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**The effects of lateralisation on detour based problem solving in horses (*Equus caballus*)**

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**The effects of lateralisation on detour based problem solving in horses (*Equus caballus*)**

**By**

**Hannah Savin**

**A thesis submitted to the University of Plymouth in partial fulfilment for the degree of**

**RESEARCH MASTERS**

**School of Biomedical and Biological Sciences**

**June 2015**

## **The effects of lateralisation on detour based problem solving in horses (*Equus caballus*)**

Potential impact of motor laterality on equine performance has resulted in research into this aspect of equine behaviour. Many studies demonstrate that equids exhibit a preference for one side over the other but there is little evidence for directional biases. In modern day equestrian practices, equids are frequently required to manoeuvre around objects and laterality preferences may hinder or aid in this movement. The aim of this study was to investigate if horses consistently show a directional preference during a detour task. Twenty three horses of various breeds, ages and sexes were required to obtain a goal, a piece of carrot placed in a food bucket located behind a barrier. Horses were started from an initial position of 4 metres from the goal. Each horse was released simultaneously after observing the carrot being placed in the bucket. The time (s) taken from release to reach the goal was recorded where the subject was considered to have attained the goal once it touched the carrot. A maximum duration of 180s was allowed to achieve the goal. Successful trials were followed by extension of the barrier-goal distance at 2m intervals until a maximum length of 8m was reached. If a horse failed to complete a trial within 180 seconds the trial was terminated. An additional study was conducted to determine whether horses consistently show a directional preference in their detour behaviour, regardless of distance to the goal. Five horses completed the task and there was no directional bias evident during the detour task  $\chi^2(1, N = 5) = 6.4, p > .05$ , with only one horse showing a directional bias to the left. The 4m trial was successfully completed by 15 horses, 6m trial was completed by 12 horses and the 8m trial was completed by 12 horses. At 4m there was a greater tendency to manoeuvre around the object to the left as opposed to the right  $\chi^2(1, N = 15) = 8.07, p < .05$ . There was no significant difference in the direction moved at the 6m trial  $\chi^2(1, N = 12) = 0.6, p > .05$  or the 8m trial  $\chi^2(1, N = 12) = 1.33, p > .05$ .

There were no significant differences in the solving times exhibited for each trial  $H_2=1.37$ ;  $P > .05$ , performance did not improve during subsequent trials. The exhibition of lateral preference changed as the detour tasks became increasingly difficult. The fact that solving times did not change throughout subsequent tasks may imply learning during this task did not occur. The overall absence of laterality biases in this study could be attributed to lack of congruity between ability of subjects and experiment requirement. This finding has importance for future studies as it must be recognised that horses should not be required to perform task outside of their behavioural ability and repertoire. This finding can be applied within the equestrian practical context for example when training and preparing horses for work.

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All procedures in this study were approved by the Animal Ethics Committee at the University of Plymouth.

## **Authors Declaration**

At no time during the registration for the degree of Research Masters has the author been registered for any other University award without prior agreement of the Graduate Committee.

During no time during the registration for the research degree has the author been registered for any other University award, without prior agreement of the Graduate Committee,

This study was partly financed from the European Social Fund through the combined universities of Cornwall.

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Relevant scientific seminars and conferences were regularly attended at which work was often presented.

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## 1 Introduction

Motor laterality is defined as a preference for one side of the body over the other, also known as side preference or sidedness (Austin & Rogers 2007 ; Berta 2011). Many studies demonstrate that equids exhibit a preference for one side over the other but there is little evidence for specific directional biases. Directional biases can be an indicator of motor laterality (Facchin, Bisazza & Vallortigara 1999). The importance of understanding non-human directional biases can further our understanding of their preferences and interactions with the environment (Ganskopp 1995) and subsequently highlight their capabilities and limitations with movement in the environment.

The direction in which the subject moves around a barrier, often referred to as directional or turning bias, is of great interest to both scientists and practitioners. Detour tasks are used to assess laterality preferences and have been successfully investigated in many species including birds (Zucca, Antonelli & Vallortigara 2008), rats (*Rattus norvegicus*) (Jovalekic, Hayman, Becares, Reid, Thomas *et al.* 2011), chickens (*Gallus gallus*) (Vallortigara, Regolin & Pagni 1999), horses (*Equus caballus*) (Murphy, Sutherland & Arkins 2005) , donkeys (*Equus asinus*) (Zucca, Cerri, Carluccio & Baciadonna 2011) and cats (*Felis catus*) (Schiller 1950).

Detour tasks usually require the subject to navigate around a barrier to reach a goal, whereby the subject distances itself from the goal by moving around the barrier (Wynne & Leguet 2004). The goal is usually a food or social reward (Vlamings, Hare & Call 2010). Smith and Lithchfield (2010) used chicken carcass mince as a food reward in a detour study, observing dingos (*Canis dingo*). Murphy *et al.* (2005) used a conspecific during a detour task in domesticated horses. A favourite toy has been used as a reward in a detour study of domesticated dogs (*Canis lupus familiaris*) (Pongracz, Miklosi, Kubinyi, Topal & Csanyi 2003).

The earliest detour tasks were introduced by Kohler in 1925 with the purpose of addressing insight learning (Vallortigara & Regolin 2002). At present detour tasks can be used to assess spatial problem solving abilities (Smith & Litchfield 2010). They are also used to measure spatial reasoning (selecting the shortest route to the goal by past familiarity of the test area or of visual assessment of the goal) and spatial learning (experience of different routes throughout the task before developing a tendency to manoeuvre the shortest way). By examining behaviour during the detour task it is possible to understand whether the subject is using spatial reasoning or spatial awareness (Wynne & Leguet 2004).

### **1.1 Displays of lateral preferences**

The broader subject of laterality is gaining substantial research attention within the discipline of equitation science (McGreevy 2007) and was introduced over a century ago (Wood 1997). Lateral preferences within a species exist at the individual level or the population level. If more than 50% of the population studied show a preference for the same directional bias, then lateralisation is considered to be apparent at the population level (McGreevy & Rogers 2005 ; Vallortigara & Rogers 2005). Lateral preferences are widely documented in many species. Previous research has shown a population level bias in cattle (*Bos primigenius*) that showed a preferred side of the milking parlour upon entering (Hopster, Van der Werf & Blokhuis 1998). Sheep (*Ovis aries*) displayed a right directional bias when required to manoeuvre around an object (Versace, Morgante, Pulina & Vallortigara 2007) and domestic goats (*Capra aegagrus hircus*) displayed a laterality bias when observed on a random walk test (Ganskopp 1995). However Folse, Packard & Grant (1989 cited in Ganskopp 1995) suggest that models based on random walks should not be used to represent lateral and spatial tendencies as they are not a true measure of lateral preferences.



## 1.2 The origin of laterality

Despite a considerable amount of research the argument as to whether cerebral and behavioural lateralisation is caused by genetics or environmental factors is still ongoing. Vallortigara *et al.* (1999) suggest that lateral preferences in a wide variety of species, including lower vertebrates may have an ancient evolutionary origin. This theory aligns with that of Ward and Cantalupo (1997) who also agree that laterality has evolved from a common ancestor. Furthermore the authors suggest that the adaptive advantage of lateral preferences are significant and therefore have been favoured in the natural selection process and subsequently they have become a governing characteristic.

Many theories suggest that the cause of lateralised behaviour may be predetermined (Murphy *et al.* 2005). Human lateralisation research has primarily focused on postnatal occurrences such as handedness and footedness. Interestingly side preferences have been found in fetuses, manifested by thumb sucking (Hepper, Shahidullah & White 1991). A correlation has been found between prenatal handedness and postnatal handedness (Hepper, Wells & Lynch 2005). Apparent lateral tendencies at birth may indicate a genetic inheritance (Lane & Phillips 2004). An alternative theory is that cerebral and behavioural lateralisation is influenced by environmental factors. Events in early life might impact the organisational and development of brain asymmetry (De Boyer des Roches, Durier, Richard Yris, Blois-Heulin, Ezzaouia *et al.* 2011). In domesticated horses it has indeed been suggested that many handling practices may have an effect on lateral preferences (McGreevy & Rogers 2005 ; Austin & Rogers 2012). A common concept is that the true cause may be an amalgamation between genetics and environment (Murphy *et al.* 2005). Schaafsma *et al.* (2009) supports this view stating that advancements in modern biology have accepted that the phenotype develops under the constant interaction that is found between genetic and environmental influences.

The earliest suggestion of human-horse interaction was 6000 years ago (Van Dierendonck & Goodwin 2005) and it is possible that present day handling techniques date back to that time, which include handling (i.e. mainly leading) from the left side of the horse (McGreevy & Thompson 2006) and mounting the horse from his/her the left side (Sankey, Henry, Clouard, Richard-Yris & Hausberger 2011). It is supposed that such training and handling practices can greatly influence the innate biases. If it is a combination of genetics and the environment then it would not be surprising that such training and handling practices can greatly influence the innate biases and overall behavioural preferences exhibited by equids.

Guide dogs are trained to work on the left side of their handler (Tomkins, Thompson & McGreevy 2012). Investigating lateral preferences in guide dogs compared to dogs that are kept as a pet would be of interest. It is easy to embrace the idea that training and handling practices may influence the innate biases of animals but consideration should be given to the fact that despite these handling practices, left and right motor preferences are documented in some studies (Baragli, Vitale, Paoletti, Mengoli & Sighieri 2011a).

### **1.3 Environmental impact on lateral preferences**

The performance of mammals, birds and fish during detour tasks has been widely investigated (Kight, Steelman, Coffey, Lucente & Castillo 2008), however despite this interest, there are fewer documented studies on directional biases and detour tasks in horses. Domesticated horses are frequently challenged by detours such as hurdles on a trail ride or a knocked down fence during a show jumping competition. Also they are challenged by hurdles in their husbandry practices such as gateways in their fields and placement of objects such as hay nets, salt licks, water drinkers, feed buckets. Moor ponies often encounter boulders and moor plants in their natural habitat. These physical challenges require the subjects to make spatial judgements by manoeuvring around objects in close

proximity. Insight into directional biases in domesticated horses may also aid in stabling and housing design. There are few documented studies on how the environment is having an impact on laterality biases in domesticated horses. In an unpublished study, Savin and Randle 2010, found that domesticated horses were always leading with a favoured limb when manoeuvring in a small proximity even if they had to take more steps. Furthermore specialised husbandry techniques and sympathetic training methods could be developed and implemented to allow for innate biases (Warren-Smith & McGreevy 2010)

The ability to deal with obstacles in natural environments is likely to have a degree of adaptive significance, whereby animals have a higher survival rate if they are able to move efficiently in order to find food and avoid predators (Smith & Litchfield 2010). Surprisingly there have been few laterality studies on wild animals (Sakai, Hishii, Takeda & Kohshima 2006) but that could be due to logistical difficulties. Greening and Randle (2012) report an absence of lateral motor preference in semi-feral Koniks. Further investigation into laterality biases in wild animals could provide an indication of whether these biases exist, the degree of the biases, or provide further evidence to decide whether this phenomenon is a trait that can be influenced by handling and training practices.

Austin and Rogers (2007) examined avoidance behaviour in 30 domestic horses by presenting a novel stimulus (the opening of an umbrella) to horses from both the left and right side of their neck. A higher incidence of horses moving to the left (when the umbrella was opened on their right side) than to the right (when the umbrella was open on their left side) was observed. Horses also moved further away from the stimulus when it was presented to them on their left side. These results agree with Sankey *et al.s* (2011) findings that domesticated horses displayed more asymmetrical responses when a human displaying dismissive behaviours approached them on their left than from their right.

Murphy *et al.* (2005) found that a lateralisation preference was not evident during a detour task where domesticated horses were required to manoeuvre around a barrier and through a gap of 1.3 metres (45% moved around to the right, 42.5% moved to the left and 12.5% displayed equal lateralised behaviour). However, more recently Baragli, Vitale, Paoletti and Sighieri (2011b) found that there was a higher occurrence of left directional bias displayed by domesticated horses undertaking a similar detour task in which they had to negotiate a barriers in order to obtain a goal. The authors also found that horses are able to perform detour tasks with both symmetrical and asymmetrical barriers (where one side is longer than the opposite side). Lateralised behaviour was found in over 50% of the sample studied and subjects changed their preferred direction as a result of an increase in the asymmetry of the barrier which suggests that horses which don't have a bias may be more adaptable at modifying their behaviour. These are examples of relevant studies that have identified laterality preferences in horses, however further studies can be customised to identify the desired objective. Scientific investigations are now applying suitable, quantitative methods, which can provide further information about domesticated horses.

#### **1.4 Hemispheric dominance**

These functions cause differences in the use of the left and the right side of the body which can be seen in both motor and sensory tasks (Tomkins, Thompson & McGreevy 2010 ; Tomkins *et al.* 2012).

It has been suggested by Austin and Rogers (2007) that the side biases in reactivity observed in response to being approached by a novel stimulus (the opening of an umbrella) from either the horse's left or right are a result from hemispheric differences in processing visual information rather than being motor biases and that avoidance behaviour is controlled by the right hemisphere of the brain. The right hemisphere of the brain is known to process the

information seen from the left eye. It is the contralateral hemisphere that processes information in animals that have laterality placed eyes (Hemond, Kanwisher & Op de Beeck 2007) particularly in animals that have laterally placed eyes.

French born physician Broca (1824-1880) theorised that certain capabilities and abilities of behaviour and cognition are located in specialised parts of the brain (Vallortigara & Rogers 2005). Understanding cerebral functions may provide an insight to cognitive abilities, behavioural complexity (meaning that individuals are able to perform complicated comparisons of behaviour in response to environmental, physical, social and psychological challenges) and behavioural lateralisation (Takeuchi, Hori & Oda 2012). Hemispheric lateralisation has received considerably more recent attention than motor lateralisation, although it is only recently that studies have moved from the laboratories into the field allowing an investigation of a broader variety of species including equids (Vallortigara & Rogers 2005). Hemispheric lateralisation is summarised as the unique function of the left and right sides of the brain.

Different behaviours (Schaafsma *et al.* 2009) and emotions (De Boyer des Roches, Richard Yris, Henry, Ezzaouia & Hausberger 2008) are produced in specific parts of the cerebral hemispheres. Fagot and Vauclair (1991) suggest some tasks can be controlled by both hemispheres but not equally. The left hemisphere is responsible for processing language and producing speech in humans and can focus on stimuli without being distracted

The left hemisphere controls behaviour in conjunction with learnt routines (Rogers 2010) and is responsible for motor function (McGreevy & Rogers 2005).

The right hemisphere of the brain responds to novel stimuli situations. It also controls a range of social behaviours (Rogers 2010) and is used when reacting to emergency

occurrences. Strong emotions and fearful faces (when faced with a potentially fear inducing situation) are processed in the right hemisphere which is also responsible for spatial processing. The relationship between these processes and laterality have been comprehensively investigated and exist in many vertebrate species (Kaarthigeyan & Dharmaretnam 2005).

### **1.5 Expressions of lateral preferences**

Each motor cortex of the contralateral hemisphere largely controls the movement of the limbs (Vallartigara and Rogers 2005) Motor laterality in quadrupedal grazing herbivore species can be investigated by examination of extended limb preference whilst grazing. McGreevy and Rogers (2005) suggested that horses very rarely graze in a square position in which the forelimbs are parallel with each other and the hind limbs parallel to each other and to the forelimbs so that the weight of the animal is distributed evenly. Appendage use has been suggested to be an outward manifestation of cerebral asymmetry in primates (Corballis 2008). Warren-Smith and McGreevy (2010) propose that assessment of a non-human's use of its thoracic appendages (i.e. paw, hand or hoof) could provide a reliable indicator of motor laterality.

Warren-Smith and McGreevy (2010) found a sample bias to extend the left forelimb in a sample of six grazing horses. A left sample bias was also found in McGreevy and Thompson's (2006) study of the extended limb preference in a group of 40 Standardbred horses, 40 Quarterbred horses and 106 Thoroughbred horses. Despite the small sample size of only six horses used in Warren-Smith and McGreevy's 2010 study it allowed further verification of the methodology being used.

Often, studies using small sizes raise the question about species applicability (Hanggi 2010) (i.e. whether the method used can be tailored to the species studied). The same method was

used to investigate extended limb preference in non-domesticated zebras (*Equus burchellii*) and non-domestic impalas (*Aepyceros melampus*). This study found there was a population bias to extend the left forelimb, although, this bias was stronger in impalas than it was in zebras (McGreevy, Landrieu & Malou 2007). The methods used to gain data, behavioural data, in particular need to be validated. For example, videoing behavioural analyses in their entirety would allow validation. Savin and Randle (2010) and Warren-Smith and McGreevy (2010) provided validation of the pedometers using this method.

Austin and Rogers (2012) employed the same method to investigate laterality preferences in a herd of 30 non-domestic adult horses (*Equus ferus caballus*) and found no population bias. These results agree with Wells and Blache's (2008) who found no population bias in 15 un-ridden horses of three years and under. Despite the age and associated stage of maturity differences within the groups being studied in social organisation both studies show no lateral preference. Furthermore, Greening and Randle (2012) did not find a population level laterality preference in their study of a herd of semi-feral Konik ponies, also using measures of position of the forelimbs whilst standing, the hind leg used to initiate movement and a preferred side in sternal and lateral recumbency. This study also used a small sample size of seven subjects. The authors have recognised the small sample size used and advocate that a larger population would provide greater confidence in the results however constraints on study samples are not uncommon especially in the Koniks study, by having a method that can be reliably used for a range of equid species under various experimental conditions. It could be argued that the evident lack of a laterality bias in the studies on wild horses may result from the lack of handling. They are not subject to practices such as being led and mounted from one particular side (generally the left) that may have inadvertently influenced lateral biases in domesticated horses.

Humans determine the nature of the environment in which the animals are kept including the size of their immediate environment – for equids that means field paddock stables and even the area that they are worked in e.g. school size. Currently there are limited studies investigating the effect of the environment on motor laterality. Zucca *et al.* (2011) investigated whether environmental constraints have an impact on lateral preferences in adult donkeys (*Equus asinus*). Subjects in their study showed a population bias to extend the right limb during standing behaviour. Observations were carried out over a 30-45 minute period whilst subjects were in their residential paddock of approximately 600m<sup>2</sup>. After the subjects were transferred and habituated to a paddock of half the size i.e. 300m<sup>2</sup>, the same procedure was used to identify whether this change in space availability had an impact on the lateral preference of the subjects. Interestingly after the reduction in space availability the population bias for a right lateral preference in extended forelimb disappeared. The results from this study show that environmental aspects can influence the occurrence of motor laterality. The effects of environment on laterality biases is an area that needs further examination and the outcome may have a significant benefit for those responsible for animals in captivity to enable them to provide suitable housing.

### **1.6 Measures of laterality**

Pedometers have been used to simultaneously record the activity of both forelimbs in domestic horses (Savin & Randle 2010) (for review see appendix 1) (Warren-Smith & McGreevy 2010). The use of pedometers may provide a reliable indicator of lateral preference based on the assumption that the advanced limb may have taken more steps than the non-advanced limb. Although small sample sizes were used (24 horses and 6 horses respectively) Savin and Randle (2010) and Warren-Smith and McGreevy (2010) both found that significantly more steps were taken with the left leg than the right leg in both populations of horses studied. This method does not introduce any operator effect as



pedometers can be securely attached to each subject and they can then be left in the environment i.e. without human interference. However, as only small sample sizes have been investigated using this method, results may not indicate a population bias and it would warrant further studies of larger populations.

It is important to consider Warren-Smith and McGreevy's (2010) proposal that the extended limb is the stronger limb as it would have encountered more steps through movement. This opposes McLean and Mclean (2008) that the non-advanced limb in grazing behaviour is supporting the weight of the horse and is better positioned to initiate the flight response, therefore it is the stronger forelimb. This is an area that would warrant further examination, possibly with sensor pads where weight distribution can be measured. The observational methods used in Warren-Smith and McGreevy (2010) and Zucca *et al.s* (2011) studies do not introduce any unwanted influencing factors such as observer effect, therefore this method can be applied to all quadrupedal grazers (McGreevy & Thompson 2006 ; McGreevy *et al.* 2007 ; McGreevy & Rogers 2005). Corballis (2008) suggests that when referring to wild animals that move freely in their natural environment, bilateral symmetry is adaptive and symmetrically placed limbs allows better linear movement therefore more efficient motion, whereby domestication and unnatural practices greatly influence the innate laterality biases in non-humans.

### **1.7 Physical attributes of lateral preferences**

Lateralised grazing behaviour has led to the occurrence of physical hoof asymmetries in grazing quadrupeds (Van Heel, Kroekenstoel, Van Dierendonck, Van Weeren & Back 2006). These asymmetries form in the equid's early years. As the grazing posture is developed, repeated and maintained, limb loading between both forelimbs for prolonged periods causes the hooves to develop asymmetrically and become uneven (Van Heel *et al.* 2006).

Horses that displayed a significant motor laterality bias had a higher likelihood of the occurrence of uneven feet compared to the horses that did not show a laterality bias. Over time, the protracted limb develops a more acute hoof angle (Van Heel, Van Dierendonck, Kroekenstoel & Back 2010).

Hoof symmetry is seen as an important conformational trait and Breed societies assess hoof symmetry at stud book inspection (a set of rules that lists all pedigree horses in a particular breed). Horses with uneven feet are rejected as it is believed that the unevenness in the hooves is a heritable trait that can be reduced by selection (Durco, Bovenhuis & Black 2009). Casanova and Oosterlinck (2012) provide further evidence of hoof conformation show this trait may be inherited. Analysis of the hooves of a group of 32 pre-slaughter horses whose hooves had received no attention found there was a prevalent left-right symmetry. Lateral preferences have also been shown to affect motor performance in the domesticated horse (Van Heel *et al.* 2006). In many species, limb preference in locomotion has received increased attention as the limbs are the primary element in motion. Martin and Lopez (2001) propose limb asymmetry may hinder the body's movement and have negative consequences on locomotive performance. Consideration should be given to prey animals as the authors went on to find a decrease in escape behaviour in Lizards (*Psammodromus*) that had larger limb asymmetry. Motor laterality may have negative consequences on musculoskeletal health (McGreevy & Rogers 2005) and consequently safety implications for the horse (Murphy & Arkins 2008).

It is likely that the occurrence of asymmetry in appendages will result in disrupted movement patterns. There have been reports of uneven limb structures in many other species including the Thoroughbred (TB) horse. For example it has been documented that TBs have larger left hind limb bones compared to the right (Pearce, May-Davis and Greaves

2005 cited in McGreevy and Thompson 2006) and longer bones in the right forelimb compared to those of the left forelimb (Davies, Gale and Baker 1999 cited in McGreevy and Thompson 2006). These studies do not identify which actual bones are responsible for these overall differences in limb size. Conformation traits have shown a significant left-right difference in the hoof and heel measurements of National Hunt horses (Weller, Pfau, May & Wilson 2006). Carmeli, Patish and Coleman (2003) found the human hand-arm system is subject to many physiological and anatomical changes over a life span.

McGreevy and Rogers (2005) suggest there is no lateralisation found in the flexing of the hind limb in domesticated horses and any slight bias does not associate with any fore limb bias. Singh (1971) observed hind limb dominance in rabbits (*Oryctolagus cuniculus*) and frogs (*Anura temporaria*). They reported that dominance of the fore limb is not the same as dominance in the hind limb and there was variation in the bone weight of the favoured limb compared to that of the non-favoured limb in both rabbits and frogs.

The fact that handling and training of non-humans may modify motor preferences exhibited for a particular side must be acknowledged. Traditionally equids are handled (McGreevy & Thompson 2006 ; Farmer, Krueger & Byrne 2010) and mounted (Sankey *et al.* 2011) from the individuals left hand side. This may lead to adaptation of the innate laterality preferences and as Zucca *et al.* (2011) indicated could certainly affect the strength extent of and direction of the bias exhibited. Moreover McGreevy (2007) previously suggested that side biases in handling can affect behaviour, even when the subject is not being handled. In modern day equestrian disciplines such as dressage, the horse is required to be supple on both sides and be able to maintain an even balance whilst in motion. Being evenly balanced on both sides assists with athletic performance (Wells & Blache 2008) and is crucial for the performance required in disciplines such as dressage. As the horse moves in a straight line,

maximal biomechanical and motor efficiency is achieved (Murphy *et al.* 2005). In addition, some training practices have shown to exacerbate existing motor asymmetry due to differences between the left and right hind limb kinematics (Dalin, Magnusson & Thafvelin 1985). Kinematic (the study of motion) differences between the left and right limbs of eight month old Standardbred horses have been reported (Drevemo, Fredricsson, Hjerten & D. 1987). Fraser (1992) found most horses are thought to lead with the right leg whilst jumping. As McGreevy and Rogers (2005) previously expressed, this study did not take into account the direction of approach to the obstacle and moreover that the majority of horses involved within the study were found to lead with their right limb during the canter phase. Preference for forelimb leading will also depend on hind limb take off (first limb moved to initiate a pace)

Forelimb preference was investigated in 21 freestyle jumping horses (Baragli, Vitale, Cipollini & Sighieri 2012). Horses were required to complete three jumps on an anticlockwise oval circuit. Jump one was 20cm in height, jump two was 40 cm in height and jump three was 60cm in height. Laterality preferences exhibited differed at each jump. There was a higher incidence of a right lateralised bias at jump one, with five horses out of 21 (23.81%), jumping with their right forelimb ahead. There was a reduction in laterality bias seen at jump two, with three out of 21 (14.29%) horses showing a significant lateralised bias. Jump 3 resulted in three out of 21 (14.29%) horses showed a left bias and four out of 21 horses (19.05%) showed a right bias. The authors suggest that the expression of laterality preferences could be influenced by the height of the jump. Understanding how horses approach and jump obstacles may provide a further consideration to how horses interact with the environment. It may also give us better guidance on safety and handling measures around horses in our care.

Racehorses are required to perform at high speeds whereby they must use their leading limb whilst turning on the racetrack. Race courses are traditionally oval or circular and can be either anti-clockwise or clockwise. Whilst travelling on the straightest part, each horse can opt for which leading leg to use but around turns racehorses are biomechanically inclined to use their inside limb (i.e. the left forelimb would lead on an anti-clockwise circuit) (Adams 1979). Williams and Norris (2007) found that the racehorses in their study on an anti-clockwise race-track showed a preference for stride pattern whilst travelling on the straight, 90% of the horses preferred their right lead and the remaining 10% preferred their left lead. The authors note that experimental conditions including observers and equipment may have influenced the results. It is also important to note that these results contrast with an earlier study where a left lead preference was found, yet it is not stated if the horses were on a clockwise or anticlockwise circuit (Deuel and Lawrence 1987 cited in (Williams & Norris 2007).

McGreevy and Thompson (2006) suggest that breeding selection and/or training may have led to favoured motor preferences within a species. Thoroughbred and Standardbred horses showed a preference to extend the left forelimb in grazing behaviour, whereas Quarter horses did not exhibit a bias. This would agree with the notion that training practices influence biases, as the Thoroughbred and Standardbreds are predominately bred for racing. Motor differences have also been documented within domestic dog breeds (McGreevy, Brueckner, Thompson & Branson 2010).

Limb preference has recently been investigated by a first stepping test. This novel assessment has been primarily studied in domestic dogs. It involves recording the limb that initiates movement from a standstill and it is proposed that first stepping behaviour is a reflection of loco-motor behaviour (Tomkins *et al.* 2010). A favouring element to this

method is that it is easily measurable and observer effect can be kept to a minimum. This technique can be easily applied to the horse. Despite its uncomplicated method there are few documented studies involving this method on horses. Murphy *et al.* (2005) found that in a group of 40 horses of mixed breed sports horses there was a higher incidence of lateralised behaviour shown in limb movement as opposed to equal limb movement but there was no difference between the numbers of horses that displayed left or right responses to initiate movement. Grzimek (1968 cited in Murphy *et al* 2005) found that there was an overall bias to use the right forelimb to initiate the walk. This area would warrant further studies and can be easily applied.

Corballis (2008) states that the most prevalent case of limb asymmetry in non-humans is that seen in birds. Reflecting the outcome of Rogers (1980) who found that 90 per cent of parrots (*Psittaciformes*) will raise their left foot during feeding. The New Caledonian crow (*Corvus moneduloides*) displayed prominent lateralised behaviour during tool manipulation (Hunt, Corballis & Gray 2001). The Japanese Jungle Crow (*Corvus macrorhynchos*) displayed lateralised behaviour during scratching behaviour and holding behaviour (Izawa, Kusayama & Watanabe 2005).

### **1.8 Sensory laterality**

Sensory dominance is another subfield of laterality. It is manifested by ocular dominance, olfactory dominance and auditory dominance. These preferences are controlled by specialist hemispheres of the brain. Sensory dominance is an attribute seen in humans and mammals. This was originally not understood due to the lack of knowledge of hemispheric specialization, for example for visual attention (Roth, Lora & Heilman 2002). Rogers (2010) proposes eye, nostril and ear preferences can be used to understand more about cognitive

processes. By identifying which eye, ear and nostril are being used can also represent how the subject is processing the environmental stimuli.

Visual lateralisation is easily measured in non-humans that have laterally placed eyes (De Boyer des Roches *et al.* 2008) such as some breeds of birds, fishes and reptiles (Sovrano, Rainoldi, Bisazza & Vallortigara 1999). Chicks were found to be better in some tasks when only sight from one eye was available (Tommasi, Andrew & Vallortigara 2000). The left eye use was associated with better performance in spatial tasks (Rashid & Andrew 1989). The horse has almost absolute decussation of the optic fibres (Cummings and De Lahunta 1995 cited in Austin and Rogers 2012). This means what is seen in one monocular field is processed with the contralateral hemisphere (Sankey *et al.* 2011). It has been documented that horses prefer to view negative emotionally valued objects such as veterinary shirts (De Boyer des Roches *et al.* 2008) with their left eye, which agrees with the earlier findings from Austin and Rogers (2007) and Sankey *et al.* (2010) where there is a greater reaction to adverse stimuli presented to them on the left and it is viewed with the left eye. Farmer *et al.* (2010) found that horses preferred to view humans with their left eye, even if the horses were trained from both sides. The greater response to left presented stimuli may be attributed to regular handling practices (i.e. being led and mounted from the left). Another notion may be because it is the result of a right cerebral hemisphere function. However, Nicol (2002) suggests that startle responses in horses may occur because the object has a different appearance when viewed from the opposite direction and is not associated with any neural shortfall in information processing capability. De Boyer des Roches *et al.* (2008) also suggest that stimuli with different emotional significance could induce different lateralised responses as measured through lateralised perception. If lateralisation is stimulus

specific this can be an indicator of eye preference (Bisazza, Facchin, Pignatti & Vallortigara 1998).

### **1.9 Conceptual theories on lateral preferences**

A fundamental point that must be remembered is however laterality is manifested, whether cerebral, motor or sensory, it should be regarded as a matter of degree rather than as an absolute (Rogers 2010). Results of a growing number of experimental studies show laterality must be considered as a continuous phenomenon (Eling 1981 ; Tommasi 2009). Since results of the majority of species studied show a high degree of individual variation in the strength of lateralisation exhibited (Reddon, Gutierrez-Ibanez, Wylie & Hurd 2009) it is important that the existence of individual differences must be taken in to account.

Several studies have found laterality preferences exhibited can alter with age in a number of different species including horses (McGreevy & Thompson 2006). Unhandled Thoroughbred foals above two years of age displayed a greater lateral bias in extended limb activity compared to unhandled foals that were under two years of age (McGreevy & Rogers 2005). Studying laterality in adults in many species including humans, poses various challenges, due to the many factors that may affect asymmetry. As Lane and Phillips (2004) suggest studying neonates allows many of those factors to be eliminated.

Measuring laterality does not come without its challenges. At present there is not one single test to measure lateral preferences and there are many factors that may affect the strength and the preference of the bias. The longstanding measure of hand preference in humans is now found to be a weak indicator of laterality and Elias, Bryden & Bulman-Fleming (1998) suggested that foot preference should be used as a measure instead. To support this suggestion there is evidence that suggests handedness in humans is a learnt behaviour (Klar



1999) and its manifestation can, as with other forms of laterality increase with practice (Santin, Begega, Rubio & Arias 1996 ; Vallortigara & Rogers 2005).

Motor laterality can be task dependent as shown in Tomkins *et al.* (2010) study. The lateral preference that dogs displayed during a first stepping test decreased when the same subjects performed a foraging based task. Squirrel monkeys (*Saimiri sciureus*) displayed different lateral preferences in a series of food reaching tasks (Laska 1996). These differences diverge from the evidence Murphy *et al.* (2005) present during their study where there was a correlation between first limb to initiate movement and directional bias around a barrier.

Displays of motor laterality have been found to be species-specific (Corballis 2008) as shown in the rhesus monkey (*Macaca mulatta*) (Vogels, Saunders & Orban 1994 ; Hopkins, Wesley, Russell & Schapiro 2006) and the Poeciliid fish (Bisazza *et al.* 1998). Vallortigara and Rogers (2005) suggest that it is hard to establish whether species variations in the direction of laterality reflect the differences in laterality or whether they reflect different behavioural strategies used in animal behaviour. Anatomical differences between different species may be responsible for the outward manifestations of laterality displayed such as grip use. The physical capabilities may limit some species in outward displays of lateral preferences.

### **1.10 Cognition**

Despite many years of research, the effects of laterality have not been documented. Over time, breeders of equids may have affected the laterality preferences by selecting for different flight responses as there is a strong relationship between laterality and emotionality (McGreevy & Thompson 2006) which was explored earlier (e.g. novel situation and eye preference). A difference in cerebral lateralisation may show a relationship with

individual variation manifesting in individual characteristics and behaviours (Reddon & Hurd 2009). Individual differences will have an impact on the laterality measure shown.

Vallortigara and Rogers (2005) express the apparent disadvantages to having an asymmetrical perceptual system. Prey animals may be vulnerable to attack on one side due to cerebral dominance and the specific functions of each hemisphere. Rogers, Zucca & Vallortigara (2004) maintains that lateralised brains are more efficient in terms of cognition and fitness and problem solving is aided by lateralisation (McGreevy *et al.* 2010). This finding agrees with the suggestion that laterality preferences can be dependent on cognitive function (Fagot & Vauclair 1991). Farmer *et al.* (2010) and Zucca *et al.* (2011) suggest that laterality could provide important information about the horse's cognitive processes and cognition tasks such as detours can be enhanced by cerebral lateralisation. Cognition is commonly defined as the process by which we detect and respond to information around us (Davenport 1995). It is also the general term which we give to mental activities, such as remembering, forming concepts, using language or attending to things (Hayes 1998). It is also described as variety of mental abilities from perceiving and sensing through conceiving and understanding a notion (McLean 2001).

Animal cognition is a growing subject that has seen substantial advancements in the last century, particularly in the areas of both evolution and ecology (Church 2001). The first studies on animal cognition primarily involved non-human primates and now include mammals, birds and fish. Despite the progressive knowledge that has been attained from these studies, it must be appreciated that our understanding of such a vast and complex subject is still limited. A major hurdle in this sphere is that interpreting the mental abilities in non-humans is not straightforward (McLean 2001).

Pearce (1987) theorises that the study of any mental process in non-humans is problematic because the subject matter is not directly observable.

Many of the cognitive tests that were once applied to horses did not take into account their cognitive limitations. It was once a common belief that domesticated horses are not very intelligent and they were only kept for farm labour and for the racing industry. A limited understanding of the complexity of animal minds has meant some cognitive abilities have been underestimated (McLean 2001 ; Hanggi 2005). It is important to appreciate the mental abilities of non-humans so that adequate training and husbandry regimes can be introduced (Sankey *et al.* 2011), subsequently enhancing equine welfare.

Spatial cognition and the ability to successfully navigate are vital for both domesticated horses and feral equids. In the wild, horses will travel over substantial distances (Hampson, de Laat, Mills and Pollitt 2010) to obtain sufficient grazing and have displayed seasonal migratory behaviour (Leblanc & Duncan 2007). In order to move and obtain a goal, navigation has to be precise. There are several cues such as land marks that can be used to aid navigation and different species use different strategies. The significance of each cue can also vary. It appears that horses discriminate by spatial cues more than any other stimulus features, including visual specific cues (Nicol 2002 ; Hothersall, Gale, Harris & Nicol 2009).

Cognitive maps have been used by scientists to describe how animals develop a complex representation of their environment. These maps encompass routes and relationships between objects so the animals can make decisions about where to go (Tolman 1948). Lund (2002) states there are opposing theories on cognitive maps and the differences among species may reflect the differences shown on performance, but there are also different interpretations on cognitive maps. Cognitive maps have seldom been described in horses, despite the horse's spatial ability.

### 1.11 Spatial awareness

The hippocampus is a structure in the brain that is important for spatial awareness and navigation, including spatial memory and visuo-spatial abilities. It plays a fundamental role in long term memory acquisition and information consolidation (Clayton 1998) and has long been associated with spatial memory tests. It is responsible for associating a conditioned stimulus with an unconditioned stimulus (Bevlin, Gandhi, Wood, Talk, Matzel *et al.* 2001). Many studies note the differences between the hippocampus size and spatial behaviour between male and female mice (*Mus musculus*) (Bian, Zhu, Guo, Xiong, Cai *et al.* 2012). Voles (*Arvicola amphibious*), rats (*Rattus*) and cowbirds (*Molothrus*) also show a sex difference in comparative size of the hippocampus (Peterson & Sherry 1996), with the majority of males having the larger hippocampus. A difference in the hippocampus size between mares and geldings has not been fully investigated.

Males in many species may have a genetic and hormonal mechanism to ensure visuo-spatial superiority (Stavnezer, McDowell, Hyde, Bimonye, Balogh *et al.* 2000). They also have superior spatial abilities compared to females (Murphy, Waldman & Artkins 2004). This primacy may have progressed through evolution (Ecuyer-Dab & Robert 2004). It is probable that spatial cognition would have been primarily shaped by the sexual selection pressures to compete for navigational behaviours such as foraging and mating (Ecuyer-Dab & Robert 2004).

Bradshaw (1991) stated that females of any species show higher motor lateralisation in general compared to males. Studies in rats have found males and females use different spatial cues when solving maze style tasks (Roof & Stein 1999 ; Murphy *et al.* 2004). Female mice show a motor bias to the left when placed in a maze style enclosure (Andrade, Alwarshetty, Sudha & Chandra 2001). Female sea lions (*Zalophus californianus*) have a

preference for swimming in a counter clockwise direction, where the males had a preference for swimming clockwise (Wells, Irwin & Hepper 2006). In a study of 40 horses Murphy *et al.* (2005) demonstrated that males displayed more substantial left lateralised behaviour compared to females who displayed significantly more right lateralised behaviour.

Within many equestrian competitive disciplines there is anecdotal evidence to suggest geldings are considered more successful than mares. This proposition has since been challenged by Whitaker *et al.* (2008) who reported no difference in the event ranking of mares and geldings in a population of >1000 horses. However despite the outcome the authors acknowledge that there are difficulties in understanding the connection between performance and equine gender.

Motor laterality and spatial performance are probably influenced by the visuo-spatial abilities of the subject and not just the sex of an individual. Furthermore the performance of the subject during a detour task can be influenced by many factors. Consistency in the direction manoeuvred around the barrier may be a consequence of the first choice being successful (Regolin, Vallortigara & Zanforlin 1995 ; Baragli *et al.* 2011b). Pongracz, Miklosi, Kubinyi, Topal & Csanyi (2001) found dogs exhibited a preference for the side that they found initially successful during a detour task. Moreover the preference to return to the successful side was apparent after the first trial. During this study only dogs older than one year were included and a variety of breeds were used. The goal in the detour study was either a piece of food or a favourite toy. The researchers asked the dog owners which would be more appropriate for motivating the dogs behaviour.

This agrees with the findings of Hosoi, Swift, Rittenhouse & Richards (1995) who found that during a T-Maze style task both goats and sheep tended to return to the side that was previously successful, this is termed a win-stay strategy. The win-stay strategy seen in this

experiment may be a result of laterality preference and is often seen in maze style settings. Subjects within test conditions adapt more readily to situations that favour their preferred side (Andrade *et al.* 2001). Lateralised behaviour appears to differ and alternate as a result of altered experimental schedules (Fagot & Vauclair 1991)

Maze style studies were introduced to quantify a variety of behaviours including behavioural lateralisation and spatial navigation, which is often studied in the T-Maze or Y-Maze experiment (subjects are placed at the end of the long corridor and are given a choice of which arm to proceed along). Kight *et al.* (2008) found that in a sample of giant water bugs (*Heteroptera: Belostomatidae*) studied in a T-Maze, displayed a higher tendency for the same direction bias where there was no reinforcement strategy in either arm. This population was not displaying the win-stay strategy. Marinier and Alexander (1994) have demonstrated that horses are capable of successfully completing maze style experiments, which may suggest evidence of a win-stay strategy.

### **1.12 Factors affecting laterality**

Other factors that affect laterality include domestication; differences have been discussed in domesticated horses and feral horses. Smith and Litchfield (2010) found that dingos completed detour tasks more quickly and showed no signs of behavioural frustration or confusion and completed the task with fewer errors compared to that of the domestic dogs.

Factors in the experimental design can all affect the behaviour displayed during a detour task. These include number of trials, complexity of task, angular deviation of the available path or paths that lead to the goal and the nature of cues whereby the goal can be located (Rogers & Andrew 2002). Gregorios-Pippas, Tobler & Schultz (2009) advocate that temporal delay can devalue a goal.

Detour tasks incorporate the delayed response task, whereby not only do the subjects have to move around a solid barrier to reach a goal but remember the location of the goal after it disappears behind the barrier. The delayed response is a behaviour that presents a demonstration of a well-developed temporal cognitive process. McLean (2004) proposes that mental representations induce the potential capability of higher mental abilities because the subject must recall the location of the goal when it has disappeared. Successful problem solving relies on subjects having the ability to act on certain responses that have either been pre-programmed or have been reinforced in the past (Vlamings *et al.* 2010).

A knocked down fence can be classified as a barrier during show jumping events. Stachurska Pieta & Nesteruk (2002) found that the wall style jump was more problematic for show jumping horses. It caused more horses to refuse jumping the obstacle. The authors theorise that it may be because of the solid appearance of the wall which may be responsible for the horses refusing the jump. Equine trainers will often concentrate on areas of weakness but the consistent problems that are caused by the solid barrier style jump may imply the difficulty that horses have with solid barriers.

### **1.13 Temporal delay and the delayed response**

The barrier plays a fundamental role in the detour task. Transparent barriers cause bigger problems than opaque barriers (Vlamings *et al.* 2010) and this occurrence is common across species (Pearce 1987). If the barrier is transparent and the subjects can see the goal the more direct route is taken. This shortfall can inhibit problem solving. Shiller (1949 cited in Rogers and Andrew 2002) trained Minnows (*Phoxinus phoxinus*) to perform a detour task. The subjects performed better at the task if they could not see the goal on approach. A similar occurrence was reported in chicks (Regolin *et al.* 1995).

Detour tasks require subjects to have an internal representation of the hidden goal. Having the awareness to recognize that objects are separate to their surroundings and will still exist when they are moved out of the observer's sight is termed object permanence (Mendl & Nicol 2009). Object permanence is important in human cognitive processes as it is an indicator of cognitive development. The question has been raised as to whether object permanence exists in non-humans. It has been documented in chickens, parrots and dogs (McLean 2004). Previous research has shown that horses are able to successfully complete detour tasks, indicating the existence of object permanence. An opposing theory is that, horses have limited recall ability and have difficulty with temporal delays (Murphy & Arkins 2007). Studies have demonstrated that temporal delay can have an impact on recall ability in species, including Monkeys (Stevens, Rosati, Ross & Hauser 2005) and gold fish (*Carassius auratus*) (Gee, Stephenson & Wright 1994).

The delayed response element during the detour task can be an inhibiting factor on performance. The preference for small immediate rewards over larger rewards after a delayed period of time is called temporal discounting and different species diverge in their capability to wait for delayed rewards in temporal choice tasks (Stevens & Muhlhoff 2012). Investigation of temporal discounting was once restricted to studying this process in primates and rodents (Freeman, Green, Myerson & Woolverton 2009). Lemurs (*Lemuriformes*) do not appear to maximise their food intake. Stevens and Muhlhoff presented 12 lemurs with a choice having two food rewards immediately or six food rewards after a delay. After this choice test the authors introduced a time delay to obtain the larger reward (based on the performance of the subject in the previous session). It was found that neither the short or long term rates accounted for the in-temporal choice patterns that were observed. There are few documented studies on temporal discounting in prey species,



further investigation into temporal discounting in prey species would greatly be welcomed to understand more about foraging behaviour.

McLean (2004) investigated object permanence along with the delayed response in horses. His study required subjects to remember which feed goal contained the reward. He found subjects were able to make a correct choice after observation and immediate release. But after observation and then a 10 second delay before being released, subjects were unable to distinguish between the correct feed goal and the empty feed goal. At present there are contrasting findings on the limited studies involved in equine short-term memory. Baragli *et al.* (2011a) examined equine short-term spatial memory, with the use of delayed response during a detour task. His study consisted of a feed goal that disappeared behind either one of two identical barriers. Subjects were released after a 10 second or a 30 second delay with the intention of obtaining the feed goal. The authors established that subjects would make more correct choices than incorrect choices in both time trials. The study concluded that the subjects had encoded and precisely retrieved the spatial location of the feed goal.

Spatial memory with regards to food choices has been documented in other species. Cattle can remember where preferred food is located for up to a period of 48 hours (Ksiksi & Laca 2002). Gerbils (*Gerbilinae*) can remember where food is based on just one landmark (Collett, Cartwright & Smith 1986). Sheep can form different associations between different cues and different food rewards (Edwards, Newman, Parsons & Krebs 1996 ; Edwards, Newman, Parsons & Krebs 1997). The importance of grazing herbivores to have the ability of remembering food locations will help with survival.

#### **1.14 Equine behaviour**

Attention, fearfulness and motivation will establish the achievement in both test and real life situations (Nicol 2002). Mendl, Burman, Parker & Paul (2009) suggest that in human

psychology, an individual's cognitive processes and memory are influenced by the individual's emotional state. This theory can be applied to the animal sciences. The willingness for horses to work towards obtaining a goal may be reliant on their motivational state. The amount of work performed during a cognitive based task may be dependent on the magnitude of the reward.

Horse riding and involvement with horses has seen a rapid growth in the United Kingdom. The British Equine Trade Association national equestrian survey 2011 reports that horse riding related activities are now considered a major leisure activity. It also reports that during 2010-2011 an estimated 3.5 million people partook in leisure riding activities with approximately 1.6 million people riding at least once a month (British Horse Industry Confederation 2011). Riding schools are the conventional way that people can learn about handling and riding equids (Kiley-Worthington 1997) and are the first opening to the equine industry.

The domesticated environment can be difficult for animals as many challenges they are required to deal with are neither solvable or escapable (Morgan and Tromberg 2006 cited in (Meehan & Mench 2007). At present many domesticated horses including riding school horses are kept in largely unsuitable environments and they are required to suppress natural instincts (Hanggi 2005). Many of the equines kept and used as riding school horses are ridden in enclosed areas, for several hours a day (Kiley-Worthington 1997) with limited access to grazing and conspecific interaction. It has been recognised that some management practices such as small housing and long periods in isolation without interaction from conspecifics may introduce stress and subjects may show unresponsiveness to certain stimuli (Hall, Goodwin, Heleski, Randle & Waran 2008).

Behavioural responses have been identified by scientists as a reliable indicator of the animals quality of life and their well-being (Mills & Nankervis 1999). To measure the comfort of riding school horses, behavioural tests that examine exploratory behaviours and the ability to learn could be implemented and used as a measure of assessing the welfare of riding school horses (Hall *et al.* 2008). Nicol, Badnell-Waters, Bice, Kelland, Wilson & Harris (2005) introduced novel objects to foals from 2-40 weeks and found the greater the amount of time subjects interacted with a novel object compared to the subjects who spent their time only looking at it appeared less stressful.

Randle (2008) identified three groups where behaviours can be categorised, during a cognitive task using equine subjects. They focused on task related behaviours, non-task related behaviours and human directed behaviours. This method may act as platform to objectively assess the welfare of the subject.

It is important to remember the physical and cognitive limitations of some non-humans and mismatching of subject to tasks may undermine the objective being investigated. Often when non-humans are forced with a challenge, there may be an inconsistency between what is expected of them and the situation in which they are required to cope (Meehan & Mench 2007). Careful matching of tests to particular non-humans may give us greater confidence in the results.

Regardless of the increase of scientific interest, there are still areas where knowledge is sparse (Nicol 2002). A further understanding of laterality biases in equids may help us understand what modern day handling and husbandry practices are having on innate lateral biases, and whether the lateral preferences hinder or aid this movement. This study may contribute to our understanding of equine motor lateralisation and its relationship to

cerebral dominance. It is intended to increase our appreciation of the limitations and capabilities of equine cognition and the potential problems with laterality.

The aim of these studies was to examine the effects of lateralisation in horses when presented with a detour-based problem solving task. Study 1A required the subject to navigate around barrier at 3 different distances (4 metres, 6 metres and 8 metres). Behaviours exhibited throughout the detour task were recorded and measures of behavioural intensity and behavioural diversity were derived and analysed this same method was used by Randle (2008). Study B was carried out to examine whether horses consistently show a directional preference in their detour behaviour. Lateralisation preferences of the subjects were also examined during a ridden exercise, study 2. The Null Hypothesis ( $H_0$ ) was that there is no evidence of lateralised behaviour when assessing preference using a detour task and the Alternative hypothesis ( $H_a$ ) was that there is evidence of lateralised behaviour when assessing preference using a detour task were tested. The same hypotheses were tested for detour study part B. In the ridden exercise The Null Hypothesis ( $H_0$ ) was that horses do not exhibit a preferred limb when faced with an obstacle when ridden. The Alternative Hypothesis ( $H_a$ ) was that horses do exhibit a preferred limb when faced with an obstacle when ridden.

## **2 Methodology**

### **2.1 Pilot Studies**

Two pilot studies were conducted to assess the intended experimental design and the accuracy of data obtained using the planned methodology, after approval from Plymouth University was gained. The first pilot study was performed during May 2011 at a private yard. Four subjects (of various ages, breeds and sexes) were required to obtain a goal, which was a piece of carrot place in a food bucket. The goal was placed behind a 1m x 1m plywood

barrier. The barrier was positioned 3m from the goal and each subject was positioned at a distance of 1m from the opposite side of the barrier. Each subject was released simultaneously they observed the carrot being dropped in the bucket. The time in seconds from release to reaching the goal was recorded. Successful trials were followed by extension of the distance from the barrier to the goal, to 4m and then to 5m. One observer stood behind the goal videoing all behaviours and after completion of the task at 4m, moved the goal so it was 5m away from the barrier. A trial was deemed successful once the subject had touched the goal. If a subject failed to complete the trial within 180 seconds, the observation period was terminated and recording was terminated in accordance with Randle (2008). All trials were videoed in their entirety to provide a continuous record of behaviour exhibited by subjects during the trial. Individual behaviours were identified and their frequency and duration recorded. Behaviours were categorised as task related, non-task related and human directed (shown in Table 1). Further measurements included which forelimb initiated movement, the direction moved around the barrier and extended limb at the goal.

Each pilot study was conducted at the subjects' own yard. The first pilot study was carried out in a large concreted area in between the subjects' fields and the entrance to the barn. The barn is used to house the subjects during the night and short periods during the day, depending on husbandry and veterinary practices. At the time of the study three conspecifics were housed in the barn. The presence of environmental stimuli, including a conspecific in a neighbouring barn and noise distraction such as road traffic and machinery may have influenced the subjects performance on the task behaviour. It was therefore decided that subsequent studies should take place in a controlled environment where external distractions could be kept to a minimum.

During the study the barrier seemed a little small in proportion to each subject used. In particular the barrier appeared to be very narrow. The 1m x 1m barrier needed enlarging to increase the physical effort/work required by the subject to reach the goal. After expansion the size of the barrier was similar to those used in other current studies. Similarly the distance between the barrier and goal at each trial appeared too short. A decision to lengthen the distance between the barrier and goal at each trial was taken based on the more steps each subject has to take. There are few documented studies discussing the appropriate size of barrier used in a detour task compared to the subject used and the distance between the barrier and the goal.

## **2.2 Pre-test training**

A pre-test training (PTT) task was implemented and completed by each subject. The subject was required to observe a piece of carrot being dropped in to the bucket and on immediate release to move towards the goal and touch the goal without detouring around the barrier. Each subject had to complete three consecutive successful trials to be included in the main study; if the subject failed they were eliminated from the study. Pre-test-training allowed the subject to associate the bucket with a food reward primarily through classical conditioning. All subjects who took part in the PTT completed the task and then went on to the detour task.

A second pilot study was conducted during August 2011. The yard was independent of that used in the first pilot study. Different subjects were used so there was no chance that learning had taken place. A revised design was used, a larger barrier was made and the distance from the barrier to the goal was extended. Four subjects were involved in this study. One horse failed to complete the pre-test training task and was eliminated from further trials.

Once the procedural changes had been confirmed the study was re-submitted for ethical approval which was accepted by Plymouth University.

### **3 Study 1(a)**

This study took place at two locations, first, Duchy College Equestrian Centre at (part of the University of Plymouth) and second, Bridgwater College Equestrian Centre. The equestrian centres are similar in set up. Fixed term-time is 30 weeks per year, horses work up to 3 times per day on Monday to Friday and have the weekends off. All horses are cared for by students supervised by industry qualified personnel. The breed profiles of horses at each establishment are also similar.

#### **3.1 Subjects and Ethics**

A selection process of all subjects within the study depended partly on being informed by yard managers which subjects were available at the time of data collection. Evaluation of the suitability of each subject was conducted by those responsible for the health and wellbeing of the subjects. All subjects available at the time of data collection were deemed suitable for each task. Rejection would have occurred for example if subjects were visually impaired as they would not have been physically capable of engaging in the required task. Visual assessment of subjects is conducted when they are first brought to the college, therefore visual analysis had already been tested.

Twenty three subjects were used. Ten subjects were from Duchy College Equestrian Centre and 13 subjects were from Bridgwater College Equestrian Centre. Subjects consisted of 5 mares and 18 geldings of various breeds and all were used as riding school horses. They ranged from 6 to 27 ( $14.4 \pm 4.79$ ) years of age. Subjects were owned either by the college or by students. When stabled at the colleges, water and forage is provided *ad libitum*. All subjects have come from different backgrounds and have all been handled predominantly

from the left as per industry training (The British Horse Society 2005). They were therefore considered representative of the general owned horse population. During the study, subjects wore standard head collars and were manoeuvred using standard lead ropes (which were removed when testing commenced).

### **3.2 Observers**

Two observers assisted in all phases of the experiment at both Duchy College and Bridgwater College. Behaviours were recorded on a Flip video <sup>TM</sup> (Ultra HD) by an observer who stood at the back of the experimental area, 2m behind the goal. This observer was also responsible for dropping the carrot into the bucket (i.e. the goal). The second observer led the subject (from the left side) out of their stable (which was in an adjoining barn) to the starting point. Once in position the subject was stood square (both pairs of fore and hind limbs parallel, no limb in advance of its pair, and no limbs resting) released by detaching the lead rope simultaneously with when the carrot was dropped in to the bucket. This procedure was used during all three phases detour testing (as in figure 1).

### **3.3 Materials**

The experimental locale at Duchy College consisted of a rectangular area 4.43m x 9.7m concreted semi enclosed area which is used as the farriery area and practical area within the Duchy College Equestrian Centre as shown in Figure 1. Yellow chalk was used to mark the 4M point, 6M point and 8M points on the floor. These points were situated along the centre line of the area. The barn's stone construction allowed the minimisation of environmental stimuli ensuring that potential visual, auditory and other environmental distractions were kept to a minimum. A replica size area was made at Bridgwater College in part of the indoor school as the study area. In both establishments a 1.82m long and 0.60m wide barrier was constructed from shaving bales, Baragli *et al.* (2011b) also used a shaving bale in their study.



The barrier was a similar size used in Murphy *et al.*'s (2005) study. A yellow bucket was used to hold the goal. Yellow was specifically chosen because equids have been shown to be able to easily discriminate the colour yellow from other i.e green, purple and red (Hall & Cassaday 2006) ; (Blackmore, Foster, Sumpter & W. 2008). Other cognitive based studies have used deliberately used yellow objects (Cozzi, Lafont Lecuelle, Monneret, Articlaux, Bougrat *et al.* 2011).

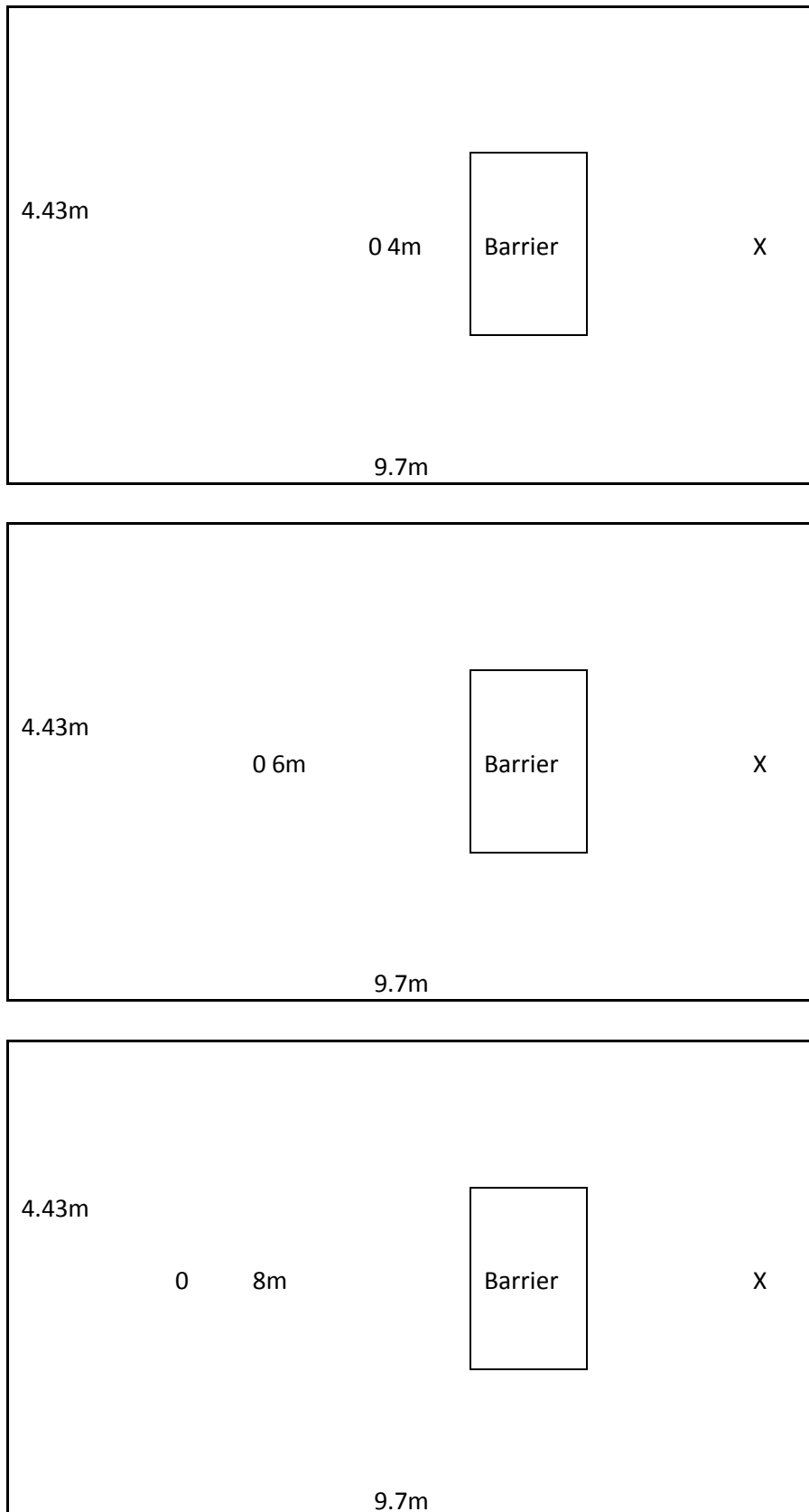


Figure. 1 The study area at all trials X =positioning of subject release at test start O = observer behind goal.

### **3.4 Experimental Conditions**

This experiment included four different trials: pre-test training (PTT); detour task at 4 metre (4m); detour task at 6 metre (6m); and detour task at 8 metre (8m).

### **3.5 Pre Test Training**

Each subject was required to successfully complete three pre training tests in order to be involved within the main study. The subjects stood three metres away from a bucket into which the goal (a piece of carrot) was dropped; the subject was immediately released. The intention was that the subject would move to the goal and touch the carrot. After three successful trials the subject had met the inclusion criterion and could be included in the main study.

### **3.6 Procedure**

The barrier was placed 1m inside the experimental area and observer two led the subject to the starting point. Observer two made sure the subject stood square (fore and hind legs parallel to each other). Observer one stood behind the goal bucket, which was 4 metres the other side of the barrier from the subject. Observer one dropped the carrot into the bucket. Once the carrot touched the bottom of the bucket, observer two immediately released the subject by detaching the lead rope and remained stationary. The intention was that the subject navigated around the barrier to reach the goal. A trial was deemed successful when the subject touched the carrot, regardless of whether they ate it or not. The subjects were allowed a maximum time of 180 seconds to reach the goal. Successful trials were followed by expansion/extension of the barrier to a distance of 6m and 8m. If a subject failed to complete a trial successfully within 180 seconds the trial was terminated.

### **3.7 Measurements**

In all trials the first limb moved was recorded, based on the method used by Tomkins *et al.* (2010 and 2012). The direction taken around the barrier was recorded, based on the method

used by Baragli *et al.* (2011b). The extended forelimb at goal was recorded, based on similar methods used by McGreevy and Rogers (2005), McGreevy *et al.* (2007), Wells and Blache (2008) and Greening and Randle (2012).

### 3.8 Behaviours recorded

All behaviours were recorded using a continuous time sampling method for a maximum of 180 seconds. Recorded behaviours were subsequently categorised into task related, non-task related and human directed (see Table 1 behaviours and descriptions). The frequencies of these were totalled. In addition two overarching measures of behavioural activity were subsequently derived: Behavioural Diversity (BD, total number of different behaviours displayed) and Behavioural Intensity (BI, total number of behavioural actions displayed) using the same methodology as Randle (2008). Behaviours displayed were categorised in accordance with the ethogram (shown in Table 1) which was verified by equine personnel and based on other published ethograms (McDonnell 2003). Solving time between subjects will also be compared, as will the behavioural intensity and the behavioural diversity.

Table 1. Ethogram of behaviours displayed during the detour tasks.

Behaviour	Description
<b>Task related</b>	
Moves in direct line with goal	Facing goal whilst walking
Touching barrier with muzzle	End of muzzle or side of muzzle and face are moved backwards and forwards or side to side on barrier
Walk around barrier	Body parallel with body whilst in motion
Goal touch	End of muzzle is in contact with yellow bucket
<b>Non-task related</b>	
Snort	Fast expulsion of air from nostrils
Walk away from goal	Consecutive 4 strides with each leg in opposite direction from goal
Tail swish	Dock of tail is raised or moved from side to side
Pawing ground	Forelimb is raised, extended forward, dropped to the ground and moved back

Muzzle touch floor	Muzzle is brushed along the ground whilst horse is in motion
Wall touch	End of muzzle or side of muzzle and face are moved backwards and forwards or side to side on the wall
Ear move	Pinna is rotated or moved backwards or forwards
Head move	Head is moved from side to side or up and down
One step	One limb is raised and then lowered
Nose touch floor	Head is lowered until the tip of the muzzle is brushing along the floor
No movement	Horse is stationary
<b>Human Related</b>	
Observer touch	End of muzzle or side of muzzle and face are moved backwards and forwards or side to side on the observer

The categories presented in this ethogram, were based on an object related investigation. (Randle 2008)

## 4 Study 1 (b)

The aim of the detour study part B was to determine whether subjects consistently show a directional preference in their detour behaviour, regardless of distance to goal.

### 4.1 Methods

The study took place at Duchy College Equestrian Centre (part of Plymouth University). Ten subjects were selected at random from a population of 35 working horses eliminating subjects that are visually impaired (all horses had vetting in 2011). Each subject was required to eat a piece of carrot from a yellow bucket as a pre-test training task (as used in experiment one December 2013). The experiment was conducted in a 4.43m x 9.7m concreted semi enclosed area (as used in experiment one). A solid 1.82m x 0.60m barrier, made from shaving bales (as in experiment one), was placed 1m inside the experimental area. A yellow bucket was placed 4 metres from the barrier (as in experiment A). Three observers were present during all stages of the experiment. Observer one was located

directly 2m behind the goal, videoing the trials in their entirety and dropping the reward into the bucket at the start of each test. All behaviour occurrences were videoed. The frequencies of behaviours were subsequently extracted, recorded due to the behaviours being independent and of short duration. Observers two and three stood on either side of the subject and lead them to the starting point which was 1m directly in front of the barrier. Subjects wore a head collar with two lead ropes attached to the head collar, thus allowing them to be led from both sides at the same time by observer two and three, in order to control for a handler induced bias. The subject was be required to stand square (front limbs parallel with each other and hind limbs parallel with each other), and once in position observers two and three simultaneously released the subject and walked back towards the entrance of the study area. Each subject had 180 seconds to navigate around the barrier. Once the subject's shoulders passed the barrier, the direction taken was recorded. Other measures recorded were first limb moved, extended limb at goal and the time to get to the goal. This method was then repeated until 10 trials were repeated or a subject failed to pass the barrier within 180s.

## **5 Study 2**

This study took place and involved the same subjects as Study 1. Study 2 took place 3 months after experiment 1.

### **5.1 Duchy College Subjects**

Before commencing any work at the educational establishment each horse was required to complete a 10 minute ridden assessment by qualified staff (BHS level 3 and 4). All staff had been employed at the college for a minimum of 2 years. The ridden assessment involved the horse walking, trotting and cantering on both reins. Working on both reins, can be defined as travelling around the arena in a clockwise direction and then in an anti-clockwise direction.

The purpose of the assessment is to match the subject to a specific area of work and also a focus on safety and is done annually for all horses. (The Duchy College Working Horses Grading System can be found in Appendix 2). At the time of the study the subjects had not taken part in any work for the study. Subjects were ridden in their usual saddle and bridle and riders did not use any artificial aids (i.e. whip and spurs) to encourage the horse to move in a particular direction. The riders maintained their usual riding contact. Contact is used to describe the feeling between the riders hands and the horse's mouth through the reins. Rein contact was not measured as this was outside of the scope of the study. No instruction was given to the riders on the contact the subjects would not be encouraged to move in a particular direction.

## **5.2 Bridgwater College Subjects**

This study took part during mid-term and observers collected data during a standard riding lesson.

## **5.3 Observers**

The observer was standing in the centre of a 60m x 40m arena at Duchy College and a 42 x 22m arena at Bridgwater College. All subjects being worked on both reins, in both directions were recorded. The observer recorded all behaviours using a continuous sampling method using a Flip video <sup>TM</sup> (Ultra HD).

## **5.4 Materials**

Three trotting poles that were white and blue, white and yellow or white and red, 3m long x 80mm in diameter made of heavy plastic were placed 1.2m apart on the quarter line, which is the line ridden half way between the centre of the arena and the outer line of the indoor arena at both establishments.

## **5.5 Procedure**

All subjects were ridden in trot on both reins and approached and moved over the trotting poles. Riders maintained their usual contact.

## **5.6 Measurements**

As the trot is initiated from the diagonal hind limb, opposite to the leading foreleg, this can be used to indicate the preference. During the ridden exercise the first limb over the first trotting pole was recorded.

## **5.7 Statistical Analysis**

All data were collated in Microsoft Excel prior to statistical analysis. The statistical analyses for both experiments were performed using Minitab 16 statistical software 2010, State College, PA. A level of  $P < 0.05$  was used to determine significance. Normality of behaviour and limb related data was determined using a series of Anderson Darling tests. Associations between direction taken around barrier, first forelimb moved and extended limb at barrier were analysed using Chi square analysis. Relationships between first limb moved and direction around barrier were also analysed using Chi squared tests of association. The Kruskal-Wallis test was used to examine solving time under different experimental conditions i.e 4M, 6M and 8M trails. Paired t-tests were conducted to examine behavioural intensity and behavioural diversity. Paired t-tests also assessed differences between those subjects who solved the task and those that didn't. Gender differences were investigated using an analysis of variance between groups.

# **6 Results**

## **6.1 Completed tasks**

The pre-test training was completed by all subjects ( $n=23$ ). Fifteen subjects (65.2%) went on to complete the task at 4m. Twelve subjects (52.2%) completed the task at 6m and 12



subjects (52.2%) completed the task at 8m in study 1a. All horses (n=7) successfully ate a piece of carrot from the yellow bucket before trials started, in the detour study part B.

## **6.2 Detour Task part A**

There was a higher incidence of left directional bias exhibited in the 4m task  $\chi^2(1, N = 15) = 8.07, p < .01$ . No directional bias was evident at 6m  $\chi^2(1, N = 12) = 0.6, p > .05$  or 8m  $\chi^2(1, N = 12) = 1.33, p > .05$ . No preference for leading limb to initiate movement was evident during the 4m task  $\chi^2(1, N = 15) = 0.39, p > 0.5$ , the 6m task  $\chi^2(1, N = 12) = 0.6, p > .05$  or the 8m task  $\chi^2(1, N = 12) = 0.33, p > .05$ .

Similarly no preference was displayed for extended limb at the goal during each task; 4m  $\chi^2(1, N = 15) = 0.07, p > .05$ , 6m  $\chi^2(1, N = 12) = 0, p > 0.5$  and 8m  $\chi^2(1, N = 12) = 0, p < .05$ . A chi squared analysis confirmed there was not a significant relationship between the first limb moved by a subject and the direction they detoured around the artificial barrier. This was consistent throughout all tasks (4m  $\chi^2(2, N = 15) = 0.19, p > .05$ , 6m  $\chi^2(1, N = 12) = 0.17, p > .05$ ) and 8m  $\chi^2(1, N = 12) = 2.74, p > .05$ ).

## **6.3 Detour task part B**

The results are from 7 horses during one detour task with the barrier set at 4m from the goal. Five out of 7 horses completed the task each carrying out 10 trials. With all 5 horses completing all 10 trails. No directional bias was evident during the detour task  $\chi^2(1, N = 5) = 6.4, p > .05$ , with only one horse showing a directional bias.

No horse showed a preference for first limb moved in any trial task  $\chi^2(1, N = 7) = 0.04, p > .05, \chi^2(1, N = 7) = 1, p > 0.5, \chi^2(1, N = 7) = 0.04, p > 0.5, \chi^2(1, N = 7) = 0.00, p > 0.5, \chi^2(1, N = 7) = 0.04, p > 0.5, \chi^2(1, N = 7) = 0.00, p > .05$  and  $\chi^2(1, N = 7) = 1, p > .05$ .

No horses showed a significant preference for extended limb at goal  $\chi^2(1, N = 5) = 0.04, p > .05, \chi^2(1, N = 5) = 3.6, p > .05, \chi^2(1, N = 5) = 0.00, p > .05, \chi^2(1, N = 5) = 0.04, p > .05, \chi^2(1, N = 5) = 1.6, p > .05$ .

There was no significant relationship between first limb moved and direction around barrier  $\chi^2(1, N = 5) = 0.074, p > .05$ , between direction around barrier and extended limb at goal  $\chi^2(1, N = 5) = 0.094, p > .05$ , or between first limb moved and extended limb at goal  $\chi^2(1, N = 5) = 0.14, p > .05$ .

#### **6.4 Trotting Pole**

Analysis of the trotting pole data demonstrated that there was no relationship between the leading limb over the trotting poles on the right rein and the first limb moved during the detour task at the 4m  $\chi^2(1, N = 23) = 0.0, p > .05$ , 6m  $\chi^2(2, N = 23) = 0.76, p > .05$  and 8m  $\chi^2(2, N = 23) = 2.88, p > .05$ . Likewise there was not a relationship between the leading limb over trotting poles on the left rein and the first limb moved during the detour task at 4m  $\chi^2(1, N = 23) = 0.0, p > .05$  at 6m  $\chi^2(1, N = 23) = 0.19, p > .05$  and at 8m  $\chi^2(1, N = 23) = 2.74, p > .05$ . There was not a significant relationship between the leading limb over the trotting poles on the right rein and direction moved around the barrier during the detour task at 4m  $\chi^2(1, N = 23) = 0.64, p < .05$ , 6m  $\chi^2(1, N = 23) = 0.51, p > .05$  and 8m  $\chi^2(1, N = 23) = 0.0, p > .05$  and the leading limb over the trotting poles on the left rein and direction moved around the barrier during the detour task at 4m  $\chi^2(1, N = 23) = 0.09, p > .05$ , 6m task  $\chi^2(1, N = 23) = 2.96, p > .05$  and at 8m  $\chi^2(1, N = 23) = 0.19, p > .05$  did not exist.

There was not a relationship between the leading limb over the trotting poles on the right rein and the extended limb at the goal during the detour task at 4m  $\chi^2(1, N = 23) = 1.03, p > .05$ , 6m  $\chi^2(1, N = 23) = 0.44, p > .05$  and at 8m  $\chi^2(1, N = 23) = 0.44, p > .05$ . There was no relationship between the leading limb over the trotting poles on the left rein and extended

limb at the goal during the detour task at 4m  $\chi^2(1, N = 23) = 0.71, p > .05$ , 6m  $\chi^2(1, N = 23) = 1.50, p > .05$  and at 8m  $\chi^2(1, N = 23) = 0.44, p > .05$ ).

Solving time data were non-parametric (AD = 1.37, 2.44, 2.162 all  $p < .05$ ) for 4, 6 and 8 metres respectively.

The average solving times for each task decreased with subsequent tasks. At the 4m task an average solving time of  $33.8 \pm 27.35$  seconds was recorded. The 6m task showed an average solving time of  $32.17 \pm 35.07$ , whereas the 8m task had an average solving time of  $26.33 \pm 24.41$ . There was no significant difference in the solving times at each trial at 4m, 6m and 8m ( $H_2=1.37$ ;  $P>0.05$ ; Figure 2).

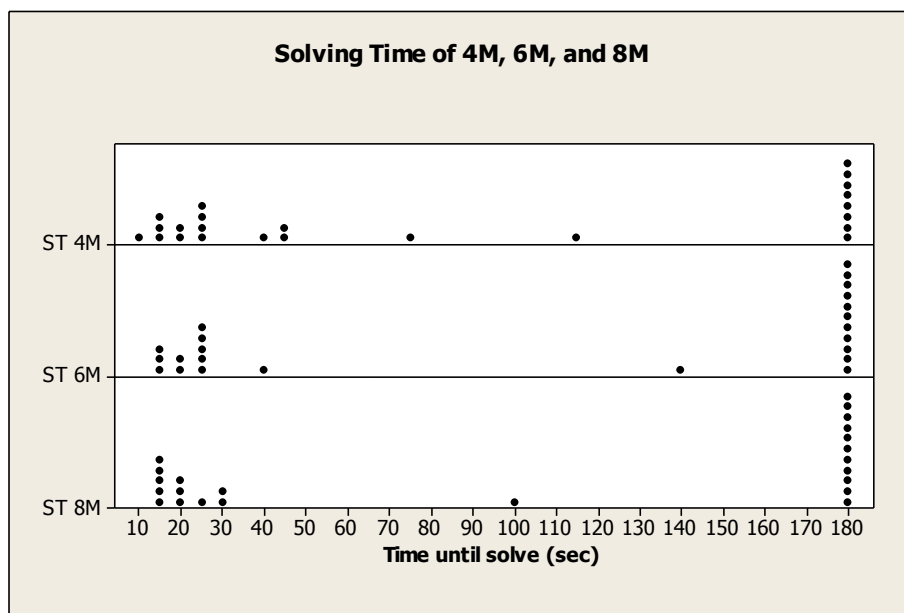
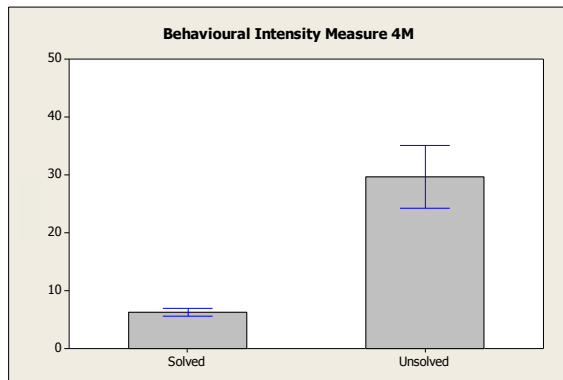


Figure. 2 Solving time(s) of subjects at each task.

## 6.5 Behaviours Displayed

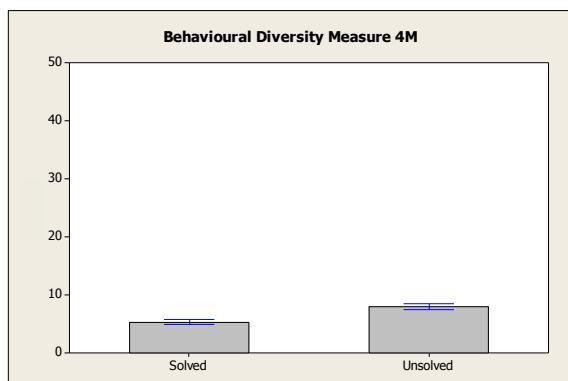
All behaviours throughout each task were recorded using a continuous time sampling method. The time behaviours were displayed were compared for each subject. Behaviours were recorded for up to a maximum of 180s. Behaviours were then categorised into task related, non-task related and human directed. All behaviours were recorded according to a verified ethogram which can be found in Table 1.

During the 4m task there was a significant difference of behavioural intensity displayed between subjects who solved the task and who did not solve the task ( $W=120.5$ ;  $p < .01$ ). Solvers displayed more task related behaviours than non-solvers (Figure 3).



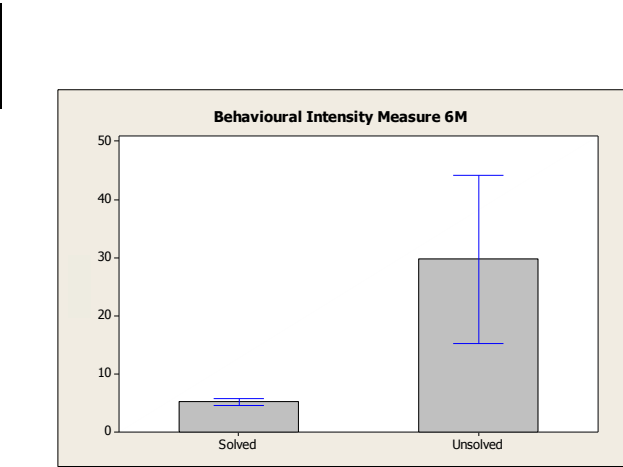
**Figure. 3 Behavioural intensity for subjects which completed the 4m task.**

Behavioural diversity during the 4m task was significantly different between solvers ( $W = 132.5$ ,  $p < .001$ ). Solvers displayed less behaviour than non-solvers.



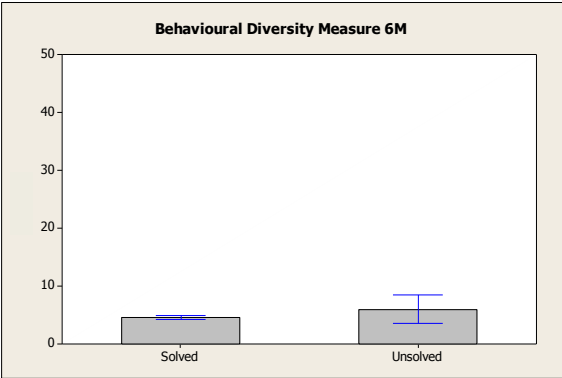
**Figure. 4 Behavioural diversity for subjects which completed the 4m task.**

At the 6m task there was a significant difference of behavioural intensity displayed between subjects who solved the task and who did not solve the task ( $W=90.0$ ;  $p < .05$ )



**Figure. 5 Behavioural intensity for subjects who completed the 6m task.**

There was no difference in the behavioural diversity displayed between solvers and non solvers ( $W=90.0$ ;  $p > .05$ ) at the 6m task.



**Figure. 6 Behavioural diversity for subjects which completed the 6m task.**

The 8m task was completed by all subjects that started the task. Behavioural intensity for subjects that completed the 8m task.

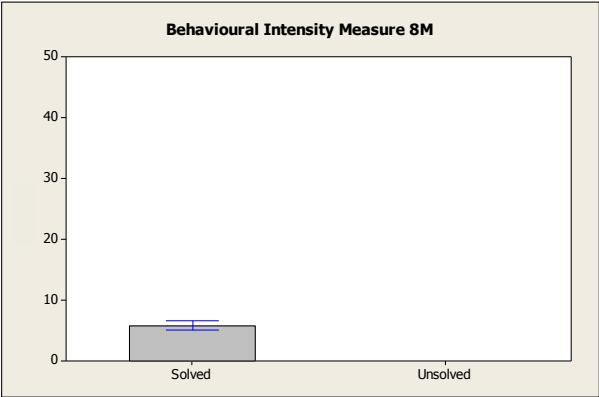


Figure. 7 Behavioural intensity for subjects which completed the 8m task.

Behavioural diversity for subjects that completed the 8m task.

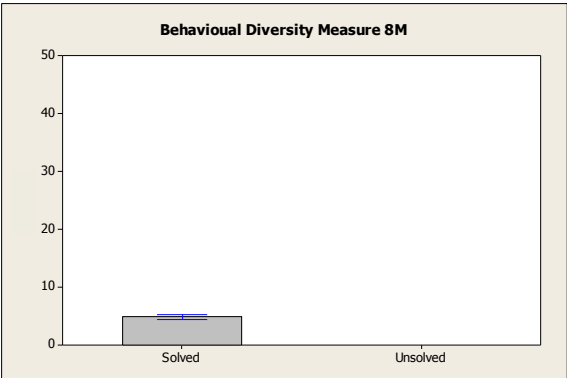
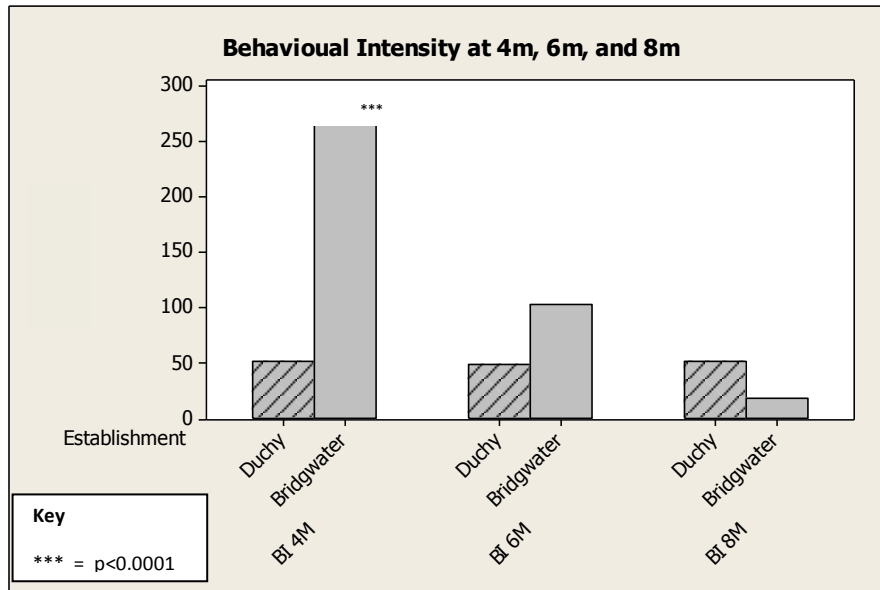


Figure. 8 Behavioural diversity for subjects which completed the 8m task.

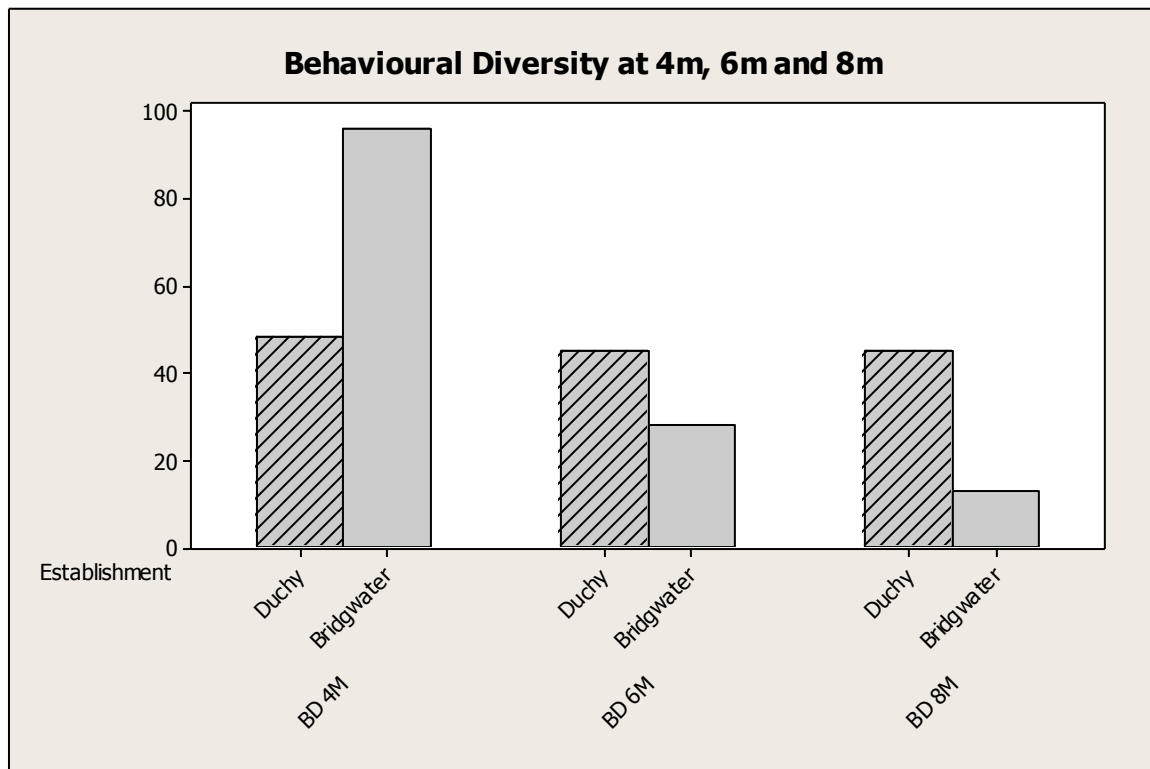
A Mann Whitney test revealed that there was a significant difference in the behavioural intensity displayed between subjects at Duchy College and Bridgwater College at 4m

( $W=214.0$ ;  $p<0.001$ ), but not at 6m ( $W=45.0$ ;  $p>.05$ ). A two sample t-test demonstrated that behavioural intensity at 8m also did not differ between the two establishments  $t(1) = 1.25$ ,  $p < .05$ .



**Figure. 9 Behavioural intensity displayed between Duchy College subjects and Bridgwater College subjects at each task.**

There was a significant difference in the behavioural diversity displayed between the two establishments  $t(20)=4.39$ ,  $p < .01$ ). There was no significant difference in behavioural intensity  $t(4)=1.63$ ,  $p > .05$  or behavioural diversity  $t(4)=0.71$ ,  $p > .05$ ) between the Duchy College Equestrian Centre subjects and Bridgwater College Equestrian Centre subjects at the 6m task. No significant difference was found in behavioural intensity  $t(1)=1.25$ ,  $p > .05$ ) or behavioural diversity ( $t=1.30$ , d.f.1:  $p > .05$ ) during the 8m task.



**Figure. 10 Behavioural diversity displayed between Duchy College subjects and Bridgwater College subjects at each phase.**

Average behaviours displayed by subjects at each task.

**Table. 2 Average numbers of behaviours (frequency) displayed at each establishment**

	Behavioural Intensity	Behavioural Diversity
4m Duchy College	5.20±1.99	4.80±1.32
4m Bridgwater College	21.5±16.0	7.38±1.50
6M Duchy College	4.80±0.79	4.50±0.52
6M Bridgwater College	20.6±21.7	5.60±3.44
8M Duchy College	5.20±1.69	4.50±1.08
8M Bridgwater College	9.00±4.24	6.50±2.12

A Kruskal-Wallis revealed there was no significant difference in the solving times between mares (n=4) and geldings (n=11) at the 4m task ( $H = 0.02$ ,  $p > .05$ ), the 6m task ( $H = 0.123$ ,  $p > .05$ ) and the 8m task  $t(7) = 1.21$ ,  $p > .05$ .

## 7 Discussion

### 7.1 Completed Tasks

This study demonstrated that all subjects selected were capable of completing the PTT in both part A and part B of the detour study. Both tasks required the subject to observe a



piece of carrot being dropped in to the food bucket, followed by immediate release from handler, with the intention for the subject to lower their head and touch the carrot. The aim of the PTT was that subjects could form an association with the food bucket and reward through classical conditioning. Each subject was required to successfully complete 3 PTT tasks in task A and 10 PTT in task B. The occurrence for all horses achieving this PTT could be associated with a previously learned response to associate humans with the delivery of food (McLean 2004).

In study 1a 23 subjects started the 4M task and 15 successfully completed it. 14 subjects started the 6M task with only 12 subjects completing it. All 12 subjects that completed the 6M task then went on to complete the 8M task. In detour task B, 7 horses started the detour task but only 5 horses completed the task. The early success in the detour task could represent novelty of the experimental area, despite subjects already being familiarised with the area used. A decrease in the number of subjects completing subsequent tasks could be due to a lack of congruity between ability of subjects and experiment requirement. Piaget (1936 cited in Regolin *et al.* 1995) suggests that the difficulty in tasks may reflect the lack of object permanence. Researchers have reported that horses may also lack object permanence (Murphy & Arkins 2007) and that temporal delay may prevent some success during detour tasks. The ability to solve tasks that require a temporal delay is an expression of well-developed temporal cognitive processes (Murphy *et al.* 2004).

Subjects who successfully completed the detour tasks in either study A or B may be attributed to the subject's success being simply due to trial and error. However, ruling out trial and error learning, it could be suggested that that the subject's success is due to classical conditioning on subsequent trials and not because of object permanence. i.e. their ability to perceive objects as permanent regardless of their visibility.

The horse is a social species and it is known that social individuals usually learn better in social tasks (Wilkinson, Kuenstner, Mueller & Huber 2010). Conspecifics have been used in many studies to assess the social benefits on performance as found in rats (Levine & Zentall 1974). Dalla Costa, Allegrini, Cerrire & Minero (2011) suggests that using a conspecific rather than a food reward may result in advancements in cognitive based studies. However, other studies utilising a conspecific during a detour task did not result in increased success rates shown by test subjects. Hartmann, Christensen & Keeling (2011) found that naive foals placed in a familiar test situation had to re-learn the process after the removal of a conspecific. However, the use of a conspecific in Murphy *et al.s* (2005) detour study was considered to contribute positively to the number of horses that successfully completed the detour task.

## **7.2 Direction around barrier**

This study shows that within the sample studied during study 1(a), there were significantly greater incidences of left directional biases whilst detouring around the barrier during the 4M task throughout detour study A. Previous detour studies have documented the preference to detour to the left of the barrier (Baragli *et al.* 2011a). During detour task B only one horse showed a directional bias to move to the left of the barrier. No directional biases were evident during Murphy *et al.'s* (2005) study and although there were some directional differences seen these differences were non-significant. Individual variation in lateral biases must be considered. In detour study A, one subject moved to the right of the barrier whilst the other 14 subjects moved to the left of the barrier at the 4m trial. This population bias was not evident during the 6M task or the 8M task. During the 6M task six subjects moved to the right of the barrier and eight subjects moved to the left of the barrier. During the 8M task four subjects moved to the right of the barrier and eight subjects moved to the left of the barrier. There was no significant difference of directional bias during the

6M task and the 8M task. However there was still a minor preference displayed to manoeuvre around the left of the barrier but this was non-significant. Like study A there were no significant differences but there was still a preference shown by one subject to move to the left of the barrier. Directional biases have been documented in a range of species including cattle (Hopster *et al.* 1998), sheep (Versace *et al.* 2007) and tadpoles (Oseen, Newhook & Wassersug 2001). Directional biases and the presence of are important to understand as Grandin (1993) fittingly states that understanding behavioural patterns in livestock can contribute to the development of sympathetic and safer handling practices. Not only is it important to implement enhanced handling practices, but by understanding behavioural patterns, consideration can be given to the interaction between animal and environment. This study primarily investigated the interaction between animal and environment and observed subjects behaviours throughout. The Null Hypothesis ( $H_0$ ) that there is no evidence of lateral behaviour when assessing preference using a detour task was accepted. The Null Hypothesis ( $H_0$ ) was that horses do not exhibit a preferred limb when faced with an obstacle when ridden was also accepted. These results mirror those of Wynne and Leguet (2004) who also found that increasing the barrier size in their detour task reduced the lateral bias displayed in Quokkas.

### **7.3 First forelimb moved**

There was a distinct absence of a population bias for a preferred limb to initiate movement in all 3 tasks during detour task A. Minor differences were documented during the 4M, 6M and 8M task. Study B also revealed minor differences and no significant difference for a preferred limb to initiate movement. These results are consistent with the findings of Murphy *et al.* (2005) who also found no bias during a first step test. A justification of no bias may be because as each horse was released immediately after the carrot was dropped in to the bucket, they appeared to take smaller steps. A bias may only be present during larger

movements i.e. stride not step movements and these larger movements may not have been apparent during this study.

#### **7.4 Extended limb at goal**

In detour task A, there were no significant differences shown for a preferred limb to be extended at the 4M task, the 6M task or the 8M task. Individual differences with extended limb preferences demonstrated an overall preference to extend the right limb. Even though there were differences these were marginal. During the 4M task eight subjects extended their right limb with seven subjects extending their left limb. The 6M task revealed what would be expected by chance where six subjects extended their left limb and six subjects extended their right limb. Detour task B also revealed no significant differences for a preferred limb to be extended at the goal. Whereby, subject 1 extended their right limb at the goal in 4 trials and extended their left limb at the goal in 6 trials. Subject 2 extended their right limb at the goal limb in 2 trials and extended their left limb at the goal in 8 trials. Subject 3 extended their right limb at the goal in 5 trials and extended their left limb at the goal in 5 trials, which is what is expected by chance. Subject 4 extended their right limb at the goal in 4 trials and extended their left limb at the goal in 6 trials. Subject 5 extended their right limb at the goal in 3 trials and extended their left limb at the goal in 7 trials. The findings from this study are not consistent with earlier studies, McGreevy and Thompson (2006) and Warren-Smith and McGreevy (2010) both found population level bias to extend the left forelimb in grazing horses.

The absence of a population bias towards a preferred extended limb whilst obtaining the goal may be due to the short amount of time each subject was in this stance/position. A bias may only be present over longer periods of time. Earlier studies that have used the same method to observe grazing position have used longer observational periods. McGreevy and

Rogers (2005) observed extended limb preference in Thoroughbred horses for two hours, similarly McGreevy and Thompson (2006) also used a two hour observational period.

### **7.5 Relationship between first limb moved and direction around barrier**

There was not an overall significant relationship between the subject's first limb moved and their direction around the barrier. This opposes the finding from Murphy *et al.* (2005) who found a significant positive relationship between first limb moved and the direction the subject moved around the barrier.

### **7.6 Trotting Poles**

Failure to change leading leg on approach to the trotting poles on either rein may imply that larger obstacles trigger lateral responses. Further investigations may demonstrate the degree to which the introduction of an obstacle (such as a series of trotting poles) will have on the showing of lateral preferences. The apparent absence of a relationship between, first limb moved and leading limb over trotting pole, the direction around barrier and leading limb over the trotting pole and the extended limb at goal may suggest that this does not affect leg choice.

### **7.7 Solving time at each task**

There was no significant difference in the solving times for each task. The average solving times for each task decreased with subsequent tasks, however these differences were marginal. These results align with those of Baragli *et al.* (2011b) who also found that detour task completion did not improve. It has been suggested that horses are quick learners and perform well at simple operant learning tasks (Sondergaard, Bak Jensen & Nicol 2011) yet these studies revealed no differences in task completion speed rate.

### **7.8 Behavioural intensity and Behavioural diversity displayed during each task – Detour Study A**

Behaviours were recorded on a continuous time sampling method. Behaviours were recorded for a maximum of 180 seconds. Significant differences were seen in both the behavioural intensity and the behavioural diversity scores of solvers and non-solvers during the 4m task. The behavioural intensity was higher in non-solvers than it was in the solvers, meaning that the non-solvers displayed more behaviours i.e more behavioural activity than the solvers. The behavioural diversity exhibited was greater in the non-solvers than it was in the solvers which demonstrated that the non-solvers displayed a wider range of behaviours than the solvers.

There was not a significant difference of behavioural intensity displayed between the solvers and non-solvers in the 6M task. Interestingly the 6M task may act as a cut off for the subjects who could complete the task and those who could not successfully complete the task. All subjects that successfully completed the 6m task, then when went on to successfully complete the 8m task. The decrease in the total amount of behaviours displayed may be a result of the eliminated non-solvers from the 4M task leaving a higher proportion of solvers in the 6M task.

There was no significant difference in the behaviour diversity displayed between solvers and non-solvers in the 6M task which would imply the amount of different behaviours did not vary between solvers and non-solvers. There is no comparison between the solvers and non-solvers during the 8M task, as interestingly all subjects completed the 8M task.

### **7.9 Behavioural Diversity and Behavioural Intensity Measures in Solvers and Non-Solvers**

Behavioural diversity and behavioural intensity measures were observed in all tasks during study 1(a). Non-solvers were observed for a longer period of time, due to the non-solvers not completing the tasks, as when the solvers reached the goal behaviour recording ceased.

This method provided data for analysis to investigate behaviours during each task, however non-solvers were recorded for longer (because they were given a maximum time of 180s in which to complete the task). However, this design meant that non-solvers were inevitably observed for longer. A future recommendation would be to record all subjects for the same amount of time (here 180s) despite completing the task. Recording subjects for the same amount of time may allow greater confidence in the results analysed. An alternative approach would be to standardise behaviour scores so that they are expressed as number of occurrences per specified unit of time for example number of goal touches per minute this would allow for a more rigorous comparison of solvers and non-solvers. As equine behavioural science knowledge expands future studies comparing behavioural intensity and behavioural diversity may provide a better understanding to the complex cognitive abilities in equines.

#### **7.10 Comparison between Duchy College Equestrian Centre subjects and Bridgwater College Equestrian Centre Subjects**

Overall fewer subjects from Bridgwater College Equestrian Centre completed all detour tasks. Different observers were used at each establishment. Both observers were instructed to use the same procedure. Despite this instruction there may have been some slight inconsistencies with actions and behaviours displayed from each assistant, which could have inadvertently affected behaviour from each subject. All subjects were previously familiarised with the observer that led them. As they were either, in the case of Duchy College Equestrian Centre a student, or Bridgwater College Equestrian Centre a member of staff, who both had contact of at least several times a week with the subjects. As Hothersall and Nicol (2007) suggested different reactions to handlers may have had an impact on the standardisation of the method and interpretation of the results.

It has been documented that in studies measuring animal behaviour, any observer effect should be kept to a minimum. However inconspicuous the observers and research assistants may appear and how carefully planned the study is there still might be an effect on the behaviour of the subject (Iredale, Nevill & Lutz 2010), regardless of how well subjects are habituated to the observers, for example olfactory cues may be given off by the observers (Martin & Bateson 2007). Some authors have documented the observer effect during their studies (Williams & Norris 2007). In order to control for any form of observer effect Baragli *et al.* (2011b) controlled the goal bucket with a cord. The famous story of the 'counting' horse Clever Hans is now widespread and a perfect example of how small unintentional cues can directly affect/influence the behaviour of the animal. In the early 1900's Dr Wilhelm von Osten demonstrated that Clever Hans could apparently accurately solve mathematical problems by tapping his hoof the correct amount of times on the ground. This was not due to possessing arithmetic capabilities, it was later found out that Clever Hans was simply, mechanistically, reacting to the subtle unintentional cues that were elicited from his handler, Dr Von Osten. When Clever Hans reached the correct answer Dr Von Osten would inadvertently raise his head and Clever Hans would stop pawing (Hergenhahn 2009). They also showed that he could produce the desired numerical answer in response to the crowd leaning forward in anticipation as he approached the correct answer. This demonstrates what appears to be a highly intelligent equine response (Murphy & Arkins 2007) although arguably some would suggest that this is just operant conditioning (Ladewig 2007). What is now known as the Clever Hans phenomenon has been recognised in other human-animal interactions such as Lit *et al.* (2011) reported that the performance of working dogs is affected by their handler beliefs.



Many studies involving animal behaviour are subject to the logistical challenges in controlling the effect of the presence of the human observer. Effective measures in animal behaviour are often conducted over several days, to avoid single day anomalies. Study A was conducted with the aim to eliminate any single day anomalies and to reduce subjects learning. This study investigated all behaviours displayed during the task. Further tasks that exposed the subjects to learning may have unintentionally skewed the results. Further tasks may have revealed different results, but in order to measure all behavioural responses during this study, observers had to be present as they were an additional factor in the cognitive task.

There was a significant difference in the behaviour intensity displayed between subjects at Duchy College Equestrian Centre and the subjects at Bridgwater College Equestrian Centre. These results yielded significant differences during the 4m task. Although there were differences of behaviour intensity throughout the 6m task and the 8m task these differences were small. The higher amount of behaviours displayed from the Bridgwater subjects may be a result of incompleteness of the detour task, whereas more subjects from Duchy College completed the task, therefore engaging in task directed behaviours. The subjects at Bridgwater College displayed more non-task related behaviours and human directed behaviours than the subjects at Duchy College, where there were a higher number of solvers in each task.

The behaviour exhibited by an animal or a group of animals is frequently used to objectively quantify the welfare of the subject being studied, not least because the actions that are performed can be related to the animal's mental state (Asher, Collins, Ortiz-Pelaez, Drewe, Nicol *et al.* 2009). The subjects that displayed more human directed behaviours may have

been anticipating a cue from the observer. It has been documented that the emotionality of a subject will establish the success of the task (McCall 1990).

### **7.11 Gender**

The differences between visuo-spatial abilities of males and females have been documented in a number of species (Stavnezer *et al.* 2000), but seldom do studies of equine cognition and learning report sex differences (Murphy *et al.* 2004). No sex differences were found in a visuo-spatial task where subjects had to seek a food reward (Murphy *et al.* 2004). As Whitaker *et al.* (2008) suggest, contemplation of sex in relation to behaviour is worth some consideration particularly as sex differences are associated with different hormonal effects on brain development (Zucca *et al.* 2011). In this study no significant differences were evident in the solving times achieved by mares and geldings during the detour tasks. Reinforcing that sex differences do not have an impact on success.

### **7.12 The importance of laterality**

Participation in leisure riding is increasing and in 2011 there were an estimated 900,000 privately owned horses in the United Kingdom ([www.bhic.co.uk](http://www.bhic.co.uk)). Many of these horses are kept in restricted housing (Baragli *et al.* 2011b) that does not provide the opportunity for normal behaviours to be performed. Many equine husbandry systems that are currently in place also restrict normal behaviours, when they should be promoting them (Rogers, Bolwell, Tanner & Van Weeren 2012).

Laterality has become topical within the Equitation Science discipline (McGreevy & McLean 2007) and many of the current studies reflect the importance of implementing training techniques that take innate biases into consideration (Austin & Rogers 2007 ; Warren-Smith & McGreevy 2010). These studies also emphasise that assessments of laterality for young stock should be introduced to assess potential for certain performance disciplines (Austin &

Rogers 2007 ; Warren-Smith & McGreevy 2010). However there has been little appreciation of how lateral preferences hinder or aid the domesticated horse in relation to current husbandry practices. Reddon and Hurd (2008) indicate that another probable source of the variation in laterality preference is the effects such as environmental constraints such as space. Ganskopp (1995) highlighted that the understanding of a non-humans directional-bias will help us recognize their preferences and interactions with the environment. Having this understanding will allow us to make better judgements on the capabilities and limitations that innate biases are having on the horse. Unfortunately current equestrian management practices and methods are governed by human requirements, but often ignore the basic needs of the horse (Van Dierendonck & Goodwin 2005). Furthermore an understanding of the epigenesis of laterality may provide an insight to the evolution and possible constraints on the adaptability of a species within its environment (Schaafsma *et al.* 2009). Having this understanding considerate practices can be implemented.

The study of animal behaviour is still being widely investigated. Cognition studies in other species have advanced those studies in equids, which is surprising considering the enormous human-horse relationship and how the horse has played a big part in history. At present there is a vast knowledge base, which means it is possible to have a greater understanding and by gaining an appreciation of the limitations and capabilities of equines we can be more sympathetic.

### **7.13 Challenges with measuring laterality**

Despite the increasing amount of research, the complex areas of motor laterality and cerebral dominance remain hard to understand. What constitutes motor laterality is still in debate. Rife (1940 cited in Murphy *et al.* 2005) stated that studies of true motor behaviour must be conducted over a wide range of tasks and preferably all motor tasks. This idea

conflicts with the hypothesis that laterality is task dependent and further examination of this notion would be welcomed. Results from detour study A, B and the ridden exercise do not support the theory that laterality preferences should be tested over several tasks, however the results also revealed there was not a preferred bias in a particular task, so neither does it support the view that biases are task dependent.

The absence of a bias shown across the majority of the detour tasks undertaken in this study may either show little lateral preferences in the subjects or it could be that the displays of laterality preferences are task dependant (Tomkins *et al.* 2010). It is also important to consider whether there are differences in lateralisation behaviour displayed or whether it is differences in behaviour strategy. A further idea taken from Fagot and Vauclair (1991) may be that failure to show any lateralisation preference/s may reflect an inability of the task to reveal any preferences that exist. However, as Rogers and Andrew (2002) suggest, the absence of asymmetry shown in tests within a particular species does not mean that lateral preferences does not exist.

At present there is not one single assessment to measure laterality and consequently assess laterality bias (colloquially known as handedness and/or footedness in humans or sidedness in horses) and at present, different tests are used to measure different lateral characteristics. If there was a true understanding of the origin of laterality this may provide suitable grounds on which to base further studies. Another problem scientists face is that unlike studies on humans, research on animals does not have the benefit of written or spoken language to assess its subjects (Thorpe, Jacova & Wilkie 2004) and decisions are commonly based on the behaviours observed. When quantifying motor lateral preferences in horses it is vital to avoid external influences (Warren-Smith & McGreevy 2010), such as those introduced as part of usually carefully planned experimental conditions. Fagot and

Vauclair (1991) suggest that temporal and spatial characteristics should be evaluated in tasks of increasing difficulty.

#### **7.14 Cognition and lateral biases governing behaviour**

It is important to consider whether lateral biases or cognitive processes are predominately determining the behaviours displayed throughout each task. Individual processes for each hemisphere have been recognised (De Boyer des Roches *et al.* 2008 ; Schaafsma *et al.* 2009) and it could be argued that the existence of a left bias during the 4M task may indicate right hemisphere dominance in the population studied. This may not be surprising given the right hemisphere has been found to be responsible for spatial cognition in birds, rats and humans (Vallortigara & Rogers 2005), however in this study no further lateral preferences were found in the 6m and the 8m tasks. Rogers and Andrew (2002) found that enhanced performance and faster responses were found in lateralised subjects compared to subjects who did not show a bias. Higher level tasks should show a hemispheric specialisation. Fagot and Vauclair (1991) stated the strength of lateral preference will increase with tasks that require intense cognitive function. Furthermore, Farmer *et al.* (2010) suggests that subjects that show a greater strength of lateralisation are more effective in cognitive based tasks. A common theory is that having a lateralised brain should result in an increased ability to multitask (Reddon & Hurd 2008). This theory is challenged as during the current study the strength of laterality did not increase with the tasks that required more cognitive functions. The strength of laterality disappeared during subsequent tasks.

It has been reported that differences in cerebral lateralisation levels relate to differences in behaviour (Reddon & Hurd 2008 ; Reddon & Hurd 2009). This is because of the variation in the degree to which one hemisphere assumes control of a given function (Vallortigara, Rogers & Bisazza 1999). The occurrence of some subjects to complete the tasks may be

attributed to individual and personality (temperament, stress, copying and behavioural syndromes) differences. There are limited studies investigating the relationship between personality behaviour and lateral preference (Reddon & Hurd 2008).

The possibility that non-lateralised responses may mirror lateral preferences for how objects are observed should also be taken into account (Farmer *et al.* 2010). It has been suggested that stimuli are processed differently depending on which hemisphere is responsible for the processing. Additionally the type of mental processing a certain stimulus receives will determine the behavioural response that is elicited by that stimulus (Vallortigara & Andrew 1991) has been reported that horses perform better during tasks where they can see the goal. During this study horses were able to view the goal at all times, although it would appear that none of the horses maintained visual contact with the goal during each task.

This study did not incorporate sensory laterality where some other laterality studies have. As Pointer (2012) proposes, that eye dominance is not related to limb preference and McGreevy and Rogers (2005) advocate that nostril use is not linked to motor laterality. Sensory laterality is an area that needs further investigation. Yet in studies where motor and sensory laterality have found to have no correlation may indicate that brain lateralisation happens on two different levels of neural organisation (McGreevy & Rogers 2005) and a brain can be lateralised without the outward manifestation of a paw or hand preference (Rogers 2009).

### **7.15 Task dependence**

The results of this study concur with Laska (1996) and Tomkins *et al.s* (2010) proposals that laterality can be task dependent. The 4m detour task was the only task that revealed a significant lateral preference and the lateralised responses that were expressed during the 4m task were not maintained throughout following tasks. Lateral preferences were found in

the first limb moved observation, direction around the barrier observation and the extended limb at goal observation. However these preferences were minimal and no subject displayed consistent lateral responses throughout all tasks. Rogers (2009) considers that some animals may not show a preference for a particular limb if the task is perceived as too difficult..

The individual variation in the strength of lateralisation maybe because of the individuals variation in behaviour (Reddon & Hurd 2009). Rogers (2002 cited in McGreevy and Thompson 2006) states that lateral preferences have been found in all vertebrae species studied, so an absence of any preferences is unusual. Baragli *et al.* (2011b) suggested that horses that do not show a laterality bias may be able to alter their detour strategy as the complexity of the task increases. The subjects that did not show any lateralised behaviour may be demonstrating a higher ability of spatial awareness and exploratory behaviours. Findings from detour study A and B may suggest occurrences of such behaviours.

This study did not examine the effects breed differences have on lateral preferences, as it has been reported that lateral differences have been reported within different breeds of a species. This study did not provide a varied number of breed differences to be analysed. Studying breed differences during cognitive based studies should be considered for the future studies. Breed differences may be responsible for variations in performance and behaviours displayed during each detour task. It has been recognised breed differences have a strong influence on emotionality (Lesimple, Fureix, LeScolan, Richard Yris & Hausberger 2011). Breed differences were found in McLean's (2004) study, whereby Thoroughbred horses showed a higher amount of frustrated behaviours as their success rate decreased in a cognitive based task. It has been suggested that there is a relationship between laterality and emotionality. Riding school horses are inspected prior to entering a riding school and some horses are not accepted on the grounds that they display inappropriate behaviours.

Thus, they are selected on the basis of emotionality before lateral preferences are tested, if at all tested.

At present there is conflicting evidence as to whether horses are able to successfully complete detour tasks. The results from this study contrast from earlier published studies including Baragli *et al.* 2011b. The fact that some detour tasks have been successfully completed by equids may be due to unintentional cues which may have reinforced the behaviour displayed during the successful completion of the task. Baragli *et al.* (2011b) suggest the success in his study may be linked to an association between the movement of the feed bucket and reward. Success in the current study to obtain the goal may be due to an association being formed between the observer, which was stood behind the goal and the goal in the bucket. Some researchers have reported increasing success in detour tasks after animals learn the correct route (Regolin *et al.* 1995 ; Pongracz *et al.* 2003). Further evidence of the successful implementation of strategy may be seen in cattle, who were reluctant to change their preferred side of a milking parlour upon entering (Hopster *et al.* 1998). Habits can be easily formed in some non-humans and these may simply follow a random choice. It has also been reported that in some situations the first learned is the best what learned, which is referred to as the law of primacy (Atkinson and Shiffrin 1971 cited in Murphy and Arkins 2007) and this strategy may be more commonly used than once thought. Regolin *et al.* (1995) suggest that some motor responses that are associated with environmental stimuli are easily reinforced.

Failure to successfully complete the detour task may be because the task incorporates a temporal delay, which may have compounded the difficulty of the task. Any form of learning behaviour is very much influenced by the amount of time the subject is exposed to the stimulus and the appearance of the associated reinforcement strategy (Murphy & Arkins



2007). Gregorios-Pippas *et al.* (2009) suggests temporal delays can reduce the value of rewards. In effective horse training rewards should be given immediately. Indicating that it exists in non-humans as the rapid achievement of the PTT and the inability to further solve the detour tasks. Temporal delay often causes learning difficulties in horses (Murphy & Arkins 2007). The inability of object permanence in horses may be because of the limited equine visual system that they cannot comprehend the stationary object is still there after it has disappeared out of sight. Murphy and Arkins (2007) suggest that the difficulty for horses to comprehend temporal delay may be due to a few factors such as memory limitations, motivational shortcomings, small attention span or the inability to chain behaviours with responses.

If the horses had been able to understand the criterion of the task, there may have been a higher achievement rate. It has been documented that horses are able to understand the concept of maze style settings. The success of horses to successfully complete maze style tasks has been recognized (Marinier & Alexander 1994). Such successes may be because mazes can be learned by association, discrimination and chaining (Nicol 2002) and not due to an understanding of the requirement.

The decline in number of subjects completing the detour tasks after first initial completion as seen in all detour task tasks (23 subjects started the 4m task, with 15 subjects completing the task. Fifteen subjects started the 6m task with 12 completing and all subjects that started the 8m task reached the goal). This occurrence might be because some horses may have problems with replacing former learning with new learning (Sappington, McCall, Coleman, Kuhlert & Lishak 1997), specifically reversal learning. It must be remembered that there are differences between detour behaviour and detour learning (Regolin *et al.* 1995).

### **7.16 Limitations of the study**

Martin and Bateson (2007) advocate that the form of measurement should reflect the objective. Correctly designed and conducted animal behaviour studies can make significant contributions in that field of study (Lehner 1987). The methods used in this study have been employed in earlier studies investigating lateral preferences and cognition. During this study there were some unavoidable limitations. There were a limited number of subjects available at each establishment, partly due to the administration of horse welfare based selection criteria. Small sample sizes at each location may have an impact on the statistical representation. In order to overcome this perceived shortcoming at the outset additional subjects at a similar establishment were also recruited for testing. Using subjects from two establishments has allowed a comparison between the two populations. Despite the similarities in daily routines variables such as different husbandry regimes between the two establishments may be enough to affect the performance displayed during each task.

Laterality preferences have caused physiological changes in horses (Weller *et al.* 2006), including hoof asymmetries (Van Heel *et al.* 2006). This study did not investigate hoof circumference and would be a recommendation for future studies, hoof asymmetries can be easily measured and if hoof asymmetry measurements are taken periodically, the rate of gradual changes, if apparent, can be documented. This method may identify lateral preferences developing. Comparisons can be made with physiological changes in the hoof and lateral preferences displayed throughout the task.

Young horses (i.e. those below two years of age) that have not had any training may show laterality preferences. The objective of using young horses would be to remove any influence that handling and training practices might be having in the domesticated horse. Earlier studies have documented that lateral preferences can be altered with age (McGreevy

& Rogers 2005 ; Tomkins *et al.* 2012). The average age of subjects involved within this study was  $14.39 \pm 4.79$  years. If lateral preferences change with age the population of horses studied would have seen some physiological changes, including physiological changes to the hoof. Larger bones have been found in the preferred forelimb of racehorses, but no documented studies have reported the effects of bone size in a preferred limb of non-race horses.

The use of a conspecific as a social reward may yield different results, during performance in a detour task. By using a conspecific in cognitive based tasks where behaviours are continuously recorded, may provide an understanding of preference between, task-related, non-task related and human directed behaviours. Social cues such as the use of a conspecific can be regarded as environmental stimuli and learned through association (Wilkinson *et al.* 2010).

The limited detour studies in horses have all used solid barriers. The use of a solid object to represent a barrier during this study followed the trend of what is used in other detour studies. However subjects could see over the top of the barrier. Future studies could incorporate transparent barriers, which may yield different results. The introduction of a transparent barrier may identify further cognitive limitations as transparent barriers have been found to be more problematic (Vlamings *et al.* 2010). There are no documented studies of using transparent barriers to assess detour behaviour in horses to date.

Earlier studies have recorded the attention span of each subject during a particular task (Randle 2008). The attention span was defined as the time the subject took until first contact with the apparatus. This method may be another identification of the subject's welfare and is easily measurable and further consideration should be given to understanding how animals interact with their environment.

A challenge faced by those studying animal behaviour is that decisions have to be made on observable behavioural responses displayed by the subject. Descriptions and interpretations have often been made that are based on anthropomorphic explanations. However, ethograms are used to objectively underpin categorisations of observations. Efforts made to ensure the distinction between different categories are as objective as possible. This study does not provide sufficient evidence of lateral biases in domesticated horses unlike other published studies that have used the same methods. It has discussed the many influences that may have affected the behaviour.

### **7.17 The future, welfare and ethics**

This study provides additional research in the field of equine laterality and cognition. It has discussed some fundamental issues regarding the challenges of measuring laterality preferences and behaviour. Like many other studies the aim is to try and answer questions where theory and anecdotal evidence are present.

In 2002, Nicol addressed subjects for future research such as a further understanding of equine spatial learning and further understanding of equine cognition. Over the past decade there have been substantial advances in these areas. Murphy and Arkins detailed 2007 review highlights the overall progression in this area. The authors point out that there is no documented research before 1991 that details concept learning in horses.

Despite this rapid growth of knowledge, there is still plenty of room for further developments in equine behaviour and cognition. Considerations for further studies should include how the environment impacts on innate lateral biases? Are modern day practices hindering the exhibition of innate biases? Are horse owners aware of lateral preferences their horses may have? Is this knowledge being relayed to the horse owners? What behavioural measure can be identified in cognitive based tasks?

Many equine cognitive studies concentrate on the achievement of operant tasks. They investigate the ability of horses to successfully discriminate between two goals. For example selecting the correct food bucket (McLean 2004). Consideration of the behaviours displayed from each subject during these tasks may provide an indication of their well-being and state of mind.

Further studies should focus on investigating further adaptive behaviour that may be displayed during cognitive based tasks (Goodwin 2007), rather than what it is already known that horses are capable of. In many situations animals often experience stress when they cannot adapt to cope with differences in their environment (Visser & Van Wijk-Jansen 2012). In modern day practices horses are kept in confined areas (Baragli *et al.* 2011b) and are often from away from conspecifics. Visser and Van Wijk-Jansen (2012) state that the behaviours that are being deprived of by individually kept horses may have detrimental effects on their welfare and that the learning ability of horse may be affected by the environmental conditions they are kept in. Horses are extremely social animals (Breed & Moore 2012). Often they are required to perform in studies isolated from conspecifics. Goodwin (2007) suggests that by studying them in isolation may greatly inhibit their learning ability and isolation from conspecifics has been connected with stress in feral horses (Van Dierendonck & Goodwin 2005). This factor should be taken into account for further studies.

Problems arise in determining animal intelligence levels between species. Mainly because of the difficulties as to what comprises intelligence (Murphy & Arkins 2007). Pearce (1987) has suggested that the characteristic of intelligence can be defined as how non-humans behave adaptively. The modern day view of animal intelligence is influenced by human perception (Goodwin 2007). Also equine learning and perception often reflects human suggestion rather than that of the horse (Heitor & Vicente 2007). It is not surprising because

descriptions of human behaviour were basically transferred to horse behaviour, many of these behaviours were of human mental characteristics, whereas the horse does not have the same capabilities (McLean 2012). Ethological constraints have shaped the species we see today. The horse is a horse and nothing else, through domestication it has developed its behavioural repertoire to meet its survival needs. It is not only the characteristics that have been shaped by evolution it is also their higher intellectual processes (Pearce 1987). Horses are not required to have higher mental abilities as they are within the grazing niche (McLean 2001), regardless of practitioners making assumptions that they do have higher order abilities. Banks and Flora (1977 cited in Pearce 1987) conducted a study to establish the view of college students on animal intelligence within a range of species. The authors found that horses appeared in the middle of a 10-point scale within apes scoring a rating of 9.2 and fish with an intelligence rating of 1.68. As Murphy and Arkins (2007) point out it is hard to verify if the inability to learn under situations that are ill-equipped for the horse challenges both memory and intelligence or both.

A fundamental point to be remembered is that during any study involving animals the overall welfare of the subject is paramount and that their welfare is more important than the acquisition of basic knowledge. Often animals are put in situations where they are unable to cope and paradoxically the ill-treatment of animals may undermine gaining new knowledge (Barnard & Hurst 1996). Studying animal behaviour is becoming an issue in regards to ethical regulation and legislation (Barnard 2007), such measures have been implemented to protect the subjects whilst in experimental conditions.

A crucial objective for equine scientists studying equine behaviour and learning processes is to capitalize on the benefits for both human and animal (Murphy and Arkins 2007). By

furthering our understanding equine welfare can be promoted and this knowledge shared with fellow horse men and women, academics and practitioners alike.

### **7.18 Conclusion**

This study investigated if horses consistently show a directional preference during a detour task. The investigations conducted in this study demonstrated that there was not a preference for direction, or therefore a directional bias. The horses in this study did not exhibit a favoured limb with which to initiate movement with when undertaking a task. Horses typically stand with one forelimb in advance of the other. However the horses in this study did not show a preference for a particular limb to be extended at the goal.

First limb moved and extended limb at goal are relatively simple measures that can be used to assess laterality. The methods used in this study were previously validated by industry specialists and equine scientists alike. Studies assessing limb movement and extension in connection with lateral preferences, can be easily implemented and applied in a range of environments in which horses are kept and worked.

The absence of laterality biases found in this study could be attributed to the lack of congruity between ability of subjects and the requirements of the task in the study. Despite all horses were known to be familiar with the area in which the study took place, the early success in the detour task (i.e. when the task was most simple) could be due to the novelty of being in the experimental area. Performance as judged by completing the task, and the time taken to do so, showed a slight decline as the task became more difficult. The frequency and variety of behaviours seen in interaction with the task did not vary significantly over distance and time, therefore it could be argued that this may have been due to becoming more familiar with the environment and not due to the task becoming more challenging.

Understanding directional biases would provide further information on how horses interact with their environment. This finding can be applied within the equestrian practical context for example when training and preparing horses for work. It must be recognised that horses should not be required to perform tasks outside of their behavioural ability and repertoire and that the overall welfare of the subject is of paramount importance at all times. Equally this must be acknowledged when conducting behavioural task-related studies with horses. It is crucial to take into account the horses limitation and not put them in the position of not being able to carry out the expected work.

Subsequently horse handlers and trainers can implement considerate training and handling practices based on future findings from laterality based studies. The outcome of future studies based on behaviour will provide further information on cognitive abilities of horses.



## APPENDIX 1

### **The relationship between facial whorl characteristics and motor laterality exhibited in horses (*Equus caballus*)**

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It is becoming recognised that understanding the motor laterality exhibited by individual horses may contribute to the wellbeing of the horse. In modern equitation, demands are put on the horse that interferes with their asymmetry and natural movement. It has been suggested that facial hair whorl direction (FWD) may be used as a physical indicator of laterality. Following successful validation, digital pedometers (designed for human use) were used to record the activity of the forelegs of 22 horses. Reading were taken over for 4h period whilst the horses were stabled with forage and water *ad libitum*. Three replications were conducted for 9 horses with a clockwise ( C ) facial whorl and 13 horses with a counter-clockwise (CC) facial hair whorl. There was a significant effect of whorl direction on the total number of steps recorded ( $F_{1,128}=7.77; P<0.01$ ). Horses with C whorls took more steps i.e. more mobile in general (mean = $11.4\pm 18.4$ ) than horses with CC whorls (mean  $4.39\pm 18.4$ ). Laterality Indices (LI) were derived and significance determined for resulting z scores ( $<0.05$ ). Analysis of LI indicated an overall left bias within the sample population (mean LI= $7.27\pm 18.4$ ) regardless of whorl direction, however horses with a C whorl exhibited a stronger left bias (mean LI= $11.4\pm 17.2$ ) than horses with CC (mean LI= $4.39\pm 19.4$ ). Pedometers are a low cost device which can be used to measure motor laterality in horses. A better understanding of laterality may improve the welfare and general health of the horse and improve the safety of the rider/handler. Understanding laterality limitations may lead to more effective and equally sympathetic training methods.

## The relationship between facial whorl characteristics and motor laterality exhibited in horses (*Equus caballus*)

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### The Message

- Anecdotal evidence suggests facial hair whorl direction may be used as a physical indicator of motor laterality in horses.
- In modern equitation, demands are put on the horse that interferes with their asymmetry and natural movement.

### Introduction

Temperament, sexual orientation, lateralization, learning ability and brain development has been related to the position and direction of the hair whorls in a number of species.

It has been hypothesised that handedness in humans is a factor that relates to whorl morphology and that whorl characteristics may be used as an indicator of handedness.

The aim of this study was to investigate the relationship between facial hair whorl direction and motor laterality in horses.

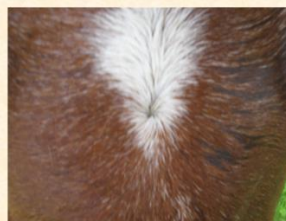
### Methods ~ laterality & hair whorl direction

- Following successful validation using videography, direct and indirect observation, digital pedometers were used to simultaneously record both left and right fore limb activity.
- 9 horses with a clockwise (C) facial whorl and 13 horses with a counter-clockwise (CC) facial hair whorl were selected from a population of 35 horses.
- Horses with 2 or more facial whorls, or a whorl of indeterminate direction were excluded from analysis.
- Step data were recorded for a 4h period whilst horses were stabled with *ad libitum* forage and water. There were 3 replications per horse.



### Results

- There was a significant effect of whorl direction on the total number of steps recorded ( $F_{1,128}=7.77$ ;  $P<0.01$ ) within the study sample.
- Horses with C whorls took more steps, i.e. were more Mobile ( $11.4\pm 18.4$ ), than horses with CC whorls ( $4.39\pm 18.4$ ).



Clockwise Facial Whorl



Counter-Clockwise Facial Whorl

- An overall left bias in forelimb movement existed within the sample (mean LI=  $7.27\pm 18.4$ ) regardless of whorl direction; however horses with a C whorl exhibited a stronger left bias (mean LI =  $11.4\pm 17.2$ ) than horses with CC whorls (mean LI=  $-4.39\pm 19.4$ ).
- In this sample of horses there was no evidence of an overt relationship between facial whorl characteristic and fore limb laterality preference ( $P>0.05$ ).

### Conclusion

- There is strong evidence of a left bias in the motor laterality exhibited by a mixed breed population of ridden horses.
- No relationship between facial whorl characteristics and laterality preference was found.
- Understanding laterality would benefit all involved in the industry subsequently improving equine welfare.

### Acknowledgements

Alison Abbey and the evening staff at Duchy College are thanked for facilitating access to the horses and allowing data collection.

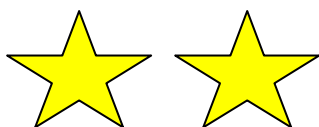
## APPENDIX 2

### Duchy College Working Horses Grading System

The descriptions of the criteria for each star rating of horse are guidelines and some horses may have elements may have two different ratings. The grading that each horse is given will be assessed by a member of staff. After a horse has had more than a three break from work, it will be reassessed. This grading criteria relates specifically to the horses work in the school and is focusing on safety.



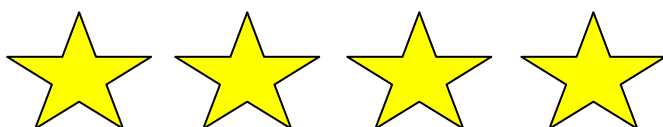
This type of horse is one that is more sensitive to ride or can be excitable. It is a horse which requires schooling and educating. The horse may have never jumped or is very green to jump. This horse is only suitable for the more experience students to ride.



This type of horse can be excitable to ride. It is a horse which has some experience in schooling but still requires educating. The horse may be green to jump. This horse is suitable for Yellow, Grey, Kiwi, Brown, Lime, Lemon and Blue students to ride.



This type of horse is educated in it's [sic] schooling on the flat and obedient to the riders aids but can be sensitive to incorrect aids. It is a horse which is honest to jump but can be forward going. This horse is suitable for all colour groups to ride.



This type of horse rarely becomes excitable. They are an honest experienced jumper. They are safe even when the rider becomes unbalanced and are forgiving by nature.

## Working Horse Assessment Sheets

Horses's Name: \_\_\_\_\_

Date: \_\_\_\_\_

Staff Assessor: \_\_\_\_\_

	Stage 3 riders	Stage 2/3 riders	Stage 2 riders	Stage 1 riders	Notes
	*	**	***	****	
Mounting					
Walk					
Trot					
Canter					
Halting					
Contact					
Jumping and Poles					
Rideability					
Group Work					
Hacking					
Other					
Grade given	*	**	***	****	

Signature: \_\_\_\_\_

## References

Adams, O. R. 1979. *Lameness in horses*, Philadelphia USA, Lea and Febiger Publishing.

Andrade, C., Alwarshetty, M., Sudha, S. & Chandra, J. S. 2001. Effect of innate direction bias on T-maze learning in rats: implications for research. *Journal of Neuroscience Methods*, **110** (1-2), 31-35.

Asher, L., Collins, L. M., Ortiz-Pelaez, A., Drewe, J. A., Nicol, C. & Pfeiffer, D. U. 2009. Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of the Royal Society of Interface*, **6** (41), 1103-1119.

Austin, N. P. & Rogers, L. J. 2012. Limb preferences and lateralization of aggression, reactivity and vigilance in feral horses, *Equus caballus*. *Animal Behaviour*, **83**, 239-247.

Austin, N. P. & Rogers, L. J. 2007. Asymmetry of flight and escape turning in responses in horses. *Laterality: Asymmetries of Body, Brain and Cognition*, **12** (5), 464-474.

Baragli, P., Vitale, V., Cipollini, M. & Sighieri, C. 2012. Motor laterality of forelimbs preference in freestyle jumping horses. *International Society for Equitation Science*, p80.

Baragli, P., Vitale, V., Paoletti, E., Mengoli, M. & Sighieri, C. 2011a. Encoding the object position for assessment of short term spatial memory in horses (*Equus caballus*). *International Journal of Comparative Psychology*, **24**, 284-291.

Baragli, P., Vitale, V., Paoletti, E. & Sighieri, C. 2011b. Detour behaviour in horses (*Equus caballus*). *Journal of Ethology*, **29**, 227-234.

Barnard, C. J. 2007. Ethical regulation and animal science; why animal behaviour is special. *Animal Behaviour*, **74**.

Barnard, C. J. & Hurst, J. L. 1996. Welfare by design: the natural selection of welfare criteria. *Animal Welfare*, **5**, 405-433.

Berta, C. 2011. Lateralized behaviour in domesticated dogs. *ESSAI*, **8** (9), Available at: <http://dc.cod.edu/essai/vol8/iss1/9>.

Bevlin, A. V., Gandhi, C. C., Wood, G. E., Talk, A. C., Matzel, L. D. & Shors, T. J. 2001. The role of the hippocampus in trace conditioning: temporal discontinuity or task difficulty. *Neurobiology of Learning and Memory*, **76** (3), 447-461.

Bian, C., Zhu, K., Guo, Q., Xiong, Y., Cai, W. & Zhang, J. 2012. Sex differences and synchronous development of steroid receptor coactivator-1 and synoptic proteins in the hippocampus of postnatal and female C57BL/6 mice. *Steroids*, **77** (1-2), 149-156.

- Bisazza, A., Facchin, L., Pignatti, R. & Vallortigara, G. 1998. Lateralization of detour behaviour in poeciliid fish: the effect of species, gender and sexual motivation. *Behavioural Brain Research*, **91** (1-2), 157-164.
- Blackmore, T. L., Foster, T.M., Sumpter, C. E. & W., T. 2008. An investigation of colour discrimination with horses (*Equus caballus*). *Behavioural Processes* **78**, 387-396.
- Bradshaw, J. L. 1991. Animal asymmetry and human heredity. Dextrality, tool use and language in evolution-10 years after Walker (1980). *British Journal of Psychology*, **82** (1), 39-59.
- Breed, M. D. & Moore, J. 2012. *Animal Behaviour*, London, Elsevier.
- British. Horse Industry Confederation 2011. *BETA Survey*. Available from <http://www.bhic.co.uk/facts-and-figures/beta-survey.html> [Online]. [Accessed 01/05/2011].
- Carmeli, E., Patish, H. & Coleman, R. 2003. The Aging Hand. *Journal of Gerontology. Medical Sciences*, **58**, 146-152.
- Casanova, P. M. P. I. & Oosterlinck, M. 2012. Hoof size and symmetry in young catalan pyrenean horses reared under semi-extensive conditions. *Journal of Equine Veterinary Science*, **32**, 231-234.
- Church, R. M. 2001. Animal cognition: 1900-2000. *Behavioural Processes*, **54** (1-3), 53-63.
- Clayton, N. S. 1998. Memory and the hippocampus in food-storing birds: a comparative approach. *Neuropharmacology*, **37** (4-5), 441-452.
- Collett, T. S., Cartwright, B. A. & Smith, B. A. 1986. Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Psychology*, **158**, 835-851.
- Corballis, M. C. 2008. The evolution and genetics of cerebral asymmetry. *The Royal Society of Biological Sciences*, **364** (1519), 867-879.
- Cozzi, A., Lafont Lecuelle, C., Monneret, P., Articlaux, F., Bougrat, L., Bienboire Frosini, C. & Pageat, P. Year. The impact of maternal equine appeasing pheromone on cardiac parameters during an cognitive test in saddle horses after transport. *In: Proceedings of the seventh International Society for Equitation Science Conference*, 2011 Hooge Mierde, The Netherlands. 79.
- Dalin, G., Magnusson, L. E. & Thafvelin, B. C. 1985. Retrospective study of hindquarter asymmetry in standardbred trotters and its colleration with performance. *Equine Veterinary Journal*, **17**, 292-296.
- Dalla Costa, E., Allegrini, M., Cerrie, E. & Minero, M. 2011. Social learning in horses: does the demonstration of a conspecific affect the ability to solve a detour task? *Proceedings of the seventh International Society for Equitation Science Conference*, p.13.

Davenport, G., C. 1995. *Introducing GSCE Psychology*, London, Davenport and Harper Collins Publishers.

De Boyer des Roches, A., Durier, V., Richard Yris, M. A., Blois-Heulin, C., Ezzaouia, M., Hausberger, M. & Henry, S. 2011. Differential outcomes of unilateral interferences at birth. *Biology Letters*, **7** (2), 177-180.

De Boyer des Roches, A., Richard Yris, M. A., Henry, S., Ezzaouia, M. & Hausberger, M. 2008. Laterality and emotions: Visual laterality in the domestic horse (*Equus caballus*) differs with objects' emotional value. *Physiology & Behavior*, **94** (3), 487-490.

Drevemo, S., Fredricsson, I., Hjerten, G. & D., M. 1987. Early development of gait asymmetries in trotting Standardbred colts. *Equine Veterinary Journal*, **19**.

Durco, B., J., Bovenhuis, H. & Black, W. 2009. Heritability of foot conformation and its relationship to sports performance in a Dutch Warmblood horse population. *Equine Veterinary Journal*, **41** (2), 139-143.

Ecuyer-Dab, I. & Robert, M. 2004. Have sex differences in spatial ability evolved from male competition for mating and female concern for survival. *Cognition*, **91** (3), 221-257.

Edwards, G. R., Newman, J. A., Parsons, A. J. & Krebs, J. R. 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: an example with sheep. *Applied Animal Behaviour Science*, **50**, 147-160.

Edwards, G. R., Newman, J. A., Parsons, A. J. & Krebs, J. R. 1997. Use of cues by grazing animals to locate food patches: an example with sheep. *Applied Animal Behaviour Science*, **51**, 59-68.

Elias, L. J., Bryden, M. P. & Bulman-Fleming, M. B. 1998. Footedness is a better predictor than is handedness of emotional lateralization. *Neuropsychologia*, **36** (1), 37-43.

Eling, P. 1981. On the theory and measurement of laterality. *Neuropsychologia*, **19** (2).

Facchin, L., Bisazza, A. & Vallortigara, G. 1999. What causes lateralisation of detour behaviour in fish? evidence for asymmetries in eye use. *Behaviour Brain Research*, **103** (2), 229-234.

Fagot, J. & Vauclair, J. 1991. Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. *Psychological Bulletin*, **109** (1), 76-89.

Farmer, K., Krueger, K. & Byrne, R. W. 2010. Visual laterality in the domestic horse (*Equus caballus*) interacting with humans. *Animal Cognition*, **13** (2), 229-238.

Fraser, A. F. 1992. *The Behaviour of the Horse.*, Wallingford, UK., CAB International.

- Freeman, K. B., Green, L., Myerson, J. & Woolverton, W. L. 2009. Delay discounting of saccharin in rehesus monkeys. *Behavioural Processes*, **82**, 214-218.
- Ganskopp, D. 1995. Free-ranging angora goats: left - or right-handed tendencies while grazing? *Applied Animal Behaviour Science*, **43**, 141-146.
- Gee, P., Stephenson, D. & Wright, D. E. 1994. Temporal discrimination learning of operant feeding in goldfish (*Carassius auratus*). *Journal for the Experimental Analysis of Behaviour*, **62**, 1-13.
- Goodwin, D. 2007. Equine learning behaviour: What we know, what we don't and future research priorities. *Behavioural Processes*, **76**, 17-19.
- Grandin, T. 1993. Teaching principles and equipment design for handling livestock. *Journal of Animal Science*, **71**, 1065-1070.
- Greening, J. & Randle, H. 2012. A preliminary investigation into limb preference amongst a herd of semi-feral Koniks (*Equus ferus caballus*). *Proceedings of the eighth International Society for Equitation Science Conference*, p.124.
- Gregorios-Pippas, L., Tobler, P. N. & Schultz, W. 2009. Short-term temporal discounting of reward value in human ventral striatum. *Journal of Neurophysiology*, **101** (3), 1507-1523.
- Hall, C. & Cassaday, H., J. 2006. An investigation into the effect of floor colour on the behaviour of the horse. *Applied Animal Behaviour Science*, **99** (3-4), 301-314.
- Hall, C., Goodwin, D., Heleski, C., Randle, H. & Waran, N. 2008. Is there evidence of learned helplessness in horses? *Journal of Applied Animal Welfare Science* **11** (3), 249-266.
- Hanggi, E., B. 2010. Short-term memory testing in domestic horses: experimental design plays a role. *Journal of Equine Veterinary Science*, **30** (11), 617-623.
- Hanggi, E. B. 2005. The thinking horse: cognition and perception reviewed. *AAEP* **51**, 246-255.
- Hartmann, E., Christensen, J. W. & Keeling, L. J. 2011. Training young horses to social separation: effect of a companion horse training efficiency. *Equine Veterinary Journal*, **43** (5), 580-584.
- Hayes, N. 1998. *Foundations of Psychology*, Surrey, Thomas Nelson and Sons Limited.
- Heitor, F. & Vicente, L. 2007. Learning about horses: What is equine learning all about? *Behavioural Processes*, **76**, 34-36.



- Hemond, C. C., Kanwisher, N. G. & Op de Beeck, H. P. 2007. A preference for contralateral stimuli in human object and face-selective cortex. *PLoS ONE*, **6**, 1-5.
- Hepper, P. G., Shahidullah, S. & White, R. 1991. Handedness in the human foetus. *Neuropharmacology*, **29**, 1107-1111.
- Hepper, P. G., Wells, D. L. & Lynch, C. 2005. Prenatal thumb sucking is related to postnatal handedness. *Neuropharmacology*, **43** (3), 313-315.
- Hergenhahn, B. R. 2009. *A introduction to the history of psychology*, 6th Edn. Belmont., Wadsworth.
- Hopkins, D. W., Wesley, M. J., Russell, J. L. & Schapiro, S. J. 2006. Parental and perinatal factors influencing the development of handedness in captive chimpanzees. *Developmental Psychobiology*, **48** (6), 428-435.
- Hopster, H., Van der Werf, J. T. N. & Blokhuis, H. J. 1998. Side preferences of dairy cows in the milking parlour and its effects on behaviour and heart rate during milking. *Applied Animal Behaviour Science*, **55**, 213-229.
- Hosoi, E., Swift, D. M., Rittenhouse, L. R. & Richards, R. W. 1995. Comparative foraging strategies of sheep and goats in T-maze apparatus. *Applied Animal Behaviour Science*, **44** (1), 37-45.
- Hothersall, B., Gale, E. V., Harris, P. & Nicol, C. J. 2009. Cue use by foals (*Equus caballus*) in a discrimination learning task. *Animal Cognition*, **13** (1), 63-74.
- Hothersall, B. & Nicol, C. 2007. Equine learning behaviour: accounting for ecological constraints and relationships with humans in experimental design. *Behavioural Processes*, **76** (1), 45-48.
- Hunt, G. R., Corballis, M. C. & Gray, R. D. 2001. Laterality in tool manufacture by crows. *Nature*, **414**, 707.
- Iredale, S. K., Nevill, C. H. & Lutz, C. K. 2010. The influence of observer presence on baboon (*Papio spp.*) and rhesus macaque (*Macaca mulatta*) behaviour. *Applied Animal Behaviour Science*, **122** (1).
- Izawa, E. I., Kusayama, T. & Watanabe, S. 2005. Foot-use laterality in the Japanese jungle crow (*Corvus macrorhynchos*). *Behavioural Processes*, **69**, 357-362.
- Jovalekic, A., Hayman, R., Becares, N., Reid, H., Thomas, G., Wilson, J. & Jeffery, K. 2011. Horizontal biases in rats' use of three-dimensional space. *Behaviour Brain Research*, **23** (2), 279-288.
- Kaarthigeyan, J. & Dharmaretnam, M. 2005. Relative levels of motivation and asymmetries of viewing and detour task in guppies (*Poecilia reticulata*). *Behavioural Brain Research*, **159**, 37-41.

Kight, S. L., Steelman, L., Coffey, G., Lucente, J. & Castillo, M. 2008. Evidence of population-level lateralized behaviour in giant water bugs, *Belostoma flumineum* say (Heteroptera: Belostomatidae): T-maze turning is left biased. *Behavioural Processes*, **79** (1), 66-69.

Kiley-Worthington, M. 1997. *Equine Welfare*, London, J.A. Allen & Company Limited.

Klar, J. S. 1999. Genetic models for handedness, brain lateralization, schizophrenia, and manic-depression. *Schizophrenia Research*, **39** (3), 207-218.

Ksikisi, T. & Laca, E. A. 2002. Cattle do remember locations of preferred food over extended periods. **15** (6). [Accessed 230812].

Ladewig, J. 2007. Clever Hans is still whinnying with us. *Behavioural Processes*, **76**, 20-21.

Lane, A. & Phillips, C. 2004. A note on behavioural laterality in neonatal lambs. *Applied Animal Behaviour Science*, **86**, 161-167.

Laska, M. 1996. A Study of correlates of hand preferences in Squirrel monkeys (*Saimiri sciureus*). *Primates*, **37** (4), 457-465.

Leblanc, M. A. & Duncan, P. 2007. Can studies of cognitive abilities and of life in the wild really help us to understand equine learning? *Behavioural Processes*, **76**, 49-52.

Lehner, P. N. 1987. Design and execution of animal behaviour research: an overview. *Journal of Animal Science*, **65**, 1213-1219.

Lesimple, C., Fureix, C., LeScolan, N., Richard Yris, M. A. & Hausberger, M. 2011. Housing conditions and breed are associated with emotionality and cognitive abilities in riding school horses. *Applied Animal Behaviour Science*, **129**, 92-99.

Levine, J. M. & Zentall, T. R. 1974. Effect of a conspecific's presence on deprived rats' performance: Social facilitation vs distraction / imitation. *Applied Learning and Behaviour*, **2** (2), 119-122.

Lit, L., Schweizer, J. B. & Oberbauer, A. M. 2011. Handler beliefs affect scent detection dog outcomes. *Animal Cognition*, DOI 10.1007/s10071-010-0373-2.

Lund, N. 2002. *Animal Cognition: comparative psychology.*, East Sussex, Routledge.

Marinier, S. L. & Alexander, A. J. 1994. The use of a maze in testing learning and memory in horses. *Applied Animal Behaviour Science*, **39**, 177-182.

Martin, J. & Lopez, P. 2001. Hindlimb asymmetry reduces escape behaviour in the lizard (*Psammmodromus algirus*). *Physiological and Biochemical Zoology*, **74** (5), 619-624.

Martin, P. & Bateson, P. 2007. *Measuring Behaviour: an introductory guide*. 3rd ed., Cambridge, Cambridge University Press.

McCall, C. A. 1990. A review of learning behaviour in horses and its application in horse training. *Journal of Animal Science*, **68**, 75-81.

McGreevy, P. 2007. The advent of equitation science. *The Veterinary Journal*, **174** (3), 452-453.

McGreevy, P., Brueckner, A., Thompson, P. C. & Branson, N. J. 2010. Motor laterality in 4 breeds of dog. *Journal of Veterinary Behavior: Clinical Applications and Research*, **5** (6), 318-323.

McGreevy, P., Landrieu, J. P. & Malou, P. F. J. 2007. A note on motor laterality in plains zebras (*Equus burchellii*) and impalas (*Aepyceros melampus*). *Laterality* **12** (5), 449-457.

McGreevy, P. & McLean, A. 2007. The roles of learning theory and ethology in equitation. *Journal of Veterinary Behaviour: Clinical Applications and Research*, **2**, 108-118.

McGreevy, P. & Rogers, L. J. 2005. Motor and sensory laterality in Thoroughbred horses. *Applied Animal Behaviour Science*, **92**, 337-352.

McGreevy, P. & Thompson, P. C. 2006. Differences in motor laterality between breeds of performance horse. *Applied Animal Behaviour Science*, **99**, 183-190.

McLean, A. 2001. Cognitive abilities — the result of selective pressures on food acquisition? . *Applied Animal Behaviour Science*, **71** (3), 241-258.

McLean, A. 2004. Short-term spatial memory in the horse. *Applied Animal Behaviour Science*, **85** (1-2), 93-105.

McLean, A. 2012. Distilling Equitation Science - objectivity versus subjectivity in equine behaviour modification. *Proceedings of the eight International Society for Equitation Science Conference*, p.148-149.

McLean, A. & McLean, M. 2008. Academic Horse Training. Equitation Science in Practice. *Australian Equine Behaviour Centre*.

Meehan, C. L. & Mench, J. A. 2007. The challenge of challenge: can problem solving opportunities enhance animal welfare? . *Applied Animal Behaviour Science*, **102**, 246-261.

Mendl, M., Burman, O. H. P., Parker, R. M. A. & Paul, E. S. 2009. Cognitive bias as an indicator on animal emotion and welfare: emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, **118**, 161-181.

- Mendl, M. & Nicol, C. (eds.) 2009. *The ethology of domestic animals.*, Oxford: CAB International.
- Mills, D. & Nankervis, K. 1999. *Equine Behaviour: principles and practice*, Oxford, Blackwell Science.
- Murphy, J. & Arkins, S. 2007. Equine learning behaviour. *Behavioural Processes*, **76** (1), 1-13.
- Murphy, J. & Arkins, S. 2008. Facial hair whorls (trichoglyphs) and the incidence of motor laterality in the horse. *Behavioural Processes*, **79**, 7-12.
- Murphy, J., Sutherland, A. & Arkins, S. 2005. Idiosyncratic motor laterality in the horse. *Applied Animal Behaviour Science*, **91**, 297-310.
- Murphy, J., Waldman, T. & Arkins, S. 2004. Sex differences in equine learning skills and visuo-spatial ability. *Applied Animal Behaviour Science*, **87**.
- Nicol, C. 2002. Equine learning: progress and suggestions for future research. *Applied Animal Behaviour Science*, **78**, 193-208.
- Nicol, C., Badnell-Waters, A. J., Bice, R., Kelland, A., Wilson, A. D. & Harris, P. 2005. The effects of diet and weaning method on the behaviour of young horses. *Applied Animal Behaviour Science*, **95**, 205-221.
- Oseen, K. L., Newhook, L. K. D. & Wassersug, R. J. 2001. Turning biases in woodfrog (*Rana sylvatica*) tadpoles. *Herpetologica*, **57** (4), 432-437.
- Pearce, J. M. 1987. *An introduction to animal cognition.*, Hove, Lawrence Erlbaum Associates Limited.
- Peterson, K. & Sherry, D. 1996. No sex difference occurs in hippocampus food-storing or memory for food caches in black capped chickadees. *Behavioural Brain Research*, **79** (1-2), 15-22.
- Pointer, J. S. 2012. Sighting versus sensory ocular dominance. *Journal of Optometry*, DOI: 10.1016/j.optom.2012.03.001.
- Pongracz, P., Miklosi, A., Kubinyi, E., Gurobi, K., Topal, J. & Csanyi, V. 2001. Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task. *Animal Behaviour*, **62**, 1109-1117.
- Pongracz, P., Miklosi, A., Kubinyi, E., Topal, J. & Csanyi, V. 2003. Interaction between individual experience and social learning in dogs. *Animal Behaviour*, **65**, 595-603.
- Randle, H. Year. Can a simple problem solving task be used to assess learned helplessness in horses. *In: International Society for Equitation Science*, 2008 Dublin, Ireland. p.64.

Rashid, N. & Andrew, R. J. 1989. Right hemisphere advantage for topographical orientation in the domestic chick. *Neuropsychologia*, **27**.

Reddon, A. & Hurd, P. L. 2008. Aggression, sex and individual differences in cerebral lateralization in fish. *Biology Letters*, **23** (4), 338-340.

Reddon, A. & Hurd, P. L. 2009. Acting unilaterally: why do animals with strongly lateralized brains behave differently than those with weakly lateralised brains? *Bioscience Hypotheses*, **2** (6), 383-387.

Reddon, A. R., Gutierrez-Ibanez, C., Wylie, D. R. & Hurd, P. L. 2009. The relationship between growth, brain asymmetry and behavioural lateralization in a cichlid fish. *Behavioural Brain Research*, **201** (1), 223-228.

Regolin, L., Vallortigara, G. & Zanforlin, M. 1995. Object and spatial representations in detour problems by chicks. *Animal Behaviour*, **49**, 195-199.

Rogers, C. W., Bolwell, C. F., Tanner, J. C. & Van Weeren, R. 2012. Early exercise in the horse. *Journal of Veterinary Behaviour: Clinical Applications and Research*.

Rogers, L. J. 1980. Lateralization in the avian brain. *Bird Behaviour*, **2**, 1-12.

Rogers, L. J. 2009. Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of The Royal Biological Society*, **364** (1519), 943-954.

Rogers, L. J. 2010. Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, **127** (1-2), 1-11.

Rogers, L. J. & Andrew, R. J. 2002. *Comparative vertebrate lateralization.*, Cambridge, Cambridge University Press.

Rogers, L. J., Zucca, P. & Vallortigara, G. 2004. Advantages of having a lateralized brain. *Proceedings of the Royal Biological Sciences*, **271** (6), 420-422.

Roof, R. L. & Stein, D. G. 1999. Gender differences in Morris water maze performance depend on task parameters. *Physiol Behaviour*, **68** (1-2), 1-15.

Roth, H. L., Lora, A. N. & Heilman, K. M. 2002. Effects of monocular viewing and eye dominance on spatial attention. . *Brain* 125.

Sakai, M., Hishii, T., Takeda, S. & Kohshima, S. 2006. Laterality of flipper rubbing behaviour in wild bottlenose dolphin (*Tursiops aduncus*): caused by asymmetry of eye use? *Behavioural Brain Research*, **170**, 204-210.

Sankey, C., Henry, S., Clouard, C., Richard-Yris, M. A. & Hausberger, M. 2011. Asymmetry of behavioral responses to a human approach in young naive vs. trained horses. *Physiology & Behavior*, **104** (3), 464-468.

Sankey, C., Richard-Yris, M. A., Leroy, H., Henry, S. & Hausberger, M. 2010. Positive interactions lead to lasting positive memories in horses, (*Equus caballus*). . *Animal Behaviour*, **79** (4), 869-875.

Santin, L. J., Begega, A., Rubio, S. & Arias, J. L. 1996. Behaviour laterality in male rats: influence of practice and stress. *Physiology & Behavior*, **60** (1), 161-164.

Sappington, B. K. F., McCall, C. A., Coleman, D. A., Kuhlers, D. L. & Lishak, R. S. 1997. A preliminary study of the relationship between discrimination reversal learning and performance tasks in yearling and 2 year old horses. *Applied Animal Behaviour Science*, **53**, 157-166.

Savin, H. & Randle, H. Year. The relationship between facial whorl characteristics and laterality exhibited in horses. *In: Proceedings of the sixth International Society for Equitation Science Conference.*, 2010 Uppsala, Sweden. p.57.

Schaafsma, S. M., Riedstra, B. J., Pfannkuche, K. A., Bouma, A. & Groothuis, T. G. G. 2009. Epigenesis of behavioural lateralization in humans and other animals. *Philosophical Transactions of The Royal Biological Society*, **364**, 915-927.

Schiller, P. H. 1950. Analysis of detour behaviour: IV. Congruent and incongruent detour behaviour in cats. *Journal of Experimental Psychology*, **40** (2), 217-227.

Singh, I. 1971. One-sided dominance in the limbs of rabbits and frogs, as evidenced by asymmetry in bone weight. *Journal of Anatomy*, **109** (2), 271-275.

Smith, B. P. & Litchfield, C. A. 2010. How well do dingoes, (*Canis dingo*), perform on the detour task? *Animal Behaviour*, **80** (1), 155-162.

Smith, B. P. & Litchfield, C. A. 2010. How well do dingoes, *Canis dingo*, perform on the detour task? . *Animal Behaviour*, **80** (1), 155-161.

Sondergaard, E., Bak Jensen, M. & Nicol, C. J. 2011. Motivation for social contact in horses measured by operant conditioning. *Applied Animal Behaviour Science*, **132**, 131-137.

Sovrano, V. A., Rainoldi, C., Bisazza, A. & Vallortigara, G. 1999. Rots of brain specializations: preferential left-eye use during mirror-image inspection in six species of teleost fish. *Behavioural and Brain Sciences*, **106** (1-2).

Stachurska, A., Pieta, M. & Nesteruk, E. 2002. Which obstacles are most problematic for jumping horses? *Applied Animal Behaviour Science*, **77** (3), 197-207.

- Stavnezer, A. J., McDowell, C. S., Hyde, L., Bimonye, H. A., Balogh, S. A., Hoplight, B. J. & Denenberg, V. H. 2000. Spatial ability of XY sex-reversed female mice. *Behavioural Brain Research*, **112** (1-2), 135-143.
- Stevens, J. R. & Muhlhoff, N. 2012. Intertemporal choice in lemurs. *Behavioural Processes*, **80**, 121-127.
- Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. 2005. Will travel for food: spatial discounting in two new world monkeys. *Current Biology*, **15**, 1855-1860.
- Takeuchi, Y., Hori, M. & Oda, Y. 2012. Lateralised kinematics of predation behaviour in a lake tanganyika scale-eating Cichlid fish. *PLoS ONE*, **7** (1).
- The British Horse Society 2005. *Complete horse and pony care*, London, Harper Collins.
- Thorpe, C. M., Jacova, C. & Wilkie, D. M. 2004. Some pitfalls in measuring memory in animals. *Biobehavioral Reviews*, **28**, 711-718.
- Tolman, E. C. 1948. Cognitive maps in rats and men. *Psychological Review*, **55**, 189-208.
- Tomkins, L., Thompson, P. C. & McGreevy, P. D. 2010. First-stepping test as a measure of motor laterality in dogs (*Canis familiaris*). *Journal of Veterinary Behavior: Clinical Applications and Research*, **5** (5), 247-255.
- Tomkins, L. M., Thompson, P. C. & McGreevy, P. 2012. Associations between motor, sensory and structural lateralisation and guide dog success. *The Veterinary Journal*, **192**, 359-367.
- Tommasi, L. 2009. Mechanisms and functions of brain and behavioural asymmetries. . *The Royal Society of Biological Sciences*, **364** (1519), 855-859.
- Tommasi, L., Andrew, R. J. & Vallortigara, G. 2000. Eye use in search is determined by the nature of the task in the domestic chick (*Gallus gallus*). *Behavioural Brain Research*, **112**, 119-126.
- Vallortigara, G. & Andrew, R. J. 1991. Lateralisation of response ny chicks to change in a model partner. *Animal Behaviour*, **41**, 187-194.
- Vallortigara, G., Regolin, G. & Pagni, P. 1999. Detour behaviour, imprinting and visual lateralization in the domestic chick. *Cognitive Brain Research*, **7** (3), 307-320.
- Vallortigara, G. & Regolin, L. 2002. *Facing an obstacle: lateralization of object and spatial cognition.*, Cambridge, Cambridge University Press.

- Vallortigara, G. & Rogers, L. J. 2005. Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioural and Brain Sciences*, **28**, 575-633.
- Vallortigara, G., Rogers, L. J. & Bisazza, A. 1999. Possible evolutionary origins of cognitive brain lateralisation. *Brain Research Reviews*, **30**, 164-175.
- Van Dierendonck, M. C. & Goodwin, D. 2005. *Social contact in horses: implications for human-horse interactions.*, Van Gorcum, 65-81 Animals in Philosophy and Science series.
- Van Heel, M. C., Kroekenstoel, A. M., Van Dierendonck, M. C., Van Weeren, R. & Back, W. 2006. Uneven feet may develop as a consequence of lateral grazing behaviour induced by the conformation of a foal. *Equine Veterinary Journal*, **38**, 646-665.
- Van Heel, M. C., Van Dierendonck, M. C., Kroekenstoel, A. M. & Back, W. 2010. Lateralised motor behaviour leads to increased unevenness in front feet and asymmetry in athletic performance in young mature Warmblood horses. *Equine Veterinary Journal*, **42** (5), 444-450.
- Versace, E., Morgante, M., Pulina, G. & Vallortigara, G. 2007. Behavioural lateralization in sheep (*Ovis aries*). *Behavioural and Brain Sciences*, **184**, 72-80.
- Visser, E. K. & Van Wijk-Jansen, E. E. C. 2012. Diversity in horse enthusiasts with respect to horse welfare: An explorative study. *Journal of Veterinary Behavior*, **7**, 295-304.
- Vlamings, P. H. J. M., Hare, B. & Call, J. 2010. Reaching around barriers: the performance of the great apes and 3-5year old children. *Animal Cognition*, **13** (2), 273-285.
- Vogels, R., Saunders, R. C. & Orban, G. A. 1994. Hemispheric lateralization in rhesus monkeys can be task-dependent. *Neuropsychologia*, **32** (4), 425-438.
- Ward, J. P. & Cantalupo, C. 1997. Origins and functions of laterality: interactions of motoric systems. *Laterality*, **2** (2/3), 279-303.
- Warren-Smith, A. & McGreevy, P. 2010. The use of pedometers to establish motor laterality in grazing horses. *Journal of Veterinary Behavior: Clinical Applications and Research*, **5** (4), 177-179.
- Weller, R., Pfau, T., May, S., A. & Wilson, A., M. 2006. Variation in conformation in a cohort of National Hunt racehorses. *Equine Veterinary Journal*, **38**, 616-621.
- Wells, A. E. D. & Blache, D. 2008. Horses do not exhibit motor bias when their balance is challenged. *Animal*, **2** (11), 1645-1650.
- Wells, D. L., Irwin, R. M. & Hepper, P. G. 2006. Lateralised swimming behaviour in the California sea lion. *Behavioural Processes*, **73**, 121-123.



Whitaker, T. C., Olusola, O. & Redwin, L. 2008. The influence of horse gender on eventing competition performance. *Comparative Exercise Physiology*, **5** (2), 67-72.

Wilkinson, A., Kuenstner, K., Mueller, J. & Huber, L. 2010. Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, **6** (5), 614-616.

Williams, D. E. & Norris, B. J. 2007. Laterality in stride pattern preferences in racehorses. *Animal Behaviour*, **74** (4), 941-950.

Wood, B. 1997. Left-right asymmetry in animal development. *Annual Review of Cell Development*, **13**, 53-82.

Wynne, C. D. L. & Leguet, B. 2004. Detour behavior in the Quokka (*Setonix brachyurus*). *Behavioural Processes*, **67**, 281-286.

Zucca, P., Antonelli, F. & Vallortigara, G. 2008. Detour behaviour in three species of birds: quails (*Coturnix sp.*) herring gulls (*Larus cachinnans*) and canaries (*Serinus canaria*). *Animal Cognition*, **8** (2), 122-128.

Zucca, P., Cerri, F., Carluccio, A. & Baciadonna, L. 2011. Space availability influence laterality in donkeys (*Equus asinus*). *Behavioural Processes*, **88**, 63-66.

