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

Sandra Nauwelaerts [a,b,*], Peter Aerts [a], Hilary Clayton [b]

[a] *Functional Morphology Laboratory, Department of Biology, University of Antwerp, Wilrijk, Belgium*
[b] *McPhail Equine Performance Center, Michigan State University, East Lansing, MI, USA*

ARTICLE INFO

ABSTRACT

Spontaneous transitions from anti-phase to in-phase manual coordination are explained in the Haken model that describes the two preferred states as stable regions that work 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 $\times$ 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 a 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-

* Corresponding author. Tel.: +32 3 2652119.
E-mail address: sandra.nauwelaerts@ua.ac.be (S. Nauwelaerts).

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; McGuigan 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 angle 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 pairs 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 outwards. 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 1%.

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 using SPSS PASW statistics 18 (IBM). To test whether joint angle CVs, 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 fet-lock angles of the trailing hind limb (Fig. 3). For all these joints, the variability decreased after the transition, but 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
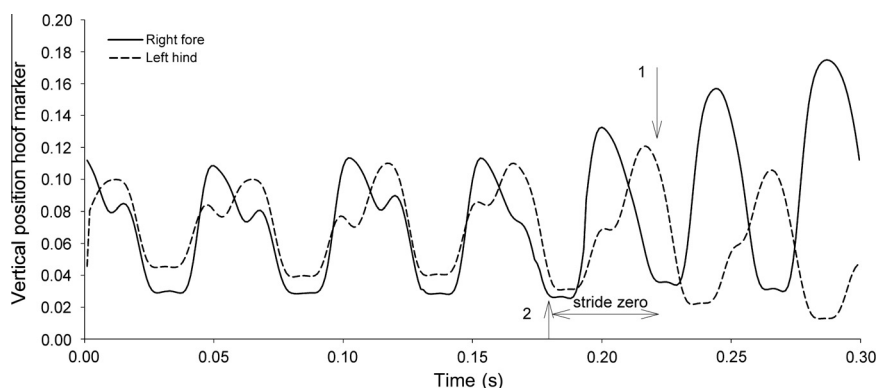

Fig. 1. Example trial of stride zero definition based on the vertical coordinates of the lateral hoof markers of one diagonal pair. Permanent dissociation (1) of the diagonal pair was detected. Stride zero started with the start of the stance phase (2) of the forelimb of the diagonal pair that dissociated.