Behavioural Processes 79 (2008) 7-12

Contents lists available at ScienceDirect

Behavioural Processes

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

Behavioural Processes

Facial hair whorls (trichoglyphs) and the incidence of motor laterality in the horse

Jack Murphy*, Sean Arkins

Department of Life Sciences, University of Limerick, Limerick, Ireland

ARTICLE INFO

Article history: Received 29 March 2007 Received in revised form 18 March 2008 Accepted 31 March 2008

Keywords: Horse Laterality Sidedness Motor behaviour Hair whorl Trichoglyph

ABSTRACT

Several species demonstrate obvious motor laterality (sidedness, handedness) in their motor function. Motor laterality in the horse affects locomotion and subsequently equine performance during training and may have inherent safety implications for equitation. Some of the most commonly used identification features in the horse are hair whorls (trichoglyphs), since their specific location and character vary to some degree in every horse. We investigated the relationship between the hair flow of single facial hair whorls and the incidence of lateralised motor bias in 219 horses when under saddle in ridden work. The horses exhibited significant differences in motor preferences with 104 left-lateralised (LL) horses, 95 right-lateralised (RL) horses compared to only 20 well-balanced (WB) horses (χ^2 = 36.9, d.f. = 2, P < 0.01). There was also a significant difference in the frequency distribution of single facial hair whorl patterns in the horses consisting of 114 horses with counter-clockwise (CC) whorls, 82 horses with clockwise (C) whorls and 23 horses, which had radial (R) whorls (χ^2 = 38.87, d.f. = 2, P<0.01). Overall there was a statistically significant association between motor behaviour and facial hair whorl patterns in the horses (χ^2 = 69.4, d.f. = 4, P > 0.001). The RL horses had significantly more C facial hair whorls and the LL horses had significantly more CC facial hair whorls than would be expected purely by chance alone (P < 0.05). The findings may provide trainers with a useful tool when attempting to identify simple, non-invasive and reliable predictors of motor laterality in the horse. Furthermore, given that efficient targeted training of performance horses during ridden work may produce WB equine athletes, the findings could assist trainers when designing individual-specific training programmes for young horses.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Numerous studies have investigated the phenomena of motor laterality or handedness (sidedness or lateralised motor behaviour) in several species including humans (Rife, 1940; Porac and Coren, 1981; McManus, 1985; Gilbert and Wysocki, 1992; Annett, 2002), primates (Ward et al., 1990; Hopkins and Pearson, 2000; Westergaard et al., 2000), dogs (Tan, 1987; Wells, 2003), cats (Tan et al., 1990; Fabre-Thorpe et al., 1993), rodents (Tsai and Maurer, 1930; Glick and Ross, 1981; Waters and Denenberg, 1994; Tang and Verstynen, 2002), whales (Clapham et al., 1995) and horses (Grzimek, 1968; Dalin et al., 1985; Deuel and Lawrence, 1987; Drevemo et al., 1987; McGreevy and Rogers, 2005; Murphy et al., 2005). In humans for example, a population bias of approximately 93% for right-handedness has been reported, irrespective of geographical location or cultural influences (Coren and Porac, 1977).

* Corresponding author. Present Address: 206 Veterinary Sciences Building, School of Agriculture, Food Science and Veterinary Medicine, University College Dublin, Dublin 4, Ireland. Tel.: +353 87 284 3070; fax: +353 1 7166104.

E-mail address: Jack.Murphy@ucd.ie (J. Murphy).

However, the specific causation of laterality still remains open to some degree of argument and theories of genetic predisposition (McManus, 1985; Klar, 1996), environmental influences (Tambs et al., 1986; Orlebeke et al., 1996) and combinations of both (Annett, 2003) have been proposed as probable aetiological models. The identification or mapping of any specific genetic locus, which could unequivocally influence lateralised motor behaviour, is it appears, as of yet incomplete or unavailable.

The ability of trainers to deal with motor laterality in the horse is important, particularly in terms of training and athletic performance (McGreevy and Rogers, 2005). It has been previously reported that equine motor function and athletic performance was compromised by laterality or gait asymmetry in the young performance horse (Drevemo et al., 1987). Various degrees of training and preparation are required in order that the horse might excel in any of the range of equestrian pursuits. In some instances, the training methods have actually been shown to exacerbate 'existing' motor asymmetry due to differences between left and right hind limb kinematics (Dalin et al., 1985). Anecdotally, at least, there is an industry acceptance that the majority of horses are 'one-sided' or lateralised to some degree and lack *balance* as a result within the various disciplines of equitation. This behaviour has also been



^{0376-6357/\$ –} see front matter @ 2008 Elsevier B.V. All rights reserved. doi:10.1016/j.beproc.2008.03.006

observed in the horse under experimental conditions (McGreevy and Rogers, 2005; Murphy et al., 2005) and supported by additional empirical research where Clayton (1990) reported that 'sidedness' or lateralised motor behaviour was undesirable in dressage horses. Powers and Harrison (2000) also showed that *balance* within motor function was vitally important in show jumping horses when participating in training and competition.

Some of the most commonly used identification features in the horse are hair whorls (trichoglyphs), since their specific location and character vary to some degree in every horse (Anon., 1984). Hair whorl patterns are determined by changes in the direction of flow of the hair from the central locus. Whorls typically present with a clockwise (C) or counter-clockwise (CC) orientation or occasionally these hair patterns may be radial (R) in nature. There are a number of additional descriptive terms associated with hair whorls such as simple, tufted, linear, crested, feathered or sinuous. depending on the pattern of the hair flow (Anon., 1984). In a preliminary study, Swinker et al. (1994) noted the position of facial hair whorls in a population of horses and suggested that facial hair whorl position might be correlated with temperament characteristics and perhaps 'sidedness' in the horse. Recently Górecka et al. (2007) investigated the relationship between reactivity scores and facial hair whorl positions in the horse, while Randle et al. (2003) had previously reported a relationship between facial hair whorls and temperament characteristics in Lundy ponies. There have been a limited number of other studies, which focused on possible relationships between facial hair whorls and some observable behavioural features in other species. In one such study, Tanner et al. (1994) reported a relationship between the location of facial hair whorls and milking parlour side preferences in a large population of dairy cows.

In a recent study, Klar (2003) described the link between hair whorl orientation and handedness in humans. Klar (2003) suggested that human hair whorl patterns resulted from a genetic basis and were not influenced by environmental factors per se. Indeed that study indicated that both handedness and scalp hair whorl patterns, including directional hair flow, might actually develop from a commonly shared genetic mechanism in humans. Others have suggested that human foetal hair patterning and brain development occurred in tandem during weeks 10-16 in utero and that these processes were intrinsically linked (Smith and Gong, 1973). More recently, Paine et al. (2003) reported that human hair whorl patterns are determined during or just prior to the events of neuralation at approximately 17-25 days in utero. In the bovine, Meola et al. (2004) showed that hair whorl patterns in cattle may be related to sperm morphology. Those authors suggested that the facial hair whorls might represent valuable indicators during breeding soundness examinations in the selection of suitable breeding bulls. Grandin et al. (1995) suggested calmer cattle could be identified on the basis of hair whorl patterns and their location on the bovine head. Facial hair whorls are generally located close to or on the mid-line at a location approximately between the lower and upper eye level in the horse. The objective of the current study was to explore the relationship, if any, between the hair flow orientations of the facial hair whorls (trichoglyphs) and the incidence of motor laterality in the horse.

2. Materials and methods

2.1. Subjects

The final test population (see Section 3) was 219 horses (males = 125, females = 94), where the male horses were geldings (n = 104) and stallions (n = 21) and the female horses were all non-pregnant intact females. The subjects were Thoroughbred (TB) and

TB × Native Breed sport horses and they were between 4 and 6 years old (mean \pm S.E.: 4.8 \pm 0.3). The horses had all been professionally produced and established in the basic requirements for ridden work (McLean, 2003; McLean and McGreevy, 2004). In an attempt to control for background effects, horses with any history of injury considered likely to bias their motor function in terms of motor laterality were not included in the current study.

2.2. Equestrian establishments

The horses were in training at different (n=8) equestrian establishments based in southeast Ireland. It is often a requirement that due to the limited availability of suitable numbers of equine test subjects, that testing and experimental protocols can be easily conducted at different locations (Le Scolan et al., 1997; Wolff et al., 1997). The eight establishments had somewhat different types of facilities and to some extent different training regimes. There was no evidence to suggest that either the training facilities or the different training regimes had the effect of causing any motor bias or specific one-directional lateralisation among the horses. There was a similar distribution of horses exhibiting left-sided, right-sided and well-balanced motor behaviour present on all equestrian establishments during the current study. On this basis therefore, our findings were unlikely to have been prejudiced because of horses influenced by similar previous handling experiences-confined to solely one specific training routine and/or exposed to only one training facility. The number of horses available at each establishment ranged from 12 to 44 and the ratio of male to female animals was not different at any of the establishments. In essence, given the similar distributions of animals in terms of sex and motor behaviour at the different equestrian establishments, the technique of comparing animals from multiple locations can help to avoid any environmental bias. This multi-facility approach to controlling for background effects among animal subjects has been previously used and validated by others sourcing hair whorl data in cattle (Grandin et al., 1995).

2.3. Trainers

The trainers (principal trainer from each establishment supported by experienced staff members) were unaware of the interest in the facial hair whorls and/or any potential association with lateralised motor behaviour prior to or during the experimental protocol. The authors readily acknowledge that motor laterality, might under certain conditions, develop in some horses due to inappropriate riding (some riders may be themselves 'one-sided') and/or perhaps inappropriate training facilities and regimes. However, the trainers that participated in the current study were selected on the basis that they were considered expert in their chosen field and that they were each acutely aware of such artefacts within equitation. The trainers were very familiar with the horses in their care and were cognisant of the behavioural and athletic idiosyncrasies associated with each individual horse. In fact, the trainers were extremely mindful of the importance of 'straightness' and 'balance' in the performance horse (basic tenets of equitation training) with respect to optimal motor behaviour and equine kinematics. Furthermore, within each of the training establishments, individual-specific programmes were already in place to address these issues with the horses in their care. Prior to the experimental protocol and for validation purposes, the trainers assessed a common group of six horses (control animals selected by the experimenters and with which the trainers had no previous experience). This was in order to establish agreement on classification of laterality among the control animals and thereafter provide high levels of consistency in their assessments of the test subjects. The expert trainers assessed the control animals in terms of motor behaviour



A horse with clockwise (C) facial hair whorl



A horse with counterclockwise (CC) hair whorl



A horse with radial (R) facial hair whorl

Fig. 1. Examples of single facial hair whorls (trichoglyphs) in the horses.

and balance and 'sidedness' when ridden (on the flat and over a small fence). Some of the techniques employed in this evaluative process have been described in detail elsewhere (Murphy et al., 2005). The assessment of motor behaviour was either: (1) left-lateralised (LL), (2) right-lateralised (RL) or (3) well-balanced (WB). There was total agreement between trainers with respect to the control animals presented by the experimenters—controls were LL (n=3), RL (n=2) and WB (n=1) and consisted of males (n=4) and females (n=2). This validation technique ensured that the expert trainers recorded the real effects of lateralised motor behaviour within both the control horses initially and then subsequently for the test subjects.

The trainers classified the individual test horses in terms of whether or not they exhibited preferences with respect to lateralised motor behaviour or exhibited any directional bias. The classification involved critical acknowledgement of whether the horses appeared to perform better—easier to ride, turn (through the body or were more supple), had better cadence or jumped more efficiently and more safely when travelling in one direction or another. Essentially, this procedure determined if an individual horse had a preference for performing (galloping, jumping, dressage movements) on either the left or right rein or if there was no detectable difference while being ridden (i.e., well-balanced or 'ambidextrous'). The trainers rated the motor behaviour characteristics of each test horse as LL, RL or WB based on the individual horse's preferences during a ridden trial to rate balance or any motor bias.

2.4. Facial hair whorl patterns

An experimenter (JM) recorded the data relating to facial whorls from the horses. The experimenter was unaware of the trainer's assessment of each horse—essentially blind to the motor behaviour data while recording the orientation of the facial hair whorls. The horses' facial features, hair whorl patterning and positioning were examined and subsequently photographed from directly in front of the animal at eye level. During the examination, the directional hair flow or orientation of the facial hair whorls was assessed as counter-clockwise, i.e., counter-clockwise hair flow from the locus of the whorl; clockwise, i.e., clockwise hair flow from the centre or locus of the whorl or radial, i.e., symmetrical hair flow from the centre or locus of the whorl (Fig. 1).

2.5. Analyses

Statistical analyses were conducted using chi-square test of independence analysis from the statistical software SPSS (SPSS, 2004).

3. Results

3.1. Subjects

Initially, 257 horses (males = 150, females = 107) were available for participation in the experimental protocol. Following preliminary assessment of the subjects, the injured and the unsound horses at walk or trot (n = 17) were excluded from further participation in the study. Furthermore, additional horses (n = 21) with multiple facial hair whorls (Fig. 2) were also excluded from the study because of the difficulty that they would have presented for statistical analysis purposes. There were no differences in any measurements between the male sub-groups (entires and geldings) and these data were amalgamated to provide one combined dataset for the male group. Thus the actual final test population consisted of 219 'sound' horses, all of which had only one facial hair whorl (total males = 125, females = 94).

3.2. Whorls

There was a significant difference in the distribution of the single facial hair whorl patterns among the horses. Overall this outcome consisted of 114 horses with CC whorls, 82 horses with C whorls and 23 horses that had R whorls ($\chi^2 = 38.87$, d.f. = 2, P < 0.01) as listed in Table 1. The male horses exhibited a significant difference in the distribution ratio between those with CC and C facial hair whorls (81 horses with CC whorls compared to 25 horses with C whorls; $\chi^2 = 15.9$, d.f. = 1, P < 0.01). However, the distribution of CC and C whorls in female horses was not significantly different (33 horses with CC whorls compared to 57 horses with C whorls; $\chi^2 = 3.20$, d.f. = 1, P = 0.07).





A horse with multiple (vertical) facial hair whorls

A horse with multiple (horizontal) facial hair whorls

Fig. 2. Examples of horses with multiple hair whorls.

Table 1

The distribution of counter-clockwise, clockwise and radial facial whorl (trichoglyph) patterns in the male and female horses

	Orientatio	Orientation of the facial hair whorls						
	СС	С	R	Total				
Male Female	81 33	25 57	19 4	125 94				
				219				

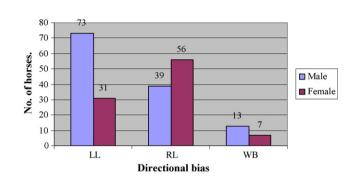


Fig. 3. Motor behavioural preferences in the horses during ridden work.

3.3. Motor behaviour

The assessment of the horses' motor behaviour indicated that there was significant laterality among the horses ($\chi^2 = 36.9$, d.f. = 2, P < 0.01) with 104 LL horses and 95 RL horses compared to only 20 WB horses (Fig. 3). When the horses' motor behaviour either was considered based on left or right laterality only, there was no difference in the number of animals displaying motor bias for predominantly left or right laterality (104 LL horses compared to 95 RL horses; $\chi^2 = 0.20$, d.f. = 1, P = 0.65). However, this trend differed between male and female horses. The male horses as a sub-group did exhibit significant left laterality (73 LL horses compared to 39 RL horses; $\chi^2 = 8.84$, d.f. = 1, P = 0.003) and the opposite trend of right laterality approached significance among the female horses (31 LL horses compared to 56 RL horses; $\chi^2 = 3.67$, d.f. = 1, P = 0.055).

3.4. Association between motor behaviour and whorl patterns

There was a statistically significant association between motor behaviour and facial hair whorl patterns ($\chi^2 = 69.4$, d.f. = 4, P < 0.001) in the horses (Table 2). The findings showed that left-lateralised horses (n = 104) had significantly more facial hair whorls with counter-clockwise rotation than that expected by chance ($\chi^2 = 36.1$, d.f. = 2, P < 0.001). Similarly, right-lateralised horses (n = 95) had significantly more facial hair whorls with clockwise rotation than that expected purely by random ($\chi^2 = 25.7$, d.f. = 2, P < 0.001). There was no difference in the distribution of whorl patterns in the WB horses ($\chi^2 = 2.65$, d.f. = 2, P = 0.27; Table 2).

Table 2

The distribution of motor behavioural bias (left-lateralised, right-lateralised and well-balanced) and facial hair whorl (counter-clockwise, clockwise and radial facial whorl) (trichoglyph) patterns in the horses

Motor behaviour	Facial hair whorl patterns					
	CC	С	R	Total		
LL	78	15	11	104		
RL	23	64	8	95		
WB	12	3	5	20		
				219		

4. Discussion

The horses in the current study exhibited significant motor laterality during locomotor behaviour (walking, cantering and jumping) when assessed by the trainers. This is interesting given that 'straightness' and 'balance' are so highly regarded and seen as basic tenets necessary for optimal performance in the competition horse (Dalin et al., 1985; Drevemo et al., 1987; Clayton, 1990; Powers and Harrison, 2000). There are further empirical examples of laterality in the horse (Grzimek, 1968; McGreevy and Rogers, 2005; Murphy et al., 2005; McGreevy and Thomson, 2006). The findings also support the consensus from within the various disciplines of equitation that the majority of horses demonstrate varying degrees of motor laterality in the ridden work. Furthermore, the findings may have basic safety implications, in that LL and RL horses may require firmer (much stronger) or more specifically targeted rider aids than WB horses, particularly when at exercise in traffic on public roads (McGreevy and Rogers, 2005). This could have specific relevance for the pleasure or novice riders, who may lack the equitation skills of more experienced professional riders. Novice and pleasure riders may not recognise or realize the extent of the potential problems associated with motor laterality in the horse or the safety implications linked to such a phenomenon when handling and riding these animals.

Although there was no difference in the numbers of LL and RL horses overall in the current study, the within sex observation for LL in male horses and contrasting RL in female horses has been previously reported in the horse based on a study of unbroken 4-year-old horses (Murphy et al., 2005). Similar trends of laterality have been reported in other species where a greater incidence of left laterality has been associated with males, including the domestic dog (Wells, 2003), chimpanzees (Hopkins and Bard, 1993) and tufted capuchins (Westergaard et al., 1998). Furthermore, the greater incidence of right laterality reported among female horses also mirrored the slightly higher incidence of right-handed preferences found in human females compared to their male counterparts (Gladue and Bailey, 1995). The LL trend observed in male horses may be due, in part, to greater numbers of male horses participating in the current study. Another possible explanation is the greater numbers of male horses participating in the various disciplines of equitation generally (Physick-Sheard, 1986; Murphy et al., 2004) combined with the convention of leading/tacking up from the left or near side of the horse. On the other hand, McGreevy and Rogers (2005) found a greater proportion of left-preferent horses in the population overall and actual breed differences in that Thoroughbreds exhibited greater LL motor behaviour than Standarbreds and Quarter horses. While, the current study found approximately even proportions of LL and RL horses, it would be interesting to monitor this outcome over an extended period to determine if more animals became LL. Although we believe that appropriate training would prevent this transformation, McGreevy and Rogers (2005) found that the frequency distribution for left directional motor bias also increased with age, probably due to equally balanced horses becoming left-preferent and those already somewhat left-preferent becoming more so.

During the current study however, the trainers did not have exclusively male or female horses in their care. While on average they worked with more male horses, it is unlikely that the training routines alone would have accounted for the opposing motor laterality demonstrated in the male and female horses, respectively. Preferences for motor laterality in the horse may be, to some extent, genetically predetermined, influenced by environmental factors or occur because of a combination of both factors. Although breeding details were available for the horses in the current study, insufficient numbers from the various familial pedigree groups prevented any possibility of investigating a genetic influence for either laterality or whorl type. In order that training/handling can be maximised for the development of WB horses, early recognition of, or useful predictors for any laterality with regard to motor behaviour could be extremely important. Where the dynamics and motor ability of the horse were adjudged as insufficient or lateralised, corrective-training schedules have been developed and are regularly employed. Klimke (1985) devised a number of exercises that 'straighten' the asymmetrical horse for improved biomechanical efficiency and enhanced athletic performance. Occasionally there may be circumstances when laterality in the horse could be beneficial, such as left-lateralised horses competing on left-handed racetracks and vice versa. McGreevy and Rogers (2005) have suggested that some competition tracks may be better and even safer for individual horses with a preference for either left or right sidedness.

In this respect the early recognition of the existence and the degree of 'sidedness' in the young horse, destined for a competitive career, is likely to be of major importance with regard to both future competition and training. This is particularly relevant with regard to the development of appropriate individual-specific training programmes designed to optimise competitive performance in individual horses. We have reported previously that scientists should be aware of and consider laterality (and associated implications) in the horse when designing experimental research protocols for the horse (Murphy and Arkins, 2007). Indeed, others have reported that more emotional horses are more likely to view frightening novel stimuli with the left eye compared to the right eye (Larose et al., 2006). Although, McGreevy and Rogers (2005) reported a lack of correlation between motor and sensory lateralisation in the horse, differences in left-right eye interpretation of stimuli could influence motor behaviour under some circumstances. In general, younger subjects (of several species) have been reported as less lateralised than older subjects and correctivetraining programmes should prove most beneficial when applied at the earlier rather than later stage. However, it has also been reported in the horse, that the absolute degree and extent of asymmetry may only become apparent following exposure to training and preparation for competition (Dalin et al., 1985). It is therefore in the interest of both the horse and trainer, to explore the possibility of determining the status of the horse's individual motor preferences prior to, or at the earliest stage of, the animal's growth and development and subsequent training.

The facial hair whorl patterns differed significantly primarily because of the smaller number of truly radial facial whorls observed in the horses (P < 0.05). The frequency distribution of CC and C whorls also differed significantly among the male horses with more CC facial hair whorls than horses with C whorls (P < 0.05). While the frequency distributions of the CC and C whorls differed, but not significantly among the female horses, overall LL horses had significantly more CC whorls and RL horses had significantly more C whorls (P < 0.05). Although environmental factors may be influential, it is however quite plausible that motor laterality in well-trained physically sound horses is innate at least to some degree. This would appear to be supported by the distribution of facial whorl patterns observed in the horses in the current study based on genetic association. These data are reflective of handedness and hair whorl patterns reported in humans (Klar, 2003), where the conclusion was that both entities emanated from the same shared genetic mechanism.

Interestingly, it has been reported that the brain, skin and hair all develop at the same time *in utero* (Smith and Gong, 1973; Paine et al., 2003) and hair patterning in early foetal life is secondary to the growth and shape of the tissues and organs that underlie the skin, especially the brain (Swinker et al., 1994). The connection between brain development, hair patterning and motor behaviour in the horse appears to be supported within the current study, given the association observed between facial hair whorl patterns and the motor behaviour patterns of the horses. The facial hair whorls may represent simple non-invasive techniques that will prove useful to trainers when investigating and understanding aspects of motor function in the horse. There may be performance or welfare issues, and increased risk of injury to both horse and rider because of horses with strong motor bias, performing in less than optimal conditions. In one study, laterality in the form of asymmetric gaits was associated with inferior performance, and, specifically affected horses tended to produce poorer racing records including fewer races per animal, fewer races won and fewer earnings overall (Dalin et al., 1985). In order that training and handling could be maximised for the development of WB horses, trainers should identify motor bias at the earliest opportunity and employ individual-specific training programmes for young horses.

5. Conclusion

The findings suggest that there is a link between the hair flow of single facial hair whorls and motor laterality in the horse. These findings may assist trainers when selecting individual horses for certain forms of equitation and designing individual-specific training programmes for young horses. Hair pattern manifestations have been linked to early foetal brain development in humans and further study of facial hair whorls may provide useful insight into both behavioural and neurobiological development in the horse. It is unclear to what extent training actually influences motor laterality in the horse and studies of younger animals, particularly untrained foals, may provide important data regarding hair whorls and the link with motor laterality in the horse.

Acknowledgements

The authors gratefully acknowledge the generosity of the owners who allowed access to the animals and the experienced trainers who took part in the study.

References

- Annett, M., 2002. Handedness and Brain Asymmetry: The Right Shift Theory. Psychology Press, Hove, East Sussex.
- Annett, M., 2003. Cerebral asymmetry in twins: predictions of the right shift theory. Neuropsychologia 41, 469–479.
- Anon., 1984. Colours and Markings of Horses. Royal College of Veterinary Surgeons, London.
- Clapham, P.J., Leimkuhler, E., Gray, B.K., Mattila, D.K., 1995. Do humpback whales exhibit lateralized behaviour? Anim. Behav. 50, 73–82.
- Clayton, H.M., 1990. Kinematics of equine jumping. Equine Athlete 3, 17–20.
- Coren, S., Porac, C., 1977. Fifty centuries of right handedness: the historical record. Science 198, 631–632.
- Dalin, G., Magnusson, L.E., Thafvelin, B.C., 1985. Retrospective study of hindquarter asymmetry in Standardbred trotters and its correlation with performance. Equine Vet. J. 17, 292–296.
- Deuel, N.R., Lawrence, L.M., 1987. Laterality in the gallop gait of horses. J. Biomech. 20, 645–649.
- Drevemo, S., Fredricson, I., Hjerten, G., McMiken, D., 1987. Early development of gait asymmetries in trotting standardbred colts. Equine Vet. J. 19, 189–191.
- Fabre-Thorpe, M., Fagot, J., Lorincz, E., Levesque, F., 1993. Laterality in cats: paw preference and performance in a visuomotor activity. Cortex 29, 15–24.
- Gilbert, A.N., Wysocki, C.J., 1992. Hand preference and age in the United States. Neuropsychologia 30, 601–608.
- Gladue, B.A., Bailey, J.M., 1995. Spatial ability, handedness, and human sexual orientation. Psychoneuroendocrinology 20, 487–497.
- Glick, S.D., Ross, D.A., 1981. Right-sided population bias and lateralization of activity in normal rats. Brain Res. 205, 222–225.
- Górecka, A., Golonka, M., Chruszczewski, M., Jezierski, T., 2007. A note on behaviour and heart rate in horses differing in facial hair whorl. Appl. Anim. Behav. Sci. 105, 244–248.
- Grandin, T., Deesing, M.J., Struthers, J.J., Swinker, A.M., 1995. Cattle with hair whorl patterns above the eyes are more behaviorally agitated during restraint. Appl. Anim. Behav. Sci. 46, 117–123.

- Grzimek, B., 1968. On the Psychology of the Horse. St. Martins Press, Inc., New York.
- Hopkins, W.D., Bard, K.A., 1993. Hemispheric specialization in infant chimpanzees (*Pan troglodytes*): evidence for a relation with gender and arousal. Dev. Psychobiol. 26, 219–235.
- Hopkins, W.D., Pearson, K., 2000. Chimpanzee (*Pan troglodytes*) handedness: variability across multiple measures of hand use. J. Comp. Psychol. 114, 126–135.
- Klar, A.J., 2003. Human handedness and scalp hair-whorl direction develop from a common genetic mechanism. Genetics 165, 269–276.
- Klar, A.J.S., 1996. A single locus, RGHT, specifies preference for hand utilisation in humans. Cold Spring Harb. Symp. Quant. Biol. 61, 59–65.
- Klimke, R., 1985. Basic Training of the Young Horse. J.A. Allen, London.
- Larose, M., Richard-Yris, A., Hausberger, M., Rogers, L., 2006. Laterality of horses associated with emotionality in novel situations. Laterality 11, 355–367.
- Le Scolan, N., Hausberger, M., Wolff, A., 1997. Stability over situations in temperamental traits of horses as revealed by experimental and scoring approaches. Behav. Process. 41, 257–266.
- McGreevy, P.D., Rogers, L.J., 2005. Motor and sensory laterality in thoroughbred horses. Appl. Anim. Behav. Sci. 92, 337–352.
- McGreevy, P.D., Thomson, P.C., 2006. Differences in motor laterality between breeds of performance horse. Appl. Anim. Behav. Sci. 99 (1–2), 183–190.
- McLean, A.N., McGreevy, P.D., 2004. Training. In: Equine Behaviour. A Guide of Veterinarians and Equine Scientists. W.B. Saunders, Edinburgh.
- McLean, A.N., 2003. The Truth About Horses. Penguin Books Australia Ltd.
- McManus, I.C., 1985. Handedness, language dominance and asphasia: a genetic model. Psychol. Med. 8, 1–40.
- Meola, M.G., Grandin, T., Burns, P., Deesing, M., 2004. Hair whorl patterns on the bovine forehead may be related to breeding soundness measures. Theriogenology 62, 450–457.

Murphy, J., Arkins, S., 2007. Equine learning behaviour. Behav. Process. 76, 1-13.

- Murphy, J., Sutherland, A., Arkins, S., 2005. Idiosyncratic motor laterality in the horse. Appl. Anim. Behav. Sci. 91, 297–310.
- Murphy, J., Waldmann, T., Arkins, S., 2004. Sex differences in equine learning skills and visuo-spatial ability. Appl. Anim. Behav. Sci. 87, 119–130.
- Orlebeke, J.F., Knol, D.L., Koopmans, J.R., Boomsma, D.I., Bleker, O.P., 1996. Lefthandedness in twins--genes or environment. Cortex 32, 479-490.
- Paine, M.L., Paine, C.T., Machin, G.A., 2003. Hair whorls and monozygosity. J. Invest. Dermatol. 122, 1057-1058.
- Physick-Sheard, P.W., 1986. I. Career profile of the Canadian Standardbred. II. Influence of age, gait and sex upon number of races, money won and race times. Can. J. Vet. Res. 50, 457–470.

- Porac, C., Coren, S., 1981. Lateral Preferences and Human Behaviour. Springer-Verlag, New York.
- Powers, P.N.R., Harrison, A.J., 2000. How can the rider help show jumpers to have better performances. In: Lindner, A. (Ed.), The Elite Show Jumper, pp. 79–90.
- Randle, H., Webb, T.G., Gill, L.J., 2003. The relationship between facial hair whorls and temperament in Lundy ponies. Annual report of the Lundy Field Society, pp. 67–83.
- Rife, D.C., 1940. Handedness with special reference to twins. Genetics 25, 178-186.
- Smith, D.W., Gong, B.T., 1973. Scalp hair patterning as a clue to early fetal brain development. J. Pediatr. 83, 374.
- SPSS, 2004. SPSS 12 for Windows. SPSS Inc., Chicago, IL.
- Swinker, A.M., Deesing, M.J., Tanner, M., Grandin, T., 1994. Observation of normal and abnormal hair whorl patterning on the equine forehead. J. Anim. Sci. 72, 207.
- Tambs, K., Magnus, P., Berg, K., 1986. Left handedness in twin families: support of an environmental hypothesis. Percept. Motor Skills 63, 155–170.
- Tan, U., 1987. Paw preferences in dogs. Int. J. Neurosci. 32, 825-829
- Tan, U., Yaprak, M., Kutlu, N., 1990. Paw preference in cats: distribution and sex differences. Int. J. Neurosci. 50, 195–208.
- Tang, A.C., Verstynen, T., 2002. Early life environment modulates 'handedness' in rats. Behav. Brain Res. 131, 1–7.
- Tanner, M., Grandin, T., Cattell, M., Deesing, M., 1994. The relationship between facial hair whorls and milking parlor side preferences. J. Anim. Sci. 72, 207.
 Tsai, L.S., Maurer, S., 1930. "Right-handedness" in white rats. Science 72, 436–
- Tsai, L.S., Maurer, S., 1930. "Right-handedness" in white rats. Science 72, 436– 438.
- Ward, J.P., Milliken, G.W., Dodson, D.L., Stafford, D.K., Wallace, M., 1990. Handedness as a function of sex and age in a large population of lemur. J. Comp. Psychol. 104, 167–173.
- Waters, N.S., Denenberg, V.H., 1994. Analysis of two measures of paw preference in a large population of inbred mice. Behav. Brain Res. 63, 195–204.
- Wells, D.L., 2003. Lateralised behaviour in the domestic dog, Canis familiaris. Behav. Process. 61, 27–35.
- Westergaard, G.C., Byrne, G., Suomi, S.J., 1998. Early lateral bias in tufted capuchins (*Cebus apella*). Dev. Psychobiol. 32, 45–50.
- Westergaard, G.C., Chavanne, T.J., Lussier, I.D., Suomi, S.J., Higley, J.D., 2000. Hormonal correlates of hand preference in free-ranging primates. Neuropsychopharmacology 23, 502–507.
- Wolff, A., Hausberger, M., Le Scolan, N., 1997. Experimental tests to assess emotionality in horses. Behav. Process. 40, 209–221.