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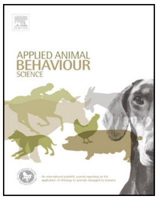

Cognitive differences in horses performing locomotor versus oral stereotypic behaviour

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ABSTRACT

Preliminary investigations reveal altered learning patterns in horses performing oral stereotypic behaviour which coincide with differential functioning of the basal ganglia group of brain structures. However, no studies to date have investigated similar differences in the equine locomotor stereotypy phenotype. The aim of this investigation was to employ behavioural probes shown previously to reveal basal ganglia dysfunction to initialise the neurologic studies of locomotor stereotypy and to compare cognitive and neural aspects of the locomotor and oral stereotypy phenotype.

Spontaneous blink rate (SBR—number of full left eye-ball occlusions by the eye-lid in 30 min) and behavioural initiation rate (BIR- Behavioural transitions in 30 min) were conducted utilising a sample of crib-biting ($n = 8$), weaving ($n = 8$) and stereotypy free ($n = 8$) animals. Horses were observed within their home box for SBR and BIR, with this being repeated three times over three consecutive days. All horses then completed an extinction learning paradigm featuring sensory specific satiety to dissect appetitive and habitual response patterns. Animals were initially shaped to press an A4 sized conditioned stimulus (CS) card mounted on an operant device for a food reward (5 g pelleted feed). The extinction schedule was then split into two separate tasks. Task 1 required animals to conduct 20 operant responses (OR) followed by sensory devaluation (1 kg freely available feed), whilst Task 2 required 40 OR prior to the devaluation phase. Following reward devaluation horses were subjected to an extinction phase where responses to the CS card were not rewarded.

Crib-biting horses demonstrated significantly lower SBR than control ($p < 0.05$) and weaving ($p < 0.01$) animals, though BIR was significantly increased for crib-biters ($p < 0.01$) and weavers ($p < 0.05$) compared to control equivalents. Both crib-biting and weaving groups acquired the initial operant response significantly faster than controls ($p < 0.001$) and thus displayed accelerated learning. Moreover, crib-biting horses performed significantly more operant responses during extinction phases 1 and 2 compared to weaving ($p < 0.001$ and $p < 0.01$, respectively) and control animals ($p < 0.001$ and $p < 0.001$, respectively). Finally, crib-biting horses required significantly more trials to reach total extinction criterion compared to control ($p < 0.001$) and weaving ($p < 0.01$) equivalents.

These findings agree with previous studies in that crib-biting horses displayed a bias towards habitual response patterns, even in the context of minimal training. This tendency corroborates previous post-mortem evidence of up-regulated ventral and down-regulated dorsomedial activity in the striatum group of brain structures. On the other hand, weaving animals were resistant to over-training and failed to display habitual responding, at any stage of the investigation. This, when taken alongside increased BIR and faster rate of learning is suggestive of enhanced ventral striatal activity but a normal functioning dorsal striatum.

1. Introduction

Stereotypic behaviours are repetitive, invariant (Pell and McGreevy, 1999; Mcbride and Hemmings, 2005) and idiosyncratic (Parker et al., 2009) induced by frustration, repeated attempts to cope or central nervous system (CNS) dysfunction (Mcbride and Hemmings, 2009), and are often utilised as an indicator of poor welfare status (Mills et al., 2002; Cooper and Albentosa, 2005; Wickens and Heleski, 2010). Crib-biting (CB) is an oral stereotypy whereby the animal grasps a solid object in the incisor teeth, and emits a grunting sound (Nicol et al., 2002; Moeller et al., 2008) with an estimated 2.4–8.3% of the equine population exhibiting the behaviour

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(Wickens and Heleski, 2010). Weaving on the other hand is a locomotor stereotypy characterised by lateral movement of the head accompanied by contralateral shifting of weight on the forelimbs, with approximately 3–10% of horses performing this behaviour in the equine population (Cooper et al., 2000; Mcbride and Hemmings, 2009).

Multiple causal factors have been suggested with regards to crib-biting although this is generally a post-prandial response (McBride and Hemmings, 2004), sometimes linked to pain induced by ulceration of the gastric mucosa (Nicol et al., 2002; Hemmings et al., 2007; Moeller et al., 2008). In contrast, weaving is thought to stem from frustration associated with deprivation of social and locomotor activities (Pell and McGreevy, 1999; McAfee et al., 2002) as well as an anticipatory response to feed (Cooper et al., 2005).

When investigating aetiology of stereotypy from a neural perspective, research efforts to date have centred on a trio of anatomically connected but functionally distinct forebrain nuclei known collectively as the striatum (Carlson, 2001). The dorsal striatum is comprised of the caudatus and putamen, two structures implicated in associative learning, and habitual response patterns that result from over-training (see Canales, 2005 for review). As they continue ventrally, the caudatus and putamen give way to the nucleus accumbens (NA) (Nolte, 2001), the function of which is generally associated with motivation and reward processes associated with the early stages of learning a new task (see Graybiel, 2008 for review). Furthermore, the striatum receives direct innervation from midbrain neurons which project dopamine onto dense populations of D1 and D2 receptors expressed across all three striatal sub-regions (Haber et al., 2000). Previous work centring on the striatum of crib-biting horses revealed up-regulation of D1 and D2 dopamine receptors in the ventral striatum and accompanying down-regulation of D1 receptor populations in the dorsally positioned caudate nucleus (Mcbride and Hemmings, 2005). This is similar to that found in chronically stressed rodents, thus highlighting the potential effect of stress on striatal functioning, particularly of the ventral striatum (Cabib et al., 1998; Cabib, 2006; Dias-Ferreira et al., 2009). Therefore, it seems plausible that stress is linked to the receptor based changes recorded in the crib-biting horse (Mcbride and Hemmings, 2009). To date no similar neural investigations have been performed on horses prone to weaving.

Alongside stereotypy, these neural changes manifest in other aspects of the animals behavioural phenotype, for example during learning. Indeed, accelerated habit learning is observed in CB horses (Hemmings et al., 2007; Parker et al., 2009). The alterations outlined above create an accelerated shift of ventral to dorsal activity in the striatum region of the brain, causing a bias towards habitual responding (Dias-Ferreira et al., 2009). Despite these findings, the weaving horse thus far has been overlooked in terms of striatal functioning, with no studies to date investigating the neural mechanisms of locomotor stereotypy. Whilst repetition of Mcbride and Hemmings (2005) work utilising weaving horses would provide details on receptor populations in weaving animals, radio-ligand binding methods are both invasive and expensive. However, behavioural probes, which investigate underlying cognitive processes using simple behavioural tests, provide a proven, non-invasive means of determining striatal functioning in a variety of species including rodents (Garner and Mason, 2002; Kaminer et al., 2011), birds (Garner et al., 2003), humans (Chen et al., 1996; Roebel and MacLean, 2007), non-human primate subjects (Karson, 1983; Taylor et al., 1999) as well as limited data within the horse (Hemmings et al., 2007; Parker et al., 2009).

For example, spontaneous blink rate (SBR), an indication of dopamine physiology in the striatum (Karson, 1983; Taylor et al., 1999; Kaminer et al., 2011), has been utilised to determine striatal functioning in stereotypy performing humans, with reduced SBR being attributed to increased postsynaptic receptor sensitivity (Roebel and MacLean, 2007). Furthermore, patients with dopamine depletion due to Parkinson's disease demonstrate reduced SBR, though this is attributed to lower dopamine availability as opposed to postsynaptic receptor sensitivity (Karson, 1983). In contrast, patients with schizophrenia exhibit significantly increased SBR as a result of elevated dopamine availability associated with this condition (Karson, 1983; Mackert et al., 1991). Additionally, dopamine agonists (i.e. elevated dopamine) and antagonists (i.e. reduced dopamine) reliably increases or decreases SBR, respectively (Karson, 1983; Chen et al., 1996; Kaminer et al., 2011). Considering the findings of Mcbride and Hemmings (2005), it is of value to conduct SBR assessment in a sample of stereotypy performing horses (oral and locomotor) to further investigate altered striatal functioning as a factor in stereotypic motor output.

Furthermore, Garner and Mason (2002) observed significantly increased behavioural initiation (BIR) (i.e. the number of behavioural transitions performed in a given period) in bank voles performing bar-mouthing, suggesting disinhibition of the striatonigral pathway of the dorsal striatum in these animals. This allows dominance of the striatopalladial pathway resulting in a significant increase in the number of behavioural 'switches' conducted (Garner and Mason, 2002; Garner, 2006). Considering the alterations in dopamine physiology observed in the CB horse (Mcbride and Hemmings, 2005) and the fact that dopamine agonists increase the rate of behavioural initiation (Garner and Mason, 2002; Garner, 2006), measurement of this phenomenon will be utilised to further elucidate the neural pathways recruited within stereotypy performing animals.

Finally, extinction learning tasks have been utilised previously to investigate the neural basis of equine stereotypy (Hemmings et al., 2007). However, traditional extinction paradigms such as that employed by Hemmings et al. (2007) have been criticised as they fail to dissect perseverance related to goal directed (i.e. directed at feeding) versus true habitual responding (see Yin and Knowlton, 2006 for review). As such, this study utilised a two phase devaluation–extinction paradigm featuring sensory specific satiety, which effectively removes feeding motivation therefore allowing accurate discrimination between appetitive and habitual responding (Dias-Ferreira et al., 2009) to further investigate behavioural differences in a sample population of crib-biting, weaving and stereotypy free control horses.

Following on from our previous post-mortem work that revealed significant alterations to basal ganglia physiology in the crib-biting horse (Mcbride and Hemmings, 2005) we hypothesised that both stereotypy performing cohorts would demonstrate a bias towards perseverative responding under extinction conditions, combined with SBR and BIR recordings that reflect altered functioning of the dopamine system.

2. Methods

2.1. Sample population characteristics and management

Eight control, eight crib-biting and eight weaving horses of various breeds, age and sex (Table 1) were recruited for the study. In order to recruit suitable numbers of stereotypy performing horses, animals from eight diverse establishments were utilised. These ranged from smaller yards of 10 animals up to larger establishments of 50, although work requirements of all three groups were similar (all were used for so called Sport Horse disciplines such as Polo). All animals were fed to meet individual dietary requirements for maintenance according to the National Research Council (2007). Furthermore, all observations and the extinction paradigm were conducted within the horses home box (3.65 m × 3.65 m) with access to forage and water. Each had eye-contact with fellow