two horses for which we were able to obtain enough strides +3 to calculate a CV, minimal values were found for all joint angles in this stride. We suggest that, because of the clear pattern in the hip of the trailing limb, the hip is the joint that initiates the transition. The response of the other joints lags behind this joint, but the overall instability that increased in the strides leading up to the transition is decreased again when the horse is cantering. Applying the notion of increased variability as an indicator of control seems to pinpoint the hip of the trailing hind limb as the main instigator of the transition. This fits with the idea of proximal joints controlling the limbs and with the observation that the trailing hind limb makes the prominent spatio-temporal changes during the transition (Nauwelaerts et al., 2013).

In the perspective of the two gaits acting like two stable regions in the coordination landscape, a transition from one gait to another would require adding energy into the system to establish the new coordination stability (Diedrich and Warren, 1995). Energy expenditure was correlated with gait instability (Kuo, 1999) and with muscle contractions to maintain balance (Malatesta et al., 2003). Instability seems to require energy due to the extra compensatory work of the muscles responsible for providing stability (Hoffman et al., 1997; Brown and Kram, 2005). Instead of containing an added factor in the explanation of the U-shaped curves between metabolic cost of transport and speed of locomotion found by Hoyt and Taylor (1981).

The kinematical variability seems to follow the predictions of the HKB model with respect to stability. This model predicts variability in the temporal patterns to occur at a moment of increased instability. Variability might not necessarily be interchangeable with stability. Recently, methods from engineering have been applied to locomotor kinematics from the principle that stability is defined by how a system responds to perturbations either in real time or from one cycle to the next (Dingwell and Kang, 2007). The data on gait transitions, however, contains an added complication to the calculation of, for instance, Lyapunov exponents, since two phenomena occur at the same moment: acceleration and a transitional phase. Also, the techniques currently available necessitate a large number of strides, which are difficult to obtain over ground.

For this study, the coefficient of variation was corrected for changes in range of motion, since the SD would be affected by changes in the joint profile. We found that, for the joint kinematics quantified by the range of motion per stride, the joints of the hind limbs experience significant changes and, contradictory to the
experimental hypothesis, these changes preferentially involved the more distal joints. At first sight, this is surprising, because we stipulated that control of the transition would originate in the more proximal joints. However, the more distal joints are actuated by tendons that are controlled by the more proximal muscles, with the forces transmitted over a longer distance. Therefore, this might not be an observed effect of control, but rather the effect of the increased compliance in the distal joints. This would make changes due to the interaction of the limbs with the substrate more apparent in the distal joints.

The kinematics pattern is generally a steady increase in ROM prior to the transition and then a sudden decrease in stride +1. These decreases are not spectacular; they range between 5° and 8° but they do represent a sudden change (abrupt changes are an inherent part of a transition) in the linear increase in ROM during the accelerating phase without the transition. Joint ROM might be the limiting factor that sets off the transition. Capsular afferents, Golgi tendon organs and muscle spindles monitor the amount of motion and detect proximity of the joint to the limits of flexion (Rossi and Grigg, 1982). For the stifle and tarsal joints of the trailing hind limb, the abrupt changes in ROM are due to the fact that joint extension is delayed and peak extension and flexion skips the stride. Maximal extension of the fetlock joints does not change in any of the limbs, which suggests that there are similar vertical ground reaction forces underneath the hooves (McGuigan and Wilson, 2003). Therefore, even though the kinematic differences between the strides are most apparent in the hind limbs, they do not seem to be the result of pronounced dynamic changes.

It is possible that the linear correlation between maximal extension and vertical ground reaction force only exists within the same gait, even though McGuigan and Wilson (2003) did not find evidence of a change in compliance due to gait, or that changes in ground reaction forces will be obvious in the horizontal forces. A study on the changes in ground reaction forces underneath the four limbs of the horse transitioning from trot to canter would therefore provide insights into whether functional changes occur during a transition.

Conclusions

Variability measurements of the joint angles of the limbs of horses transitioning from trot to canter show increased variability which supports the predictions of the HKB model. This reinforces the notion that gaits can be regarded as stable regions of coordination surrounded by regions of instability. Switching from one state to another implies overcoming this instability, which inevitably involves an energy cost. As hypothesised, the most proximal limb joints (hip, scapulothoracic and shoulder joints) followed the predictions to a large extent. The variability of the hip joint angle of the trailing hind limb showed a peak of variability at stride 0, which was quickly reduced after the transition was completed. The detection of this brief perturbation in the hip joint indicates its importance in the transition process. The hip joint is related to the movements of the limb, the pelvis and the back, which is one of the main differences between symmetrical and asymmetrical gait. It would be interesting to perform a study on the activation patterns of the muscles in this region to unravel the underlying mechanism of the transition and to assess how much control is involved in the decision to make the transition.

Conflict of interest statement

None of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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