The Veterinary Journal 198 (2013) e46–e51

Contents lists available at ScienceDirect

The Veterinary Journal

journal homepage: www.elsevier.com/locate/tvjl

Directional asymmetry of facial and limb traits in horses and ponies

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ARTICLE INFO

Keywords:
Equine
Conformation
Asymmetry
Skeletal
Laterality

ABSTRACT

Current published data on directional asymmetry (DA) in horses refer to racing Thoroughbreds. The aim of this study was to identify whether horses and ponies exhibit directionality of trait asymmetries. Eleven functional (limb) and four non-functional (facial) bilateral traits were measured on left and right sides in a cohort of 100 horses and ponies using callipers. The population was investigated as pooled data and as horse (withers height >148 cm) and pony (withers height ⩽148 cm) sub-groups. Within the pooled data, functional traits were longer on the right for the third metacarpal (MCIII, 73%) and metatarsal (MTIII, 65%) bones and wider on the left for the forelimb proximal phalanx (54%), MCIII (40%), MTIII (51%) and hind limb proximal phalanx (55%). Dimensions of the intercarpal and tarsocrural joints were larger on the right side. Differences in DA were present between horses and ponies within non-functional traits, but not functional traits. The results suggest that DA within horses and ponies is more likely to be a species trait rather than one exclusive to racing as a result of pressures from directionally orientated training or from selective breeding strategies.

Introduction

Symmetry within nature is thought to reflect the ability to defend against environmental or genetic stressors (Møller, 1990, 1993; Hosken, 2001). The ability of an individual's genotype to defend against these stressors is depicted through the symmetry of their phenotype (Tuyttens, 2003). Within bilaterally paired traits, fluctuations from the ideal symmetrical state, with no directional bias, are known as fluctuating asymmetries (FA) or phenodeviants (Van Valen, 1962; Møller, 1993; Wilson and Manning, 1996). FA has been used to measure the level of developmental stability within populations and within individuals (Thornhill and Gangestad, 1994). Although the optimum state for an individual is unknown, it is generally assumed that this should be perfect symmetry (Houle, 2000).

Within a population, a mean of zero and a normal distribution around this mean should be observed for differences between left and right sides (Van Valen, 1962). FA in the region of 1–2% of character size is usually exhibited by a population (Gangestad and Thornhill, 1999). A further indicator of imbalanced development is the measure of directional asymmetry (DA), which identifies a skewed distribution of asymmetry to the left or right side. DA has not been linked to developmental stability, but has been suggested to depict an adaptive or functional asymmetry (Tuyttens, 2003).

The athletic phenotype affects performance, with influential features including intermandibular width and length of the third metacarpal bones (Delahunty and Webb, 1991; Mostert and Householder, 2000). Symmetry of bilateral traits influences performance capabilities, especially for Thoroughbred racehorses. Dalin et al. (1985) correlated performance and asymmetries of sacral tuber height in racehorses and demonstrated that greater asymmetry was associated with decreased performance. However, the study by Dalin et al. (1985) did not consider the origin of asymmetry. The relationship between asymmetry of skeletal dimensions and performance in horses has not been studied.

Traits of lesser functional importance often display greater asymmetry than functional traits (Møller, 1993; Markow and Clarke, 1997). In a sample of 285 children in the Jamaican Symmetry Project, upper body bilateral traits exhibited greater asymmetry than lower body bilateral traits (Trivers et al., 1999). Lower ranking Thoroughbred racehorses exhibit greater asymmetry of non-functional facial traits than the functional limb traits (Manning and Ockenden, 1994).

The effects of limb length discrepancies on gait have been investigated more extensively in humans than horses; the magnitude of the discrepancy has a strong bearing on gait kinematics and kinetics (Bloedel and Hauger, 1995). Limb length discrepancies <15 mm rarely have clinical implications, whereas discrepancies of greater magnitude lead to dysfunction and pain (Subotnick, 1976). Limb length affects leverage during locomotion; therefore, an economical and symmetrical gait is achieved only with symmetrical body traits (Vagenas and Hoshizaki, 1992).

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1090-0233/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.tvjl.2013.09.032

Watson et al. (2003) reported longer right third metacarpal (MCIII) lengths than left in 76% of racing Thoroughbreds. This was considered to be a consequence of human selection rather than imbalances induced by training stresses, since growth of the MCIII bone ceases by 7 months of age (Thompson, 1995) and therefore should not be affected by subsequent training. Femoral epicondylar dimensions in Thoroughbred racehorses run on a clockwise track are greater for the left than the right limb (Pearce et al., 2005). Runners on an anticlockwise track are presumed to have a mechanical advantage if their outside (right) limb is longer (Watson et al., 2003). This finding might help explain why horses that are successful racing on an anticlockwise track may not be as successful on a clockwise track (Williams and Norris, 2003). As a dynamic structure, bone responds to the forces placed upon it and alternative theories suggest that repeated directionality could also be causal in the development of equine asymmetries (Drevemo et al., 1980; Scutt and Manning, 1996).

Currently, the only data that exists regarding directional asymmetry of horses are based on populations of racing Thoroughbreds. The aim of this study was to compare the magnitude and direction of asymmetry within functional and non-functional traits of non-racing horses and ponies.

Materials and methods

The study population consisted of male and female horses and ponies of a variety of breeds at two equestrian centres and two livery yards in Gloucestershire, UK. None of the horses or ponies had an elite competitive record and all were >5 years of age to eliminate age related changes in symmetry (Trivers et al., 1999). One-hundred horses and ponies were selected via a convenience sampling technique and were investigated both as pooled data and following separation into horses (withers height >148 cm; $n = 57$) and ponies (withers height $\leqslant$148 cm; $n = 43$). The data were reviewed as pooled data, as well as separately for horses and ponies.

Direct measurements of 11 functional and four non-functional bilateral traits (Table 1) were determined using Invicta metric callipers (1 mm accuracy), similar to previous studies (Manning and Ockenden, 1994; Manning and Pickup, 1998). The horses and ponies were made to stand squarely on level concrete while being measured; three measurements were taken at each site by one assessor and a repeated measures one-way analysis of variance (ANOVA) was used to determined intra-observer variability. Two observers repeated the measurements for selected horses following the same protocol and inter-observer repeatability (r) was calculated using the following equation (Lessells and Boag, 1987):

$$r = s_A^2/(s^2 + s_A^2)$$

where s_A^2 is the between-group variance and s^2 is the within-group variance.

Absolute (directional) asymmetries (A) were calculated by subtracting the mean of the left trait (L) from the mean of the right trait (R) ($A = L - R$) (Manning and Pickup, 1998). Positive values indicated a larger left sided trait and negative values indicated a larger right sided trait. Thus, the study determined the directionality of the data rather than the magnitude of the asymmetry in terms of frequencies; outliers were not removed. The directionality of the data was examined using two-way classification χ^2 analysis with significance declared at $P < 0.05$ to test the assumption that, if no directional bias exists, the distribution frequency of left and right for each trait should be equal.

Results

On repeated measures one-way ANOVA, there were significant variances between the three repeated measures for the length of the hind limb proximal phalanx (HPP; $P \leqslant 0.05$). However, repeatability calculations were 0.99–1.00 for all traits.

There were significant differences between the observed and expected values for the frequency of directionality of asymmetry within the pooled group data ($\chi^2 = 39.8$, degrees of freedom, df = 14, $P \leqslant 0.05$) and the pony sub-group ($\chi^2 = 31.3$, df = 14, $P \leqslant 0.05$), but not for the horse sub-group ($\chi^2 = 18.5$, df = 14, $P \geqslant 0.05$).

Higher frequencies within bilateral facial traits were recorded for greater length and width on the left (positive DA, PDA) (Table 2; Fig. 1). Mean trait values tended to be greater for the left traits within those exhibiting PDA and greater on the right for those exhibiting negative DA (NDA; Table 2); however, this was not seen for pinna length in the pony sub-group, where those exhibiting PDA had a greater mean value right-sided trait, indicating that, although there were fewer individuals with PDA of this trait, the magnitude of the asymmetries was greater.

Left forelimb proximal phalanx (FPP) length and width dimensions were frequently larger than those observed for the right for the pooled group and the two sub-groups (Table 2). Tendency for a longer right MCIII was greater in all three groups; however the pony sub-group displayed more individuals with greater width on the left, whilst the horse sub-group exhibited more individuals with greater width on the right. For all groups the carpal width and depth dimensions were more frequently larger in the right limb. The mean trait values tended to be greater for the left trait within those exhibiting PDA, and greater on the right for those exhibiting NDA; however this was not seen for MCIII length in the pooled data set, where those exhibiting PDA had a greater mean value right-sided trait or for carpal depth in the horse data set, where those exhibiting NDA had a greater mean value left side, again indicating a lower frequency of incidence, but greater individual magnitude of asymmetries.

Hind limb traits displayed high frequencies of directional asymmetry (Fig. 2). More individuals within all three groups demonstrated greater right HPP length, but greater left HPP width. Similarly to the MCIII and to the HPP, a longer third metatarsal

Table 1
Bilateral traits measured including description.

Trait	Description
Third metacarpus length (MCIII) and third metatarsus length (MTIII)	Measured laterally from the 'V' formed by the overlap of the annular ligament over the superficial digital flexor tendon at the distal portion of the limb, to the protrusion of the fourth metacarpal/metatarsal bone at the proximal region of the distal limb
Third metacarpus width (MCIII) and third metatarsus width (MTIII)	Measured on the horizontal axis half way between the carpometacarpal/tarsometatarsal joint and the metacarpophalangeal/metatarsophalangeal joints
Fore proximal phalanx length (FPP) and hind proximal phalanx length (HPP)	Measured laterally from the protuberance of the lateral cartilage of the distal phalanx to the lateral protrusion made by the proximal condyle of the proximal phalanx
Fore proximal phalanx width (FPP) and hind proximal phalanx width (HPP)	Measured horizontally at the narrowest point of the phalanx
Carpal joint width	Measured horizontally from the medial to the lateral aspects of the intercarpal joint
Carpal joint depth	Measured laterally from the dorsal aspect of the intermediate carpal bone to the palmer aspect of the accessory carpal bone
Tarsal joint width	Measured horizontally from the medial to the lateral aspects of the tarsocrural joint
Pinna length	Measured from the point at the summit of the pinna to the inverted point at the base of the pinna
Pinna width	Measured from the medial to the lateral aspect of the pinna at the midpoint of its length
Nostril length	Measured from the top of the fold on the medial aspect of the nostril to the lowest point of the nostril
Nostril widths	The width of the nostrils was measured horizontally from the alar fold on the medial aspect, to reduce the impact of nasal flaring, to the lateral border of the nostril