Stereotypies, why and how

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Abstract

This paper summarizes recent findings on the 'how' and 'why' of stereotypic behaviours. The focus will be on the 'how' question and will in particular discuss the caustions of stereotypies and the underlying mechanism in which stereotypic behaviours develop. First I will outline stereotypic behaviours from a welfare perspective and address in brief the evolutionary aspect and possible functions of stereotypies (the 'why' question). This section will be more outlined in the discussion part. Then two paradigms in sciences will be discussed about the 'how' of stereotypic behaviours. The first will be from a physiological perspective, that supports the idea that a physiological discomfort is the trigger to perform a stereotypy. The second paradigm is from a neurophysiological point of view and shows that the development of a stereotypy is caused by changes in the mesoaccumbens dopamine pathway within the brain, which forms the base for the development of a stereotypic behaviour. This paradigm will be demonstrated with a neurological model of stereotypic development and shows chronic stress and a predisposition in the genotype as being extremely important to the underlying causes. With the extend that stereotypies can have advantages and disadvantages as well, it is questionable whether we should treat stereotypies or not. This will be more outlined in the discussion part.

Keywords: Stereotypic behaviour, mechanism, dopamine, striatum, animal welfare

Contents

1. Introduction

Scientists in different fields have been attracted to the study of stereotypical behaviour, in humans as well as in animals. Stereotypies are considered a pathology or at least a result of a reduced well being, where animals went through a period of serious physical or mental discomfort [Mason 1991; Zor et al. 2009] and stereotypies are therefore commonly seen as indicators of the major welfare problems. Stereotypic behaviors are currently defined as behaviour patterns that are repetitive, invariant and have no obvious goal or function [Mason 1991] and can be individual specific. Stereotypies are most often seen in captive animals and they seem to be absent in the wild [Mason 1991]. Stereotypies are very diverse. Form and timing depend on the species and the eliciting conditions and may differ between individuals. They also differ in repetitiveness and (in)flexibility[Mason 1991]. In this paper I address the 'why' (1) and 'how' (2) of stereotypical behavior, but the focus will be on the mechanism underlying stereotypic behaviour ('how'). The 'why' is about (a) the evolution of stereotypies and (b) the function of stereotypical behaviour. With respect to evolution, the focus will be on the behavioural needs of individual animals that have been shaped by evolution under natural conditions. The original definitions of stereotypic behaviour contain the term 'no obvious goal or function', but it has become increasingly clear that stereotypies may develop as a strategy to cope with direct physical discomfort and may later on become a behavioural/physiological goal or need of their own [Mason & Latham 2004]. The 'how' questions adress the underlying mechanism of stereotypic behaviour; (c) the development of stereotypical behaviour and (d) the causations of stereotypical behavior and includes the underlying physiological and neurological mechanism of (stereotypic) behavior. In the last sections I will discuss the paradigms in science about the causations and development of stereotypies and the implication for welfare. The main focus of this paper will be on the development of stereotypies and the changes in the underlying neurological pathways where an up regulation in the midbrain dopaminergic pathway plays a central role.

2. Context

Most stereotypies involve one of the following 3 domains (1) locomotor behaviour (walking in circles in large carnivores, weaving in elephants and horses, rocking back and forward in primates), (2) feeding behaviour stereotypies (cribbiting, airsucking, floor licking in horses and tethered sows, pecking in poultry), and (3) self maintenance stereotypies (excessive grooming in cats and parrots). It is quite obvious that stereotypies are mainly found under captive conditions in both domesticated, semi-domesticated, tammed and wild animals. The captive conditions must therefore be causal to the development of stereotypies. Captive conditions are usually defined by 1) limited space 2) either an

excess, too few, and/or similar social contacts 3) extremely rich and efficient in energy and nutrients and 4) rather barren with respect to a host of environmental factors. Although these conditions have clear 'benefits for animals' but it was found that animals in a captive environment have higher cortisol levels and therefore are in a chronic state of stress [Mason et al. 2001; Clubb & Mason 2003; Liu et al. 2006]. This state of stress is induced by the animals physical and mental state to reach certain goals. Not reaching these goals result in a host of stereotypies such as: vertical weaving or head tossing in horses [McBride & Hemmings 2009], elephants and bears [Mason et al. 2007], crib-biting in horses [McBride & Hemmings 2009; Parker et al. 2009] and pacing in carnivores [Burgener et al. 2008]. Weaving in horses is a commonly observed whole body or locomotor stereotypy, which involves a weight shift from one side to the other. Weaving is usually accompanied by a lateral swaying movement of the head, though it can also involve the forequarters and sometimes hindquarters. This typically occurs whilst the horse is standing with the head over the stable door. This can lead to disadvantages to the horse. It may, for example, cause the untimely wearing of shoes and the legs to swell leading to lameness and may result in loss of condition of the horse [Cooper & Mason 1998].

In other species and stereotypic phenotypes comparable physiological disadvantages can appear. Even 'ideal' captive conditions seem to have high disadvantages to animals [Morgan & Tromborg 2007] and stereotypies are likely to evolve. Under such conditions animals may reproduce and survive relatively well and it seems reasonable that developing stereotypies under certain conditions may help animals cope with those conditions and have therefore a certain function. One of the main functions may be that the stereotypy itself becomes a rewarding behaviour. The reward would be the release of endorphins, such as dopamine, which makes the animal feel better and therefore improves its welfare (do-it-yourself enrichment) [Mason & Latham 2004] , first because the behaviour is associated with solving a problem, later this behaviour emancipates from its original stimulus but still releases endorphins. Nevertheless, another study in laboratory-bred bank voles ,*Clethrionomys glareolus*, found that survival and reproductive success are increased when stereotypies were performed [Schonecker 2009].

Because less is known about whether stereotypies are advantageous or disadvantageous to the animal, it is important to take a closer look at stereotypies in a mechanistic point of view in relation to the function of stereotypic behaviour. It was also been found, for example in Asian elephants, *Elephas maximus*, that their survivorship in captivity was reduced significant [Clubb et al. 2008].

3. Methods

For this paper the literature was reviewed using the electronic database of ISI Web Of Science. Because I aimed for recent developments, the search was limited to articles published after 1990. The keywords that were used were: stereotypical behavior/behaviour, stereotyp*, repetitive behavior or

behaviour, dopamine, brain, OCD (obsessive-compulsive disorder), captivity, psychoactive drugs. Moreover, the search initially centered around scientists well known in this field of research, such as Mason GJ or Wiepkema PR, who both studied stereotypical behaviour in captive animals and animals in the wild. The option 'Times cited' in ISI Web Of Science was used to search 'forward' in time. Some references of Masons review were also been seen, but most of it was not recent (not published after 1990).

Using this search method yielded only few studies about the underlying neural mechanisms of stereotypical behaviour. Therefore search terms were extended with 'brain' and 'rituals', because of the relative likeness of rituals and habits with stereotypies. Then a review [Graybiel 2008]was found about the way habits develop in the brain and in this review the author discusses a link between the development of habits and stereotypies. This review was very useful. Then further searching included the words 'striatum' and 'stereotypy', because the review linked brain areas such as the striatum to the development of stereotypical behaviour. Another review [McBride & Hemmings 2009]was found about the mechanism in a more neurological perspective. These last two reviews form the basis of this paper.

4. Results

4.1 'How'; stereotypies, the underlying mechanism

There are two paradigms for the mechanisms in which stereotypies develop. The first paradigm implies a physiological point of view, whereas the other is from a neurophysiological perspective.

4.1.1Physiological paradigm

The mechanism in the first paradigm is best illustrated with an example. This well known example of a stereotypy that seems to stem from a physiological need is crib-biting or 'cribbing', an oral stereotypic behaviour in horses, where a horse is gripping on a fixed object with its incisor teeth, leaning back and contracting the muscles of the neck to bring into an arched position. Depending on the individual horse, air may be drawn into the esophagus; this is known as wind sucking. Researchers that sustain this paradigm suggest that horses undergo a stereotypic behaviour, because of a discomfort that the horse experiences. It is now widely recognized that many intensively farmed (food restricted) horses suffer from gastric ulcerations and crib biting horses have higher plasma cortisol levels than normal horses. The discomfort caused by ulcerations in this setting is caused by the animal's diet. When being stabled, horses are mostly fed hay in combination with a concentrated supplement of grain to replace lost access to pasture [Johnson et al. 1998]. In physiological terms, this change in diet compared to the 'normal' diet of the horse changes oral stimulation, the pattern of ingestion and the function of the digestive

system. Due to this change, researchers suggest that the horse will perform stereotypic behaviour displays. They suggest that concentrated food stuff will have an effect on the saliva production in the way that saliva production will decrease, because the horse spends less time chewing. As a result the pH in the stomach of the horse will decrease and this is a reliable discomfort to the horse. The hypothesis is that cribbing acts as a substitute for this chewing in an attempt to increase the total saliva production (crib-biting horses also have increased wateruptake) and therefore buffer against an elevated gastrointestinal acidity [McGreevy 2004; Mills & Donnel 2005]. This is also known as the 'saliva' hypothesis. A study with horses that were given virginiamycin, a nontherapeutic antibiotic that suppresses lactic acid production in the hind gut of horses (Rowe et al in [Johnson et al. 1998], support this hypothesis. The results of this study show that virginiamycin significantly reduced the decline in faecal pH compared to when concentrates alone were given [Johnson et al. 1998]. They also showed that a decrease in faecal pH below about 6,2-6,3 was associated with a rapid rise in the occurrence of behavioural abnormalities. Due to these results they concluded that their work suggests when horses are fed high concentrated food, the control of hindgut acidosis with virginiamycin can reduce the incidence of abnormal behaviours like stereotypies. In this study it is remarkable that the displays of abnormal behaviours all had some component of oral stimulation. How the reduction in gut acidity could have effect on the appearance of stereotypic behaviours is still unclear. But due to this experiment, it could simply be that with the performance of a stereotypic behaviour, the animal has less visceral discomfort, because more saliva is produced that buffers the acidity in the hindgut [Johnson et al. 1998].

Besides the 'saliva' hypothesis, some researchers follow the 'sweetness' hypothesis which argues that the sweetness of feed concentrates triggers endorphin release in the brain, which has cribbing as a result [Mills & Donnel 2005]. The underlying mechanism of endorphin release will be discussed in the neurophysiological paradigm. The sweetness can be seen as a causational factor and will be discussed in the part about causations of stereotypic behaviour.

4.1.2 Stereotypies as extreme habits

The second paradigm approaches stereotypies from a neurological point of view. In this setting it is important to realize that there is much evidence for a comparable developmental pattern between habits and stereotypies [Graybiel 2008]. In this line a stereotypical behaviour is seen as an extreme habit, which has its development in the same pathway. Stereotypies are common seen as strongly repetitive behaviours who emancipated of the original goal [Mason 1991]. However, evidence in research suggests that in both habit learning and the development of stereotypies, a particular goal plays an important role in the development of a repetitive behaviour [Graybiel 2008]. In the initial stages of habit learning, behaviours are not automatic, but they are goal-directed (for example, press a bottom to obtain food reward) [Graybiel 2008; de Wit et al. 2009].

This goal-directed behaviour is defined as response-outcome (R-O) behaviour [Parker et al. 2009]. However, with extensive training the animals become in a state to perform the behaviour repeatedly, even when the value of a reward is reduced or even when it is no longer rewarding [McBride & Hemmings 2009]. This behaviour, where the outcome is independent from a direct stimulus, is defined as stimulus-outcome (S-R) behaviour [Graybiel 2008]. Thus, when looking at habit learning as repetitive, sequential, context triggered behaviours, habits can be defined as being preformed not in relation to a current goal, but rather in relation to a previous goal and the advanced behaviour that most successfully led to obtain that goal [Graybiel 2008]. Stereotypies seem to reflect an extreme state of functioning and conditioning of certain brain circuits, in which flexibility is minimal and repetitiveness is maximal. The same can be seen in addictions [Franken et al. 2005; Graybiel 2008]. In this setting stereotypy and habit development match in the way that the repetitive behaviour becomes uncoupled of a previous goal. One of the main points in this setting is that when a stereotypy develops, there is an enhanced switch from response-outcome (R-O) to stimulus-response (S-R) learning, whereas animals with no stereotypy did not switch from R-O to S-R, but remained in the R-O state. This was found in a study with horses where crib-biting horses were compared with control horses [Parker et al. 2009].

4.1.3 Neurophysiological perspective

Looking closer at the switch from R-O to S-R learning, there is seen an increase in striatum related brain region activity. The striatum is required for repetitive S-R behaviour [Packard & Knowlton 2002]. The striatum, a sub cortical part of the forebrain, is part of the basal ganglia and seems to have a main role in the development of stereotypical behaviour.

Neural circuits interconnect the neocortex with the striatum and related regions of the basal ganglia. Different basal ganglia-based circuits appear to operate to different types of cognitive and motor habits. However, evidence suggests that many of these basal ganglia-based sub circuits participate during the accession of habits. One of the properties of habits is that they are performed almost automatically and thus unconsciously. Moreover, habits tend to involve an ordered, structured sequence of action. These repetitive behaviours (motor or cognitive) are mostly built by the action of basal ganglia-based neural circuits [Graybiel 2008]. As habits are acquired and habitual behaviours crystallize, neural activity patterns change dynamically into specific chunked patterns [Graybiel 2008]. In addition, during early stages of habit learning it seems that the ventral striatum (nucleus accumbens) is necessary for the acquisition of behaviour, whereas the dorsolateral striatum (caudate nucleus and putamen) is active during later stages of habitual learning [Graybiel 2008; McBride & Hemmings 2009]. Reversible inactivating studies have pointed this out [Atallah et al. and Hernandez et al. in [Graybiel 2008]. In stereotypies there is a strong suggestion that there also is an early-learning ventral striatum system and a late-

learning dorsal striatum system [Graybiel 2008]. The key concept in these ganglia-based circuits, which can be seen as the active component, is dopamine. In several species, dopamine has been the primary candidate neurotransmitter underlying the development and maintenance of stereotypic behaviour[[McBride & Hemmings 2009]. From the work of several studies (zie Mc Bride linker stuk blz12) it seems that with regard at least to crib-biting in horses, stereotypies seem to be a result of increased neural transmission of the striatal region of the basal ganglia [Robbins et al and Presti et al in [McBride & Hemmings 2009]. This "sensitization" is strongly associated with significantly increased dopamine D1 and D2 receptors in the ventral striatum as well as significantly decreased density of D1 receptor subtypes in the caudate striatum [Parker et al. 2009]. These findings are very interesting given the functional role of the mesoaccumbens. The mesoaccumbens dopamine pathway is the primary neural center for initiation and control of goal-directed behaviour [Ref, Altered mesoaccumbens and nigro-striatal dopamine physiology is associated with stereotypy development in a non-rodent species [Ikemoto & Panksepp 1999; McBride & Hemmings 2005; McBride & Hemmings 2009]. Therefore, it has been suggested that an unregulated mesoaccumbens dopaminergic system could place an animal in an enhanced motivated state in relation to any given goal-oriented situation [Ikemoto & Panksepp 1999; McBride & Hemmings 2009]. But, when the environment is restricted in that goal, the animal could be maintained, within a highly motivated state with regard to goal accomplishment. The animal becomes within the so called "appetitive phase" of goal attainment and it has been suggested that it is this maintenance within this phase that is the basis for stereotypy development [McBride & Hemmings 2009]. Neurophysiologically, at this point there take place a shift in neural activity from the ventral to dorsal striatum [McBride & Hemmings 2009] and there is a shift from matrix to striosomes activity within the striatum [Graybiel 2008]. These striosomes occur mainly in the dorsal striatum and they are thought to provide a major source of input to the dopamine-containing neurons of the substantia nigra, which respond to conditioned stimuli predictive of future reward [Graybiel 1998].Therefore, it can be said that with the arising of striosomes, the system becomes self-stimulating since the substantia nigra is said to be the initiator of the release of dopamine [Graybiel 2008] and therefore, the animal becomes more and more motivated to a goal that is restricted in its environment. This is in line with the do-it-yourself enrichment theory [Mason & Latham 2004].

Several studies that administered a dopamine receptor blocker (naloxone) which was given to animals with stereotypic behaviours, caused an immediate stop in stereotypy performance [Pollock & Kornetsky 1991; McBride & Cuddeford 2001]. Some researchers suggest a hypothesis that is opposed to the current thinking about stereotypies. They suggest that when an animal received naloxone, the animal would not have the effects of endorphins anymore and therefore it should be reasonable that the animal should show an immediate increase of the behavior because the craving for dopamine is not reduced. In this way the animal wants to compensate for the lack

of endorphins. However, it can also be seen that a stereotypic animal that is given naloxone is not sensitive for dopamine anymore, and therefore is not motivated to a given (indirect) goal. In other words, the animal is removed from the "appetitive phase" right at the moment that naloxone was given. As a result, the animal will not show stereotypic behaviour after given naloxone. This could be a reliable explanation for the working of nalaxone on stereotypic behaviour. However, the 'addiction' hypothesis (where the performance of the stereotypy becomes a goal itself) contradicts this. Therefore, further research should point out the exact working of naloxone.

As described earlier, when a stereotypy develops it becomes uncoupled of a previous goal. In the past, stereotypies are often said to have no obvious goal. Nevertheless, a feature of stereotypical behaviour is that there is a strong motivation within the animal to reach a particular goal, but the environment is restricted to that goal [McBride & Hemmings 2009]. As in habits, there is a previous goal that induces the pathway to become a habit or ritualistic behaviour. However, unlike in the development of habits, there is no reward for that goal. In other words, there cannot be provided in that goal and the animal cannot perform a behaviour that is most successfully to achieve that goal. Therefore, it is reasonable that the animal performs a behaviour that comes from a behaviour system related to that goal, but since there cannot be provided in that goal, the behaviour is not successfully. The' unsuccessfully' behaviour that the animal performs is actually the stereotypic behaviour itself. For this reason it is incorrect that stereotypic behaviour is common defined as a behaviour that has no obvious goal or function, because stereotypic behaviour is indirectly related to a goal. The whole neurophysiological mechanism, as described, is shown in **Figure 1**.

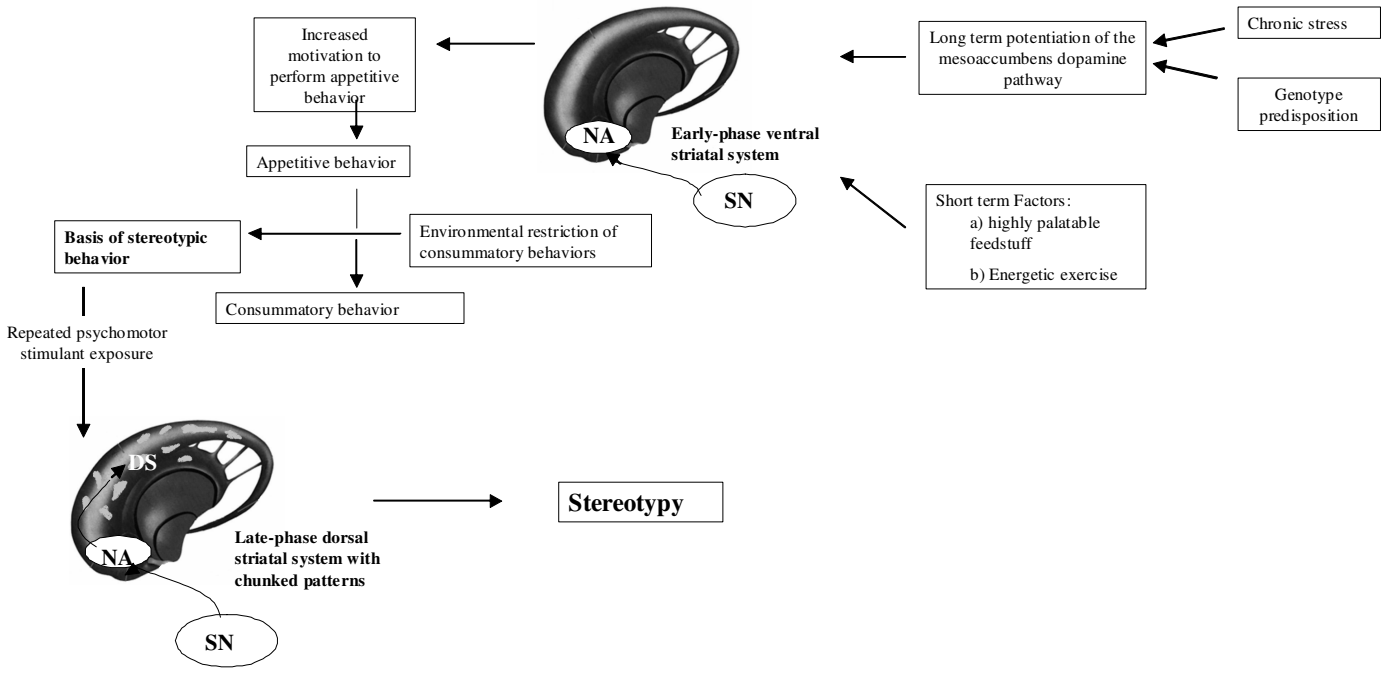

Figure 1. Mechanism of stereotypic development with considered causal factors. SN, Substantia nigra; NA, nucleus accumbens; DS, dorsal striatum.

4.2 Causations

4.2.1 Physiological

The main causation in the physiological paradigm for the performance of stereotypic behaviour is the fall in pH in the hind gut, when the animal is given concentrated foodstuff (see **Fig. 1**). This physiological discomfort of acidity triggers the animal to perform stereotypic behaviour.

4.2.2 Brain related

Underlying the neurophysiological perspective, there are two main causations of stereotypy development that induce the potentiation of mesoaccumbens dopamine pathway activity. The first causative factor is a commonly discussed issue in terms of frustration, boredom, or stress. Due to research from McBride et al, chronic stress seem to be the most likely cause for equine stereotypy development, but may also be obvious for other species. These studies support the suggestion that avoiding early life experience involving stress will prevent the neurophysiologic changes required for stereotypic development [McBride & Hemmings 2009]. This stereotypic development is directly related to the animal's species-specific behavioural needs, restricted feeding, restricted locomotion and social isolation. However, not all individuals that are housed in captive sub-optimal environments develop a stereotypy [Mason et al. 2007]. This indicates that factors other than the environment can play a crucial role in the development of stereotypies.

Another factor that researchers think that greatly influence the development of stereotypic behaviour is a predisposition in the genotype. For example, offspring of stereotypic striped mice, *Rhabdomy*, are more likely to be stereotypic than offspring from non-stereotypic parents [Jones et al. 2008]. However, the data showed that there was a greater maternal than paternal contribution to stereotypy prevalence in offspring, which indicates that genetics alone cannot explain the observed transmission pattern. In this context, chronic stress situations early in the animal's development may be critical to stereotypic predisposition. Thus, chronic stress has great influence on the susceptibility of the central nervous system that may be genotype dependant.

Nevertheless, besides these long-term effects on the mesoaccumbens dopamine pathway, there are also short-term factors that might influence the striatal 'sensitization'. Psychostimulants in humans (eg. cocaine, heroin) also cause 'sensitization' of the basal ganglia dopamine based circuits to produce high goal or reward phenotypes [Cardinal & Everitt 2004]. In this way, animals are being exposed to similar substrates and are placed in a neurophysiological state similar to that induced by human psychostimulant administration.

Examples of these substrates might be highly palatable feedstuff (that the animal have not evolved to ingest) or energetic exercise (causing excessive amounts of endogenous opioid release) [McBride & Hemmings 2009]. The 'sweetness' hypothesis, as described earlier, supports this in the way that the sweetness of the feed concentrates triggers endorphin release [Mills & Donnel 2005]. By doing so, animals become in a hyper motivated state and show reward-seeking behaviour. Further research has to point out the impact and importance of these factors.

5. Discussion

5.1 Conclusion

When taken in conclusion the underlying mechanism in which stereotypies develop, there are seen two paradigms in science that have acceptable explanations. One paradigm assumes that a physiological discomfort in the hind gut triggers the animal to perform a stereotypy to counteract for this discomfort. The other paradigm shows that a 'sensitization' in the basal ganglia dopamine pathway triggers the animal to be high motivated to a particular goal, but when that goal is restricted in the environment, the animal will become in the 'appetitive' phase for goal-attainment and this forms the base for a stereotypical behaviour. Causations for the neurophysiologically paradigm can be either for long-term potentiation of the mesoassumbens dopamine pathway (induced by chronic stress or a predisposition in the genotype) or can be short term factors (like highly palatable feedstuff or energetic exercise). When a switch takes place from ventral-striatal to dorsal-striatal activity and striosomes are formed within the matrix of the dorsal striatum, the behaviour becomes a stereotypy.

5.2 Possible explanations for both paradigms

When taken in account both paradigms, it could be reasonable that both mechanisms are involved in the development of a stereotypical behaviour. For example, when an animal is fed high concentrated feed stuff, it could be that the fall in pH motivates the animal to perform a particular behaviour. In other words, the fall in pH can be a possible causation for dopamine release in the substantia nigra and therefore triggers the basal ganglia pathway in which a stereotypy develops. When the animal is not allowed to attain in its motivated goal (the animal wants to chew to make saliva), the animal is triggered to perform a behaviour that is related to goal-attainment and therefore the stereotypical behaviour that will be performed comes from a related behaviour patter.

As described in the text, virginiamycin in combination with highly concentrated food supplements lowers the reduction of pH in the hindgut of horses [Johnson et al. 1998]. However, the study also showed that horses that were given virginiamycin take longer time to consume their ration. Johnson et

al (1998) suggest that this longer feeding time could have led to greater saliva production which could influence the neutralization of gut acidity. Anyway, it could also be that the horses eat slower because it is less tasteful and therefore they have a longer feeding time. As a result the brain of these horses could be less activated with dopamine and therefore the horses are less motivated and thus the behavioural outcome of a stereotypy will be low. Nevertheless, horses that were given concentrated feed that is highly tasteful showed significantly more stereotypic behaviour. This is in a line with the neurophysiological mechanism (**see Fig.1**).

5.3 Stereotypies; why

5.3.1 A product of evolution?

Habits occur all over the place and they seem to have evolutionary advantages. However, extreme habits such as stereotypies are very common in captivity, but seem to be absent in the [Mason 1991]. Therefore stereotypies are mostly seen as abnormal and the argument is that they cannot be the product of natural selection, nor of selective breeding for captivity, because they are not unique to domesticated species [Mason 1991]. However, the way in which stereotypies develop is in common with the development of natural habits [Graybiel 2008] and may therefore be adaptive. This means that, although stereotypies may be pathological, they cannot be seen as a self-contained behaviour and solely. Nevertheless, in the development of a stereotypical behaviour pattern, it seems that an animal is high motivated for a particular goal, but an animal in a captive environment cannot provide in that goal. This is the base of the development of stereotypical behaviour. In this context it can be seen that an animal is not evolved not to be provided in this particular goal. Another important factor is that one of the main causations of stereotypies is the presence of a predisposition in the genotype [McBride & Hemmings 2009]. Therefore, the chance whether or not a stereotypy will develop depends on the presence of a predisposition in the genotype of an individual and so stereotypical behaviour can be seen as inheriting. Nevertheless, habit formation can yield advantages to the animal and some genotypes will develop stereotypies as a result of this habit formation. However, the animal is evolved in an environment where needs and goals are available and so the animal can attain in its needs and goals. Therefore, the animal can be seen as a product of evolution in a particular environment and this environment is unequal to current husbandry. And it should also been said that in the past there has never been a selection against natural behaviours in domesticated species. Thus, research in science about natural behaviours of animals is crucial for the knowing of how to keep animals in captive environments.

5.3.2 Functional?

When animals perform perform normal habits, the behaviour is coupled to goal-attainment [Graybiel 2008]. However, when habits are learned, the behaviour being performed can also be in relation to a previous goal that most successfully led to achieving that goal. In this context the behaviour being performed is functional, because the animal will be rewarded by achieving that given goal. However, when an animal is in a captive environment, where attaining a primary goal is impossible, the animal still is motivated to perform a behaviour to goal attainment. The behaviour being performed is not related to a goal and therefore the behaviour can be seen as non-functional. For this reason, stereotypic behaviour is common defined as having no obvious goal or function [Mason 1991]. But when taken in account boredom, frustration or stress as possible causational factors, the animal counteracts these factors by performing stereotypic behaviour. Therefore, stereotypic behaviour can be seen as functional.

5.4 Treatment necessary?

A common thought about the development of stereotypies is that there can be seen three stadia: early, middle and late. Where the transition from early to middle is common seen as reversible, whereas the transition from middle to late is seen as irreversible. In the latest state the behaviour is fully crystallized and becomes inflexible. However, as described earlier, an animal that performs stereotypic behaviour is given naloxone immediately stops the performing of the stereotypy, even when the animal is in the latest state [Pollock & Kornetsky 1991; McBride & Cuddeford 2001]. This indicates that the latest state of stereotypic behaviour is actual reversible when using pharmacological treatment. The question is if it is in the advantage of the animal to stop the stereotypical behaviour, since the animal encounters advantages from the performing of the behaviour [Schonecker 2009], for example by producing endorphins (do-it-yourself-enrichment) [Mason & Latham 2004]. It can only be advantageous for the animal when the environment is also enriched so that the animal is not motivated to a particular goal, while the environment is restricted. In this setting, when the animal will have a motivation to a particular goal, the environment is allowed to provide in this goal and the animal can proceed to perform consummatory behaviour. However, it is very difficult to perform this pharmacological and environment enrichment in a right way, because little is known about the strategy of stereotypic displays. For this reason, it seems obvious to have further research about this strategy. The research has to point out in what circumstances the stereotypic behaviour is more advantageous. Moreover, the genotypic predisposition must be taken in account to. Since this predisposition in the genotype exists, it must occur in the wild and therefore it might me obvious that the stereotypic phenotype performance can be advantageous under some circumstances. However, it is known that animals that form routines have strong advantages in the wild, under a given

circumstance. Stereotypies can be seen as a same type of behaviour, because it develops in the same pattern as a routine habit (as described in this paper). A possible study can therefore be as follows: Select two groups of animals from a wild condition, one group of routine-making animals and one control-group. Put these animals in a captive environment and test which group of animals have the most advantages in terms of surviving, offspring, cortical levels and so on. Another study can be more from a predisposition starting-point. In this study captive animals that are selected on their predisposition for stereotypic behaviour should be selected in a way that two groups arise; a high stereotypic group and a low stereotypic group. These selected animals can be placed in a semi-wild or enriched environment. The aim of this study should be on routine training, for example by feeding both selected groups at a given time, also known as a 'meal' circumstance and also by feeding unpredictable. A possible hypothesis could be that animals that have a predisposition for a stereotypic behaviour will have advantages when it comes to routine forming. When this would be found, it indicates that stereotypical behaviours are in line with evolution and can have advantages in some circumstances and environments.

When taken in conclusion, the aim of the control of stereotypic behaviour should not be exclusion of the behaviour itself, but rather the exclusion of the welfare problem. It must be considered that these two are not the same.

5.5 Final conclusion

Although our knowledge about the underlying mechanisms about stereotypic behaviours has been increased in the last years, it must be keeping in mind that stereotypies are mostly multifactorial, arising from environmental and genetic risk factors in a give individual at a given time [Mills & Donnel 2005]. Further research should give more insight in the mechanisms in which stereotypies develop and therefore gives more knowledge about how to keep animals.

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