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1 Causal Factors of Oral versus Locomotor Stereotypy in the Horse

2  
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16  
17 Abstract

18 Stereotypic behaviours are commonly observed in domestic equids, as they are in  
19 a range of captive, non-domesticated species. Estimates suggest that 19.5-  
20 32.5% of horses perform a stereotypy. The presence of these behaviours is  
21 thought to indicate sub-optimal welfare status, and can result in secondary  
22 physical pathologies such as colic, ligament strain and incisor wear. Relatively  
23 little is understood about the aetiologies of oral and locomotor stereotypies.  
24 Seemingly disparate causal factors have been proposed including gastric  
25 pathology, neural adaption and genetic predisposition. In this review we propose a

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

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

38 Introduction to Equine Stereotypy

39 Stereotypic behaviours are repetitive, invariant (Pell and McGreevy, 1999;  
40 McBride and Hemmings, 2005; Ninomiya et al., 2007), idiosyncratic (Parker et al.,  
41 2009) and induced by motivational frustration (Mason, 2006), repeated attempts to  
42 cope or central nervous system dysfunction (McBride and Hemmings, 2009;  
43 McBride and Parker, 2015). Crib-biting is an oral stereotypy, in which the animal  
44 grasps a surface at chest height with the incisors, pulling back creating an arch  
45 with the neck (Moeller et al., 2008; McBride and Hemmings, 2009; Wickens and  
46 Heleski, 2010) accompanied by the sucking of air into the proximal oesophageal  
47 region, creating an audible grunting sound (Nicol et al., 2002; Moeller et al., 2008;  
48 McBride and Hemmings, 2009; Wickens and Heleski, 2010). Weaving is a  
49 locomotor stereotypy, defined as the repetitive weight shift from one forelimb to  
50 the other, often combined with lateral swaying of the head (Cooper et al., 2000;  
51 McBride and Hemmings, 2005). Box-walking, also a locomotor stereotypic  
52 behaviour, is the repetitive circular walking of the stable (McBride and Hemmings,  
53 2009).

54

55 The extent of stereotypy manifestation would appear to differ between studies  
56 dependant upon factors such as stereotypy type, breed and performance  
57 discipline. For example, utilising a questionnaire based methodology McGreevy et

58 al. (1995) reported that the prevalence of stereotypy ranged from 19.5% to 32.5%  
59 in horses from dressage, eventing and endurance backgrounds. A previous  
60 review calculated that 4.3% of horses perform the oral stereotypy, crib-biting,  
61 compared to 3.25% and 2.2%, respectively of horses that perform the locomotor  
62 stereotypies weaving and box-walking based upon previous published study (see  
63 McBride and Hemmings, 2009). Direct observations indicate that questionnaire-  
64 based estimates of stereotypy may be conservative (Cooper et al., 2000).  
65 Furthermore, certain breeds are more susceptible to stereotypy than others,  
66 indicating a genetic component to the development of these behaviours in the  
67 horse (Bachmann et al., 2003a; Albright et al., 2009; Wickens and Heleski, 2010).  
68 Thoroughbred horses are thought to be 3.1 times (Bachmann et al., 2003a), and  
69 warmbloods 1.8 times (Wickens and Heleski, 2010), more likely to perform crib-  
70 biting behaviour than other breeds. The thoroughbred is also thought to be more  
71 at risk of performing weaving behaviour (Ninomiya et al., 2007). It could be  
72 argued, however that thoroughbred and warmblood horses are utilised more  
73 greatly in performance disciplines, and that the increase prevalence of stereotypy  
74 observed in these breeds is a manifestation of their more intense management  
75 regimes.

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

85

86 Stereotypic behaviours are often viewed as 'vices' (McBride & Long, 2001), and  
87 are associated with health complications. For example, crib-biting results in  
88 excessive wear of the incisors, (McBride and Hemmings, 2009) and has been  
89 proposed by some authors to increase the likelihood of colic (Archer et al., 1998),

90 although the underlying pathologic mechanisms are unknown. Weaving and box  
91 walking have been associated with secondary muscle fatigue (Ninomiya et al.,  
92 2007). Weaving is linked to weight loss (Mills and Davenport, 2002) and leg  
93 swelling, and may ultimately result in lameness (Cooper et al., 2000). It is perhaps  
94 because of these health impacts that there is a 37% reduction of monetary value  
95 of stereotypy performing animals (Marsden, 2002; see also Williams and Randle –  
96 this issue). Establishments including riding schools, racing and competition yards,  
97 do not allow stereotypy performing animals onto the premises due to  
98 unsubstantiated anecdotal belief that these behaviours are ‘copied’ from  
99 stereotypy performing neighbours (Cooper and Albentosa, 2005). As such, 74%  
100 riding schools, racing and competition yards investigated attempt to physically  
101 prevent the behaviour (McBride and Long, 2001). Surgical procedures such as a  
102 neurectomy or a myectomy, or the use of crib-straps or cribbing rings are  
103 designed to prevent crib-biting behaviour (McBride and Long, 2001; McBride and  
104 Hemmings, 2009; Albright et al., 2015). Despite their severity, these preventative  
105 measures are not always effective (McBride and Hemmings, 2009), though in  
106 some cases can result in a reduction in crib-biting behaviour (Albright et al., 2015).  
107 Owners of weaving horses often utilise anti-weaving bars (McBride and Long,  
108 2001), so the horse is unable to put the head outside of the stable to conduct the  
109 behaviour (McAfee et al., 2002; McBride and Hemmings, 2009). This is often  
110 unsuccessful as horses continue to weave within the confines of the stable  
111 (McBride & Hemmings, 2009). Should the purpose of stereotypy be to provide a  
112 coping mechanism for the individual, the physical prevention of these behaviours  
113 could lead to further stress induced pathology (McGreevy and Nicol, 1998;  
114 McAfee et al., 2002; Hemmings et al., 2004; Houpt, 2012; Freymond et al., 2015).  
115 Indeed, following restriction of oral stereotypy with the use of a cribbing collar or  
116 surgical methods, crib-biting horses were less able to cope during a stress test in  
117 comparison to their counterparts who were not restricted from performing the crib-  
118 biting response (Nagy et al., 2009). Underlying causal and contributory issues for  
119 stereotypic behavior, e.g. poor environmental conditions, are seldom addressed,  
120 and may not be known (Cooper and Mason, 1998; Cooper and Albentosa, 2005;  
121 Nagy et al., 2009). We consider putative causal factors leading to stereotypy  
122 manifestation and suggest separate developmental mechanisms for oral and  
123 locomotory stereotypy of the horse.

124

125 Equine Oral Stereotypy: The Gastric Hypothesis

126 Gastric inflammation is common in crib-biting horses (Nicol et al., 2002; Cooper &  
127 Albentosa, 2005), suggesting that gastrointestinal discomfort may be linked to the  
128 development of this behaviour. Lending credence to this notion is the finding that  
129 crib-biting is a predominantly post-prandial response (McBride & Hemmings,  
130 2004). Horses evolved to consume a forage based diet, with approximately 16-  
131 18h of the 24h time budget utilised for mastication in the wild (Cooper et al.,  
132 2005), during which 35-40 litres of alkaline saliva is produced (Nicol et al., 2002;  
133 Moeller et al., 2008; Nagy et al., 2010). Domesticated horses tend to be fed highly  
134 palatable cereal based concentrate feeds to meet high energy requirements  
135 (Hemmings et al., 2007; Albright et al., 2009; McBride and Hemmings, 2009;  
136 Whisher et al., 2011) which reduces mastication, resulting in decreased saliva  
137 production and increased acidity in the foregut (Nicol et al., 2002; Cooper and  
138 Albentosa, 2005; Hemmings et al., 2007). This increased acidity may result in  
139 gastric discomfort. Indeed, Nicol *et al* (2002) examined the equine gastric  
140 environment endoscopically, comparing those which crib-bite and those who did  
141 not exhibit oral stereotypy. Those who performed crib-biting demonstrated much  
142 more stomach ulceration. Further study may wish to examine the gastric lining of  
143 crib-biting animals and non-crib-biting animals kept under the same management  
144 and feeding regimes, to truly dissect the gastric hypothesis of oral stereotypy.  
145 Thus it has been hypothesized that the crib-biting response may attempt to  
146 replicate the mastication process to stimulate salivary production (Nicol et al.,  
147 2002; Hemmings et al., 2007; Moeller et al., 2008; Hothersall and Casey, 2012).  
148 Saliva produced during crib-biting is similar in pH to saliva produced during  
149 mastication (Moeller et al., 2008), which supports this idea. The function of crib-  
150 biting could be to buffer the stomach in an attempt to counteract gastric pain  
151 (Moeller et al., 2008) or acidosis of the hind-gut, and such a mechanism would be  
152 consistent with the significant increase in crib-biting response 2-8 hours after  
153 feeding (Clegg et al., 2008).

154

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

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

168  
169 Archer et al. (2008) provided support for the gut based hypothesis of crib-biting.  
170 (Archer et al., 2008). Indeed, Archer *et al.* (2008) identified a strong, positive  
171 association between presence of crib-biting and risk of developing colic. Whether  
172 this relationship is causal or correlational is unknown (Cooper and Mason, 1998).  
173 An episode of colic may result in chronic stress, an area of study that certainly  
174 requires further investigation. Chronic stress in rodents contributes to  
175 sensitisation of the dopaminergic midbrain and striatum in a genotype dependent  
176 manner (Cabib et al., 1998) which has been hypothesized as a precursor for  
177 stereotypy manifestation (McBride and Hemmings 2005). Colic could be an  
178 initiating factor rather than an effect of crib-biting if the same processes occur in  
179 horses.

180  
181 To summarize, experimental evidence supports some link between feeding,  
182 gastric discomfort and oral stereotypy, but it is currently difficult to conclude  
183 whether stereotypy is an ameliorative response to stomach pathology, the  
184 outcome of neural sensitisation induced by gastric stress, or an interaction  
185 between these factors.

#### 186 187 Equine Oral Stereotypy: The Dopaminergic Hypothesis

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

190 Stressors commonly associated with stereotypy development such as feed  
191 restriction and social isolation induce significant alterations to dopamine receptor  
192 function in rodent models of spontaneous stereotypy (Cabib et al., 1998). Similar  
193 changes were also observed in crib-biting horses by McBride and Hemmings  
194 (2005) who found that D1 and D2 receptor densities were significantly increased  
195 within the nucleus accumbens (NAcc), which is associated with sensitisation to  
196 dopamine release within this ventral region. In contrast, D1 receptor density and D2  
197 receptor affinity was reduced within the caudate nucleus, indicating reduced output  
198 of this dorsal striatal structure in crib biting horses (McBride and Hemmings, 2005).  
199 This study could not demonstrate whether these changes were present prior to the  
200 emergence of crib-biting behaviour, or were as a result of crib-biting, but activity the  
201 midbrain-striatum pathway is relevant for crib-biting horses. Changes within this  
202 anatomical and neurochemical system may affect other aspects of the horse's  
203 behavioural repertoire. The caudate nucleus is crucial to the process of action-  
204 outcome monitoring. In rodent models of caudate inactivation, animals exhibit habit  
205 formation (i.e., preferentially utilize a habitual response) far quicker than control  
206 rodents (Yin et al., 2005). Similar acceleration in habit formation may be observed  
207 in horses performing stereotypy. A cross maze test was examined striatal circuitry  
208 within a sample of crib-biting versus control animals (Parker et al., 2009). Parker  
209 and his co-workers observed that crib-biting animals demonstrated an accelerated  
210 preference for a 'response' rather than a 'place' strategy, and as such were  
211 preferentially utilising a habitual response rather than action-outcome monitoring.  
212 This finding suggests that there is decreased output of the caudate nucleus,  
213 resulting in an increased reliance on the sensorimotor putamen circuitry, resulting  
214 in accelerated habit formation (Parker et al., 2008; 2009). Receptor based  
215 alterations recorded by McBride and Hemmings (2005) may be probed using  
216 carefully designed cognitive testing. Given the financial, logistical and ethical  
217 dimensions of direct physiological measurements, cognitive tests have the potential  
218 to significantly extend knowledge of stereotypy and associated neuro-mechanics.  
219 Roberts et al. (2015) a proposed two basic inferred measures of dopamine  
220 transmission consisting of spontaneous eye blink rate (SBR) and behavioural  
221 initiation rate (BIR). Both were measured in triplicate over 30 minutes, SBR values  
222 were obtained via counting of full blinks in the left eye at rest, where BIR records



223 the number of behavioural initiations i.e. the number of new behaviours performed,  
224 also at rest.

225

226 Crib-biting horses demonstrated significantly decreased SBR, consistent with  
227 studies that suggest lowered blink rate is indicative of dopamine receptor  
228 sensitisation (Roebel and MacLean, 2007; Roberts et al., 2015). This result also  
229 agrees with the receptor work conducted in the horse (McBride and Hemmings,  
230 2005). The significantly increased BIR appears to indicate adaptations within the  
231 dopamine circuitry of crib-biting animals, due to dominance of the movement  
232 activating direct pathway over the movement inhibiting indirect pathway (Roberts  
233 et al., 2015). Both the SBR and the BIR data appear to reflect the significant  
234 adaptations of dopaminergic physiology previously recorded in crib-biting animals.  
235 Further longitudinal study should reveal the scope of SBR and BIR and may  
236 identify individuals predisposed to stereotypy development. If predictive potential  
237 is revealed, given the pivotal role of chronic stress in stereotypy development, the  
238 elimination of key stressors such as feed restriction and social isolation could  
239 effectively reduce the risk that neural adaptations to receptor populations develop.  
240 Insult to the gastric mucosa may also be associated with significant nociceptive  
241 signalling to the CNS. Pain leads to liberation of neuropeptides such as beta  
242 endorphin, which bind to mu receptor populations in the ventral tegmental area  
243 (VTA), and contribute significantly to neuroplasticity in striatal brain regions (see  
244 McBride and Hemmings 2009 for review). Therefore, a mechanism is proposed by  
245 which a variety of environmental stressors lead to the neural changes that  
246 underlie the emergence of stereotypy.

247

### 248 2.3 Equine Locomotor Stereotypy: Potential Aetiologies

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

254

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

263

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

284

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

294

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

309

### 310 3.0 Motivational Basis of Stereotypic Behaviour

311 An understanding of motivational state during the development and ongoing  
312 performance of stereotypy is important. Hughes and Duncan (1988) proposed a  
313 generalised model (see Figure 1) to explain the motivational basis of a broad  
314 range of behaviours whereby in response to organism variables (i.e., declining  
315 blood glucose) the animal becomes motivated to perform a consummatory goal  
316 (i.e., feeding) and thus appetitive strategies ensue. As an example, a horse may

317 have access to two fields, though preferentially graze in one field. When this field  
318 has been grazed, the horse may experience reduced blood glucose levels. At this  
319 point the consummatory goal is to graze. The appetitive behaviour is to get  
320 additional food by moving from the first field to the adjoining field. The appetitive  
321 phase has a positive feedback effect on motivation, and is therefore self-  
322 reinforcing i.e., appetitive behaviours increase the motivation to continue to  
323 perform appetitive behaviours until the consummatory goal has been met, in this  
324 case ingesting grass from the neighbouring field. The achievement of the  
325 consummatory goal has a number of effects: 1) functional consequence (e.g.,  
326 elevated blood glucose), which leads to negative feedback on organism variables  
327 with a subsequent effect on motivation; 2) direct feedback on motivation, initially  
328 positive followed by negative; 3) an effect on perception of the animals  
329 environment which again influences the underlying motivation of the behaviour.

### 330 **FIGURE 1 ABOUT HERE**

331

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

343

344 This model can now be updated to incorporate findings from recent studies  
345 investigating locomotor versus oral stereotypy. Weaving seems to fit the Hughes  
346 and Duncan model very well. Weaving animals are not pre-disposed to  
347 accelerated habit formation, but do experience increased appetitive drive, perhaps  
348 due to neural alterations that centre on ventral striatal circuitry (Roberts et al.,

349 2015). Weaving ensues whenever the consummatory goal (e.g., grazing, social  
350 interaction) cannot be reached, though ceases when motivational end points (e.g.,  
351 turnout, social interaction) are provided. Indeed, anecdotal observations appear to  
352 support this notion, as weaving animals seldom perform stereotypy when turned  
353 out to pasture.

354

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

361

362

363

364

## **FIGURE 2 ABOUT HERE**

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

375

376

377 3.0 Conclusions

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

392

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

399

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

408

409 **Conflict of interest statement:** There are no conflicts of interest relevant to this  
410 manuscript

411

412 **Ethical Approval:** Not required

413 This invited review was written with an equal contribution of all stated authors.

414

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