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Causal Factors of Oral versus Locomotor Stereotypy in the Horse

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Abstract

Stereotypic behaviours are commonly observed in domestic equids, as they are in a range of captive, non-domesticated species. Estimates suggest that 19.5-32.5% of horses perform a stereotypy. The presence of these behaviours is thought to indicate sub-optimal welfare status, and can result in secondary physical pathologies such as colic, ligament strain and incisor wear. Relatively little is understood about the aetiologies of oral and locomotor stereotypies. Seemingly disparate causal factors have been proposed including gastric pathology, neural adaption and genetic predisposition. In this review we propose a

model of causality which presents separate pathways to the development and continuation of oral behaviours such as crib-biting, compared to locomotor alternatives (i.e., weaving). The word ‘stereotypy’ has alarmingly negative connotation among horse keepers. Stereotypic behaviours are often viewed as ‘vices’ and so a number of horse owners and establishments attempt to physically prevent the behaviour with harsh mechanical devices. Such interventions can result in chronic stress, and be further detrimental to equine welfare. Stereotypy has been proposed to be a stress coping mechanism. However, firm evidence of coping function has proven elusive. Stereotypy a range of serious welfare issues remain. This review will explore management options directed at both prophylaxis and remediation.

Keywords: crib-biting; weaving; striatum; dopamine.

Introduction to Equine Stereotypy

Stereotypic behaviours are repetitive, invariant (Pell and McGreevy, 1999; McBride and Hemmings, 2005; Ninomiya et al., 2007), idiosyncratic (Parker et al., 2009) and induced by motivational frustration (Mason, 2006), repeated attempts to cope or central nervous system dysfunction (McBride and Hemmings, 2009; McBride and Parker, 2015). Crib-biting is an oral stereotypy, in which the animal grasps a surface at chest height with the incisors, pulling back creating an arch with the neck (Moeller et al., 2008; McBride and Hemmings, 2009; Wickens and Heleski, 2010) accompanied by the sucking of air into the proximal oesophageal region, creating an audible grunting sound (Nicol et al., 2002; Moeller et al., 2008; McBride and Hemmings, 2009; Wickens and Heleski, 2010). Weaving is a locomotor stereotypy, defined as the repetitive weight shift from one forelimb to the other, often combined with lateral swaying of the head (Cooper et al., 2000; McBride and Hemmings, 2005). Box-walking, also a locomotor stereotypic behaviour, is the repetitive circular walking of the stable (McBride and Hemmings, 2009).

The extent of stereotypy manifestation would appear to differ between studies dependant upon factors such as stereotypy type, breed and performance discipline. For example, utilising a questionnaire based methodology McGreevy et al. (1995) reported that the prevalence of stereotypy ranged from 19.5% to 32.5% in horses from dressage, eventing and endurance backgrounds. A previous review calculated that 4.3% of horses perform the oral stereotypy, crib-biting, compared to 3.25% and 2.2%, respectively of horses that perform the locomotor stereotypies weaving and box-walking based upon previous published study (see McBride and Hemmings, 2009). Direct observations indicate that questionnaire-based estimates of stereotypy may be conservative (Cooper et al., 2000). Furthermore, certain breeds are more susceptible to stereotypy than others, indicating a genetic component to the development of these behaviours in the horse (Bachmann et al., 2003a; Albright et al., 2009; Wickens and Heleski, 2010). Thoroughbred horses are thought to be 3.1 times (Bachmann et al., 2003a), and warmbloods 1.8 times (Wickens and Heleski, 2010), more likely to perform crib-biting behaviour than other breeds. The thoroughbred is also thought to be more at risk of performing weaving behaviour (Ninomiya et al., 2007). It could be argued, however that thoroughbred and warmblood horses are utilised more greatly in performance disciplines, and that the increase prevalence of stereotypy observed in these breeds is a manifestation of their more intense management regimes.

Other abnormal behaviours of the horse which by some are considered stereotypic include oral behaviours such as tongue-flicking and wind-sucking, and locomotor behaviours, for instance pawing (Marsden, 2002; Cooper and Albentosa, 2005). Prevalence estimates for these behaviours remain largely unknown, and further investigation is warranted. Whether these abnormal behaviours can strictly be classified as stereotypic according to the widely accepted definition of stereotypy (above) is questionable, therefore this review will focus primarily upon the three motor anomalies (crib-biting, weaving and box walking) that reliably fit the commonly held definition.

Stereotypic behaviours are often viewed as 'vices' (McBride & Long, 2001), and are associated with health complications. For example, crib-biting results in excessive wear of the incisors, (McBride and Hemmings, 2009) and has been proposed by some authors to increase the likelihood of colic (Archer et al., 1998), although the underlying pathologic mechanisms are unknown. Weaving and box walking have been associated with secondary muscle fatigue (Ninomiya et al., 2007). Weaving is linked to weight loss (Mills and Davenport, 2002) and leg swelling, and may ultimately result in lameness (Cooper et al., 2000). It is perhaps because of these health impacts that there is a 37% reduction of monetary value of stereotypy performing animals (Marsden, 2002; see also Williams and Randle – this issue). Establishments including riding schools, racing and competition yards, do not allow stereotypy performing animals onto the premises due to unsubstantiated anecdotal belief that these behaviours are 'copied' from stereotypy performing neighbours (Cooper and Albentosa, 2005). As such, 74% riding schools, racing and competition yards investigated attempt to physically prevent the behaviour (McBride and Long, 2001). Surgical procedures such as a neurectomy or a myectomy, or the use of crib-straps or cribbing rings are designed to prevent crib-biting behaviour (McBride and Long, 2001; McBride and Hemmings, 2009; Albright et al., 2015). Despite their severity, these preventative measures are not always effective (McBride and Hemmings, 2009), though in some cases can result in a reduction in crib-biting behaviour (Albright et al., 2015). Owners of weaving horses often utilise anti-weaving bars (McBride and Long, 2001), so the horse is unable to put the head outside of the stable to conduct the behaviour (McAfee et al., 2002; McBride and Hemmings, 2009). This is often unsuccessful as horses continue to weave within the confines of the stable (McBride & Hemmings, 2009). Should the purpose of stereotypy be to provide a coping mechanism for the individual, the physical prevention of these behaviours could lead to further stress induced pathology (McGreevy and Nicol, 1998; McAfee et al., 2002; Hemmings et al., 2004; Houpt, 2012; Freymond et al., 2015). Indeed, following restriction of oral stereotypy with the use of a cribbing collar or surgical methods, crib-biting horses were less able to cope during a stress test in comparison to their counterparts who were not restricted from performing the crib-biting response (Nagy et al., 2009). Underlying causal and contributory issues for stereotypic behavior, e.g. poor environmental conditions, are seldom addressed, and may not be known (Cooper and Mason, 1998; Cooper and Albentosa, 2005; Nagy et al., 2009). We consider putative causal factors leading to stereotypy manifestation and suggest separate developmental mechanisms for oral and locomotory stereotypy of the horse.

Equine Oral Stereotypy: The Gastric Hypothesis

Gastric inflammation is common in crib-biting horses (Nicol et al., 2002; Cooper & Albentosa, 2005), suggesting that gastrointestinal discomfort may be linked to the development of this behaviour. Lending credence to this notion is the finding that crib-biting is a predominantly post-prandial response (McBride & Hemmings, 2004). Horses evolved to consume a forage based diet, with approximately 16-18h of the 24h time budget utilised for mastication in the wild (Cooper et al., 2005), during which 35-40 litres of alkaline saliva is produced (Nicol et al., 2002; Moeller et al., 2008; Nagy et al., 2010). Domesticated horses tend to be fed highly palatable cereal based concentrate feeds to meet high energy requirements (Hemmings et al., 2007; Albright et al., 2009; McBride and Hemmings, 2009; Whisher et al., 2011) which reduces mastication, resulting in decreased saliva production and increased acidity in the foregut (Nicol et al., 2002; Cooper and Albentosa, 2005; Hemmings et al., 2007). This increased acidity may result in gastric discomfort. Indeed, Nicol *et al* (2002) examined the equine gastric environment endoscopically, comparing those which crib-bite and those who did not exhibit oral stereotypy. Those who performed crib-biting demonstrated much more stomach ulceration. Further study may wish to examine the gastric lining of crib-biting animals and non-crib-biting animals kept under the same management and feeding regimes, to truly dissect the gastric hypothesis of oral stereotypy. Thus it has been hypothesized that the crib-biting response may attempt to replicate the mastication process to stimulate salivary production (Nicol et al., 2002; Hemmings et al., 2007; Moeller et al., 2008; Hothersall and Casey, 2012). Saliva produced during crib-biting is similar in pH to saliva produced during mastication (Moeller et al., 2008), which supports this idea. The function of crib-biting could be to buffer the stomach in an attempt to counteract gastric pain (Moeller et al., 2008) or acidosis of the hind-gut, and such a mechanism would be consistent with the significant increase in crib-biting response 2-8 hours after feeding (Clegg et al., 2008).

Evidence for this hypothesis includes that the addition of antacids to feed to modulate gastric pH resulted in a significant reduction of observed crib-biting

(Mills and MacLeod, 2002; Nagy et al., 2010), and improved stomach lining condition (Nicol et al., 2002). These positive results could also be attributed to increased mastication of a feed, given a lower palatability following the addition of powdered supplement.; this theory does require confirmation however. Resultant increases in saliva would then lead to more effective gastric buffering (Johnson et al., 1998). Cooper et al., (2005) found that increasing meal frequency also resulted in a significant reduction in the crib-biting response, perhaps due to the increased time taken to consume the ration, allowing a more effective buffering effect of the saliva. *Ad lib* feeding studies have also produced mixed results (Fenn et al., 2008; McCall et al., 2009) suggesting that the role of feeding regime in stereotypy development requires further research.

Archer et al. (2008) provided support for the gut based hypothesis of crib-biting. (Archer et al., 2008). Indeed, Archer *et al.* (2008) identified a strong, positive association between presence of crib-biting and risk of developing colic. Whether this relationship is causal or correlational is unknown (Cooper and Mason, 1998). An episode of colic may result in chronic stress, an area of study that certainly requires further investigation. Chronic stress in rodents contributes to sensitisation of the dopaminergic midbrain and striatum in a genotype dependent manner (Cabib et al., 1998) which has been hypothesized as a precursor for stereotypy manifestation (McBride and Hemmings 2005). Colic could be an initiating factor rather than an effect of crib-biting if the same processes occur in horses.

To summarize, experimental evidence supports some link between feeding, gastric discomfort and oral stereotypy, but it is currently difficult to conclude whether stereotypy is an ameliorative response to stomach pathology, the outcome of neural sensitisation induced by gastric stress, or an interaction between these factors.

Equine Oral Stereotypy: The Dopaminergic Hypothesis

Chronic stress can have a significant influence on dopamine physiology, particularly within the striatal brain regions (McBride and Hemmings, 2005).

Stressors commonly associated with stereotypy development such as feed restriction and social isolation induce significant alterations to dopamine receptor function in rodent models of spontaneous stereotypy (Cabib et al., 1998). Similar changes were also observed in crib-biting horses by McBride and Hemmings (2005) who found that D1 and D2 receptor densities were significantly increased within the nucleus accumbens (NAcc), which is associated with sensitisation to dopamine release within this ventral region. In contrast, D1 receptor density and D2 receptor affinity was reduced within the caudate nucleus, indicating reduced output of this dorsal striatal structure in crib biting horses (McBride and Hemmings, 2005). This study could not demonstrate whether these changes were present prior to the emergence of crib-biting behaviour, or were as a result of crib-biting, but activity the midbrain-striatum pathway is relevant for crib-biting horses. Changes within this anatomical and neurochemical system may affect other aspects of the horse's behavioural repertoire. The caudate nucleus is crucial to the process of action-outcome monitoring. In rodent models of caudate inactivation, animals exhibit habit formation (i.e., preferentially utilize a habitual response) far quicker than control rodents (Yin et al., 2005). Similar acceleration in habit formation may be observed in horses performing stereotypy. A cross maze test was examined striatal circuitry within a sample of crib-biting versus control animals (Parker et al., 2009). Parker and his co-workers observed that crib-biting animals demonstrated an accelerated preference for a 'response' rather than a 'place' strategy, and as such were preferentially utilising a habitual response rather than action-outcome monitoring. This finding suggests that there is decreased output of the caudate nucleus, resulting in an increased reliance on the sensorimotor putamen circuitry, resulting in accelerated habit formation (Parker et al., 2008; 2009). Receptor based alterations recorded by McBride and Hemmings (2005) may be probed using carefully designed cognitive testing. Given the financial, logistical and ethical dimensions of direct physiological measurements, cognitive tests have the potential to significantly extend knowledge of stereotypy and associated neuro-mechanics. Roberts et al. (2015) a proposed two basic inferred measures of dopamine transmission consisting of spontaneous eye blink rate (SBR) and behavioural initiation rate (BIR). Both were measured in triplicate over 30 minutes, SBR values were obtained via counting of full blinks in the left eye at rest, where BIR records the number of behavioural initiations i.e. the number of new behaviours performed, also at rest.

Crib-biting horses demonstrated significantly decreased SBR, consistent with studies that suggest lowered blink rate is indicative of dopamine receptor sensitisation (Roebel and MacLean, 2007; Roberts et al., 2015). This result also agrees with the receptor work conducted in the horse (McBride and Hemmings, 2005). The significantly increased BIR appears to indicate adaptations within the dopamine circuitry of crib-biting animals, due to dominance of the movement activating direct pathway over the movement inhibiting indirect pathway (Roberts et al., 2015). Both the SBR and the BIR data appear to reflect the significant adaptations of dopaminergic physiology previously recorded in crib-biting animals. Further longitudinal study should reveal the scope of SBR and BIR and may identify individuals predisposed to stereotypy development. If predictive potential is revealed, given the pivotal role of chronic stress in stereotypy development, the elimination of key stressors such as feed restriction and social isolation could effectively reduce the risk that neural adaptations to receptor populations develop. Insult to the gastric mucosa may also be associated with significant nociceptive signalling to the CNS. Pain leads to liberation of neuropeptides such as beta endorphin, which bind to mu receptor populations in the ventral tegmental area (VTA), and contribute significantly to neuroplasticity in striatal brain regions (see McBride and Hemmings 2009 for review). Therefore, a mechanism is proposed by which a variety of environmental stressors lead to the neural changes that underlie the emergence of stereotypy.

2.3 Equine Locomotor Stereotypy: Potential Aetiologies

Little work has been done on the specific aetiology of equine locomotor stereotypy. McBride and Hemmings (2004) and Cooper and Albentosa (2005) suggested that weaving is a pre-prandial response to highly palatable concentrate feed, and others propose weaving occurs in response to high environmental activity and anticipation (Cooper et al., 2000; Clegg et al., 2008).

Cooper et al. (2005) noted that the weaving response was significantly amplified when concentrate meal frequency was increased. Interestingly, the control horses whose meal frequency was not altered also performed an increase in locomotor stereotypies when the experimental group were given their concentrate ration. This may have been due to increased motivation to feed, suggesting that locomotor stereotypy may well be an anticipatory response. This reasoning is consistent with the pre-prandial nature of weaving behaviour (Cooper et al., 2005; McBride and Parker, 2015).

Absence of social interaction has previously been associated with locomotor stereotypic behaviour (Cooper et al., 2000; McAfee et al., 2002; Mills and Reizebos, 2005), an important observation given that horses are by nature social animals When stable designs were adapted to allow the horses displaying a stereotypy to observe other horses, the weaving response was significantly reduced (Cooper et al., 2000).This result agrees with a recent study indicating that adaptation of management regimes to include environmental enrichment such as increasing contact with conspecifics resulted in a positive cognitive bias, i.e. an improvement in affective state, in ambiguous situations (Löckener et al., 2016). Simulation of social behaviours using a stable mirror was also associated with reducing the weaving response (McAfee et al., 2002). It’s unknown whether the reduction was resultant from a perceived increase in social interaction or simply a distracting stimuli, and as such requires further investigation (McAfee et al., 2002). Mills and Reizebos (2005) attempted to resolve the relative potential roles of social interaction versus distraction. When a poster with a two dimensional image of a horse was present within the stable, the weaving response was significantly reduced (Mills and Reizebos, 2005). This result may suggest that the reduction in weaving response results from simulation of social behaviours. If so, weaving may be linked to social contact, though the potential distracting effect of a novel object may also have resulted in this reduction of weaving behaviour.

Weaving behaviour has also been attributed to lack of exercise (Cooper and Mason, 1998). Weaving decreases with increased turnout and exercise (Cooper et al., 2000). It is estimated that free-ranging horses take approximately 10,000 strides as part of their normal feeding regime within a social group per day. This amount of exercise is a stark contrast to the confined stable situations under which domesticated horses often live (Sarrafchi and Blokhuis, 2013). Increased turnout also increases the opportunity for social interaction and improved grazing activity. In this scenario social, exercise and nutritional requirements are met. thereby the impetus for performing weaving behaviour is removed.

One recent study sought to investigate the potential neural mechanisms governing weaving (Roberts et al., 2015). The SBR of the weaving animals was statistically similar to the control group, but significantly increased when compared to the crib-biting horses. SBR is believed to primarily controlled by midbrain projecting areas originating in the substantia nigra, and terminating in the dorsal striatum (see Karson 1983 for review). This finding suggests that dorsal striatal mechanics are comparable to stereotypy-free control horses. Approach latency and task acquisition were significantly faster in the weaving group. Heightened locomotion (reflected in reduced approach latency) and faster task acquisition are largely under ventral striatal control (see Robbins and Sahaikian, 1983 and Yin and Knowlton, 2006 for respective reviews) suggesting elevated ventral activity and normal functioning at the level of the dorsal striatum. This enhanced ventral striatal functioning is further supported by a lack of habitual responding in weaving animals, even after significant repetition of the operant response.

3.0 Motivational Basis of Stereotypic Behaviour

An understanding of motivational state during the development and ongoing performance of stereotypy is important. Hughes and Duncan (1988) proposed a generalised model (see Figure 1) to explain the motivational basis of a broad range of behaviours whereby in response to organism variables (i.e., declining blood glucose) the animal becomes motivated to perform a consummatory goal (i.e., feeding) and thus appetitive strategies ensue. As an example, a horse may have access to two fields, though preferentially graze in one field. When this field has been grazed, the horse may experience reduced blood glucose levels. At this point the consummatory goal is to graze. The appetitive behaviour is to get additional food by moving from the first field to the adjoining field. The appetitive phase has a positive feedback effect on motivation, and is therefore self-reinforcing i.e., appetitive behaviours increase the motivation to continue to perform appetitive behaviours until the consummatory goal has been met, in this case ingesting grass from the neighbouring field. The achievement of the consummatory goal has a number of effects: 1) functional consequence (e.g., elevated blood glucose), which leads to negative feedback on organism variables with a subsequent effect on motivation; 2) direct feedback on motivation, initially positive followed by negative; 3) an effect on perception of the animals environment which again influences the underlying motivation of the behaviour.

FIGURE 1 ABOUT HERE

In the context of the Hughes and Duncan (1988) model, stereotypies have been described as being appetitive in origin because the restrictive nature of the animals' environment prevents the consummatory goal from being attained. Thus a number of appetitive behaviours are being attempted in an effort to reach the consummatory goal. Lack of consummation and subsequent functional consequence means that no negative feedback on motivation to perform appetitive behaviours occurs. Consequently, appetitive behaviours continue and because they are self-reinforcing, the animal becomes locked in a positive feed-back loop. The restrictive nature of the environment 'channels' the behaviour into a limited number of discrete acts performed repeatedly. Over time, these frustrated appetitive behaviours evolve into stereotypic motor sequences.

This model can now be updated to incorporate findings from recent studies investigating locomotor versus oral stereotypy. Weaving seems to fit the Hughes and Duncan model very well. Weaving animals are not pre-disposed to accelerated habit formation, but do experience increased appetitive drive, perhaps due to neural alterations that centre on ventral striatal circuitry (Roberts et al., 2015). Weaving ensues whenever the consummatory goal (e.g., grazing, social interaction) cannot be reached, though ceases when motivational end points (e.g., turnout, social interaction) are provided. Indeed, anecdotal observations appear to support this notion, as weaving animals seldom perform stereotypy when turned out to pasture.

Crib-biting persists despite achievement of the consummatory goal. The recalcitrant nature of oral stereotypy reflects the tendency to rely on habitual response patterns recorded in various investigations (Hemmings et al., 2007; Parker et al., 2009). Indeed, minimal repetition of appetitive behaviour results in transition to automatic habitual responding, divorced from conscious motivational circuitry (see Figure 2).

FIGURE 2 ABOUT HERE

The ramifications of this extended model for management are twofold. First, weaving can potentially be reduced by providing free access to consummatory end points such as feeding and social interaction. Conversely, due the neural differences that render crib-biting animals prone to habitual response patterns, these animals will display considerable resistance to environmental intervention. Thus, crib-biting behaviour will persist despite apparent consummatory end points being reached. As such, a prophylactic approach to reducing occurrence of crib-biting behaviour is recommended, perhaps with the use of predictive tools such as SBR and BIR to identify predisposed animals and manage these animals accordingly.

3.0 Conclusions

Crib-biting horses are initially in a high state of motivation, and as such attempt appetitive behaviours (e.g., biting the stable door) in the face of poor environmental conditions, particularly in relation to thwarted feeding behaviours (e.g., lack of forage). Crib-biting is initially an appetitive behaviour and self-reinforcing. Alterations within the ventral and dorsal striatum as a result of stress and / or gastric pain increases the acceleration of habitual responding in crib-biting animals. Thus the initial elevated motivation to perform crib-biting is replaced with a habitual response pattern. As such, management regimes which allow the consummatory goal to be achieved may not necessarily reduce crib-biting behaviour. Neural changes may also account for the post-prandial increase in the crib-biting response. Following ingestion of palatable feed, an opioid mediated release of dopamine within the already sensitised striatum (McBride and Hemmings, 2005; Whisher et al., 2011) correlates with a significantly increased rate of the crib-biting response (Bachmann et al., 2003b; Whisher et al., 2011).

The weaving response appears to result from alterations to the ventral striatum which lead to a highly motivated state, resulting in locomotor stereotypy due to an unattainable consummatory goal. Weaving animals do not exhibit an accelerated reliance on habitual response mechanisms, and as such management strategies (e.g., increasing turnout) to reduce performance of locomotor stereotypy is worth attempting, by ensuring that the horse's innate needs are met.

Finally, both oral and locomotor stereotypies of the horse appear to involve neuroplasticity at the level of the striatal group of brain structures. In rodent species the function of these varies with genetic strain. The identification of genetic polymorphisms that may place horses at increased risk of stereotypy development deserve more research. The technology now exists to enable in-depth genetic research strategies. Following identification of predisposed animals, removal of key stressors will provide immense potential for prevention over and above unpredictable remedial measures.

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