



Research report

Frustration and perseveration in stereotypic captive animals: Is a taste of enrichment worse than none at all?

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ABSTRACT

Stereotypic behaviours are common in animals in impoverished housing, arising from two complementary processes: (1) thwarted attempts to perform motivated behaviours; (2) forebrain dysfunction impeding normal behavioural inhibition. When enriched animals are moved to impoverished housing, they are sometimes protected against developing stereotypic behaviour, but in other cases become even more stereotypic than animals housed lifelong without enrichment. Negative contrast-induced frustration must occur in both scenarios. We hypothesise that sustained behavioural responses to this frustration are prevented in the former by normalised forebrain function, but exacerbated in the latter by forebrain dysfunction. ICRC-1 mice reared in enriched or standard cages were re-caged at 3 months to standard conditions. Here, previously-enriched mice became far more stereotypic than mice reared from birth in such conditions. To investigate the role of frustration, we assessed both corticosterone output and motivation (break-point) to regain enrichments. We also assessed perseveration via extinction learning. As predicted, previously-enriched mice were as perseverative as standard-raised mice, and frustration seemed to play a causal role in their exacerbated stereotypic behaviour. Previously-enriched mice showed higher motivations to access enrichments, and only in this group did these correlate with corticosterone levels after re-caging; furthermore only in previously-enriched mice did corticosterone responses to re-caging predict stereotypic behaviour 30 days later (males only). All results need replicating and further investigation. However, they suggest for the first time that individual risk factors related to the HPA axis predict stereotypic behaviour following enrichment-removal, and that previously-enriched mice have lasting motivational differences from standard-raised mice, suggesting sustained behavioural effects related to the frustration of enrichment-loss.

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1. Introduction

Highly repetitive 'stereotypic behaviours' are prevalent in laboratory, farm and zoo animals: over 85 million individuals worldwide perform activities like pacing and body-rocking, and in some captive populations (e.g. zoo-housed giraffes, stall-housed pregnant sows, and single-housed laboratory primates [25]) they are nearly ubiquitous. Ethologists and neuroscientists have proposed two complementary explanations for stereotypic behaviours. Ethologists, who focus on the evolution and proximate causation of normal species-typical behaviour, explain them in terms of sustained attempts to perform highly-motivated normal behaviour patterns that are frustrated by captivity (e.g. [44]). Empirical support for this view includes the following: stereotypic digging in caged gerbils (*Meriones unguiculatus*) is triggered specifically by the lack of naturalistic burrow-like structures [64]; the motor patterns

involved in feather-plucking by hens (*Gallus gallus*) are morphologically identical to foraging pecks [9], and bar-chewing by laboratory mice (*Mus musculus*) develops from repeated escape-attempts [31]. Researchers from neuroscience and related disciplines [58,62] instead explain stereotypic behaviours in terms of Central Nervous System (CNS) pathologies similar to those underlying stereotypic behaviour in humans with schizophrenia or autism (e.g. [10,59]), subjects dosed with psychostimulants (see [42]), and severely maternally-deprived primates (reviewed [21]). Here, forebrain changes that compromise abilities to inhibit inappropriate responses induce stereotypic behaviour, along with perseveration – 'the continuation or recurrence of an... activity without the appropriate stimulus' [45] – and reduced behavioural flexibility. Evidence for similar CNS impairments in caged animals includes correlations between individual levels of stereotypic behaviour and: perseveration/reduced behavioural flexibility under test (e.g. [11,61]); altered dopaminergic receptor density/binding affinities in ventral and dorsal striatum (e.g. [29,53]); reduced striatal enkephalin, a marker for indirect pathway activity [39], and reduced cytochrome oxidase activity in the substantia nigra [51].

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Consistent with both ethological and neuroscientific accounts, captive animals' stereotypic behaviours are less prevalent and severe if individuals are raised and housed with 'enrichments', i.e. structures and stimuli that promote natural behaviour [22,27,56,57], and that are now well-documented with regard to enhancing CNS functioning/delaying the onset of neurological disorders [33]. Enriched individuals may also have reduced corticosteroid output, suggesting less stress and frustration [15], and anatomical and physiological changes in cortico-basal ganglia pathways that suggest more normal CNS functioning, e.g. increased dendritic spine densities (reviewed [22]). As one would expect, animals raised in unenriched conditions but then provided with enrichment tend to show reductions in stereotypic behaviour—as demonstrated experimentally, for instance in research rodents [4,51], as well as via meta-analyses of environmental enrichments' effects on zoo animals [47,49,50]. The beneficial effects of added enrichments vary in magnitude: different enrichments vary in efficacy [47,49,50] and individuals vary in their responses, e.g. elderly animals' stereotypic behaviours are often resistant to enrichment [4,14,54]. However, the *direction* of effects is largely consistent: stereotypic behaviours are almost always attenuated by the addition of enrichments, and sometimes even abolished altogether.

The converse treatment – removing enrichments from animals raised with them – has, however, far more unpredictable effects. As might be expected from the accounts above, providing enrichments but then removing them often exacerbates or even induces stereotypic behaviour; for instance removing the mother often triggers stereotypic attempts to escape or suckle in young mammals (reviewed [21]), while removing or delaying expected food rewards exacerbates pacing, weaving and sham-chewing in captive pigs and carnivores [16,23]. Less expected is that in some of these cases, the stereotypic behaviours of animals from whom complex natural stimuli are removed become even more prevalent and severe than those of subjects that have lived without enrichment all their lives. Thus, caged birds brought in from the wild typically show more route-tracing than captive-bred conspecifics [19]; removing temporary enrichments from laboratory primates elevates stereotypic behaviours over the levels performed before they were provided (e.g. [2]), and removing straw from pigs used to interacting with it increases abnormal tail-biting above levels in pigs never provided with this enrichment [8]. Furthermore, to complicate the picture further, in yet other cases environmental enrichment can appear to *protect* animals against later developing stereotypic behaviour, even after its removal. Thus in many mammalian species, individuals caught from the wild and caged as adults are less stereotypic than captive-born conspecifics (reviewed [24]); while bank voles (*Clethrionomys glareolus*) and deer mice (*Peromyscus maniculatus*) reared in large, enriched cages remain less stereotypic when transferred to standard cages than conspecifics housed in such conditions all their lives [14,34,38]. Thus removing enrichments has inconsistent effects, variously increasing or decreasing stereotypic behaviour relative to animals exposed to life-long barren housing.

This paradox likely reflects the relative contributions of frustrated motivation and of abnormal behavioural control caused by forebrain dysfunction. Enrichment-removal is particularly frustrating: animals with experience of valuable resources are less motivationally satisfied by poor resources than are animals without such high expectations: so-called 'negative contrast' effects or 'Crespi' effects (e.g. [6,37,65]). In negative contrast paradigms frustrative non-reward (e.g. [23,36]) typically elevates corticosteroid output and induces behavioural activation, particularly attempts to escape and/or to perform the thwarted highly-motivated behaviour [19]. However, such effects are typically transient, these behaviours extinguishing [18,36], sometimes being replaced with inactivity [3].

We therefore hypothesise that when enriched rearing protects animals against stereotypic behaviour, enrichment-removal does not lead to sustained behavioural responses indicative of frustration, despite the downshift in environmental conditions, because enriched rearing has normalised forebrain function, thereby enhancing behavioural flexibility and normalizing behavioural inhibition (see e.g. [20,30,41]). We term this the 'Protection Hypothesis'. Conversely, we hypothesise that when enrichment-removal increases stereotypic behaviour (over that of subjects raised without enrichment) the enhanced frustration induced by the downshift in environmental conditions has sustained behavioural effects due to underlying deficits in forebrain function: deficits that render abnormally perseverative the resultant attempts to escape and/or perform thwarted activities. We term this the 'Frustration Hypothesis', to highlight the role frustration now plays in the exacerbation of stereotypic behaviour. Here, our aim was to test these ideas, by assessing both perseveration and frustration in mice raised with enrichments but then moved to non-enriched cages.

2. Methods

2.1. Overall aims and rationale

If the hypotheses above are correct we would expect one of the two following outcomes. Firstly, if early enrichment decreases the stereotypic behaviour our enriched-reared subjects display after transfer to non-enriched conditions compared to mice raised in such conditions then we should find that (a) frustration measured post-transfer, as inferred from corticosteroid responses [26,68] and motivations to re-acquire the enrichments (cf. e.g. [5,23,48]), does not predict their performance of stereotypic behaviour, and (b) our enriched-reared subjects display more normal behavioural inhibition, as inferred from perseveration under test (e.g. [52]) – a proxy measure of basal ganglia dysfunction [11,61] – than non-enriched-raised mice ('Protection Hypothesis'). In contrast, if early enrichment increases the stereotypic behaviour our subjects display after transfer to non-enriched conditions compared to mice raised in such conditions, we should find that (a) frustration post-transfer does predict their performance of stereotypic behaviour, while (b) behavioural inhibition should be no more normal in our enriched-reared subjects than in non-enriched-raised mice ('Frustration Hypothesis'). As the first assessment of perseveration, frustration and stereotypic behaviour concomitantly in the same subjects, in addition to testing these hypotheses, our experiment also allowed us opportunistically to investigate whether frustration helps cause perseveration, and whether frustration and perseveration combine or summate to determine overall levels of stereotypic behaviour (see 'statistical analyses').

2.2. Differential rearing and behavioural/physiological data collection during this time

12 pregnant ICR CD-1 females at 14–16 days gestation were housed in opaque MB1 cages (45 cm × 28 cm × 13 cm, North Kent Plastics). This strain was chosen because used in previous studies of stereotypic behaviour [31,66,67], and one of the highest selling outbred mouse strains (source: Harlan UK Ltd.). All cages contained *ad lib.* food (RM3 pelleted food, Lillico, UK), a water bottle, wood-shaving bedding (PetsatHome) and nesting material (rough teabag nesting material, Lillico, UK). Cages with no further additions comprised the standard (STA) conditions. Half the cages additionally contained nest boxes (PetsatHome), plastic tunnels (B&Q) and a 'novel' object chosen from a variety of commercial rodent enrichments (PetsatHome) and changed weekly: cage furnishings chosen based on the proven preference of mice for, and welfare benefits associated with, nesting material and increased environmental complexity [35]. These comprised the enriched (ENR) cages, in which six dams and their litters were housed—see Fig. 1. Lights on/off occurred at 1 am/1 pm. Room lights were shaded so that light levels were ~10 Lux at floor level during light hours. An automated dimmer provided a 1 h dusk period prior to lights-off, and at night the room was lit by a 25 W red bulb. Temperature and humidity were maintained at 20 °C (±2 °C) and 50–70%, respectively, and animals were checked daily. Cages were not cleaned until 2 weeks after the birth of litters to minimise disturbance. After this, bedding and nesting materials were changed weekly, and cages cleaned out and washed every 4 weeks.

Weaned pups (male $N=24$; female $N=24$) were then individually-housed in cages matching their natal conditions, and kept there into young adulthood (89 days). Individual housing was opted for here to (a) try and minimise 'litter effects' while also using all pups produced (to avoid wasting surplus animals), (b) eliminate social hierarchy effects [31] that may have adversely influenced our ability (to detect each individual's underlying predisposition to frustration and perseverative tendencies), and (c) allow the in-cage assessment of motivation and perseveration (see below).

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