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Research report

Environmentally enriched rearing environments reduce repetitive perseveration in caged mink, but increase spontaneous alternation

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HIGHLIGHTS

- ► Enrichment during rearing decreased stereotypy and perseveration in mink.
- ► Environmental enrichment increased spontaneous alternation behaviour in mink.
- ► Mink with more spontaneous alternation also gained more rewards in our two-choice guessing task.
- ► Unexpectedly, stereotypy and perseveration did not co-vary in these young adult mink.

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ABSTRACT

Studies spanning 15 species (including American mink, *Neovison vison*) demonstrate that within similarly-housed populations, individuals displaying high levels of stereotypic behaviour (SB) typically show perseverative responding (e.g. during set-shifting, or reversal/extinction learning). Similar correlations in autism and schizophrenia suggest this indicates captivity-induced cortico-striatal circuit dysfunction. However, this pattern does not prove developmental impairment: SB, perseveration and their inter-correlations also occur in normal humans. We therefore differentially-reared enriched versus non-enriched mink to investigate whether treatments that exacerbate SB correspondingly increase perseveration (Study 1). Enriched-rearing did reduce SB and perseverative response repetition (in two-choice guessing tasks), while increasing spontaneous alternation: a strategy yielding more rewards, and suggesting enhanced hippocampal development. This complements previous research demonstrating cortical/hippocampal impairments and reduced behavioural flexibility in non-enriched animals, with implications for research animals and wild animals captive-raised for reintroduction into nature. Consistent with previous data, highly stereotypic subjects repeated guessing task responses most rapidly, suggesting disinhibition during repetition. However, unexpectedly, SB and perseveration did not co-vary across individuals. We therefore suggest that behavioural changes manifest as increased perseveration are important but do not fully explain captive animals' SBs, possible reasons including the contributory role of differential motivations for underlying source behaviours. Re-analyses of old data (Study 2) confirmed that spontaneous alternation is profitable; and demonstrated that the precise methods used for quantifying perseveration and SB can modify the strength of apparent relationships between them, as can statistically controlling for feeding motivation: as predicted, partialling out motivational effects increased the variance in SB predicted by perseveration.

1. Introduction

Stereotypies, traditionally defined as repetitive, highly unvarying behaviours without apparent goal or function [1], are widespread in captive animals, being performed by over 85 million worldwide [2] and statistically the norm in some populations (e.g. single-housed laboratory primates; zoo-housed giraffes [3]). These behaviours are part of a broader spectrum of abnormal, repetitive activities including self-biting and fur- or feather-plucking [4,5]. Here we use "stereotypic behaviour" (SB) to cover this range of activities, defined broadly as "repetitive behaviour induced by frustration, repeated attempts to cope, and/or CNS dysfunction" [5]. Although diverse in aetiology, captive animals' SBs generally typify unnatural husbandry: abnormal rearing environments (e.g. early weaning [6]), or sub-optimal current environments (e.g. barren, non-enriched cages [7,8]). Ethologists traditionally propose that these SBs represent sustained attempts to perform specific normal activity patterns, triggered by correspondingly specific

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motivational states that are frustrated by captivity. Evidence for this includes that feather-plucking by hens (*Gallus gallus*) involves pecks morphologically identical to normal foraging pecks [9] and is often followed by feather-eating [10] which seems to aid gut function [11]; and that bar-chewing by mice (*Mus musculus*) in laboratory cages is focused at locations sometimes permitting escape [12], and elevated in previously-enriched mice: subjects displaying higher breakpoints to leave non-enriched cages and gain enrichments [13]. Recently, however, this ethological perspective on SBs has been supplemented by explanations derived from neuroscience and human clinical psychology, focusing on forebrain pathology.

Human SBs, ranging from predictable repeats of individual actions to recurring expressions of restricted interests, are common in schizophrenia [14], autism and other pervasive developmental disorders [15–17]; Alzheimer's and other dementias [18]; people who have over-used stimulants such as amphetamine [19]; and children raised in severely deprived environments [20,21]. These SBs reflect underlying forebrain changes affecting multiple aspects of behaviour, both subtle and conspicuous, generally involving compromised abilities to inhibit inappropriate responses. These SBs are therefore often accompanied by, and even co-vary with, other forms of reduced behavioural flexibility including perseveration: the inappropriate repetition of responses or activities, or "continuation or recurrence of an activity without the appropriate stimulus" [22,23]. Perseveration, tested for via laboratory assessments involving card sorting, object naming or word list generation [22], is prominent in schizophrenia, dementia, autism, and children raised in extreme privation [4,23,24]. Furthermore, when stereotypic schizophrenics or autistics participate in simple guessing or sequence-generation games, individuals with the most repetitive motor actions and/or most circumscribed interests [14,25], also most frequently repeat answers or response sequences in a perseverative way. Corticostriatal systems are often implicated here [e.g. 26], with much evidence for this coming from pharmacologically- or genetically-modified animal models. In rats, for instance, repetitive movements induced by apomorphine, amphetamine or cocaine correlate with over-activation of corticostriatal striosome-based circuits relative to matrix-based circuits [27]; in DAT knock-out mice, repetitive locomotion is accompanied by increased dopaminergic activity, especially in the dorsal striatum and nucleus accumbens [28,29]; while in deer mice, striatal infusion of dopamine receptor antagonists selectively decreases repetitive jumping, but not other activity [30], and dysfunction of the basal ganglia's 'indirect', inhibitory pathways is implicated by reduced striatal leu-enkephalin [31] and attenuation of stereotypy by adenosine receptor agonists [32].

Correspondingly, growing evidence suggests that captive animals' SBs have similar neurobiological bases [4,26,33]. Aside from several impressive papers on non-enriched-raised deer mice [16,30–32], most evidence is behavioural, based on tests for perseveration akin to those applied to human subjects, or assessments of behavioural flexibility during reversal/extinction learning. These studies, currently spanning 16 species, typically utilise individual differences across similarly-housed and -raised subjects, either contrasting stereotypic with non-stereotypic individuals or comparing subjects that spontaneously vary in SB levels. The vast majority find positive relationships between SB and behavioural inflexibility or perseveration. Populations in which positive correlations occur include captive-bred bank voles (*Clethrionomys glareolus*) [36]; wild-caught and captive-bred striped mice (*Rhabdomys*) [37]; captive-bred laboratory mice (*M. musculus*) [38]; captive-bred adult American mink (*Neovison vison*) performing pacing and other locomotor SBs [45]; wild-caught caged blue tits (*Parus caeruleus*) and marsh tits (*P. palustris*) [34]; and captive-bred orange-winged Amazon parrots (*Amazona amazonica*) [35]. Other studies similarly exploit individual differences between similarly housed subjects, but use animals with uncertain, varying past life histories that could have shaped their current phenotypes; these reveal positive relationships between SBs and perseveration in horses (*Equus caballus*) [39,40], captive-bred rhesus macaques (*Macaca mulatta*) [41,43], lion-tailed macaques (*Macaca silenus*), squirrel monkeys (*Siamiri sceurius*), and capuchin monkeys (*Cebus apella*) [42]; and caged Asiatic black bears (*Ursus thibetanus*) and Malayan sun bears (*Helarctos malayanus*) [44]. Finally, in hens [10], genetically high and low feather-peckers may correspondingly differ in extinction learning. Exceptions not displaying such patterns are as follows: repetitive scrabbling with the forelimbs in caged mature adult mink [45]; and bar-mouthing and similar behaviours in both ICR-CD1 laboratory mice [13,47] and deer mice (*Peromyscus maniculatus*) [46], although, as we review below, these rodent behaviours are affected by differential rearing.

This substantial body of data does not, however, conclusively demonstrate captivity-induced dysfunction. First, not all repetitive behaviours indicate impairment: while the specific forms and frequencies of captive animals' SBs rarely occur in the wild [33; although see 48,49], repetitive or ritualistic behaviours do occur naturally [reviewed in 50; also see 5,49]. Likewise, SBs can occur in normal humans: in normal children, for instance, ritualistic and repetitive behaviours are part of daily life [51–53]. Second, perseveration also occurs to varying degrees in normal adults and children [54,55]. Third, this perseveration may statistically co-vary with SB in non-clinical subjects, reflecting normal, stable aspects of individual variation: thus positive correlations occur between SBs and tests of response inhibition and/or set shifting in normal children and adults [55–58]. Without controlled, well-documented differences in ontogeny, we thus cannot determine whether captive animals' responses represent differential pathology caused by detrimental housing, or instead similar normal individual variation. To assess any causal role played by captivity, we need experimental comparisons of animals from different, known developmental backgrounds.

Only a few studies have both manipulated animals' rearing or adult housing environments, and assessed SB and perseveration. Decades ago, severely deprivation-reared rhesus monkeys were found to be both perseverative [59] and more stereotypic than mother-reared controls [e.g. 60]. Similarly, capuchins captive-bred as pets seem both more stereotypic and poorer at extinction learning than mother-raised animals (although they lived at different facilities, making location a confound: [61,62]). However, in neither of these studies were perseveration and SB statistically compared. African striped mice maturing to adulthood in the wild were less perseverative in a 4-arm maze, and less stereotypic, than captive-raised conspecifics [37] (as mentioned above, perseveration and SBs also significantly co-varied at the individual level). In deer mice, enriched rearing environments were similarly found to reduce both SB and reversal deficits compared with mice reared in standard non-enriched cages [46], despite the two traits *not* co-varying within each group. Likewise, in laboratory ICR CD-1 mice, one study found that enriched rearing environments reduced perseveration and SB, but again independently: the two aspects of behaviour did not co-vary [47]; while another study found no effects of enriched versus non-enriched past rearing conditions in adults currently housed in standard cages [13]. Finally, Dallaire et al. [45] differentially-raised juvenile mink until early adulthood in either enriched or non-enriched housing: enriched rearing significantly reduced locomotor SB, but had no effect on perseveration in two-choice guessing tasks. In addition, these authors provided mature, non-enriched-raised adult females with enrichments. Enrichments again reduced SB but not perseveration; they also weakened the covariance between perseveration and SB evident in the animals' original, non-enriched housing.