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Can't stop, won't stop: is stereotypy a reliable animal welfare indicator?

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Abstract

We estimate that stereotypies are currently displayed by over 85 million farm, laboratory and zoo animals worldwide. This paper investigates their reliability as welfare indicators, by surveying studies relating stereotypy to other welfare measures and by analysing the mechanisms underlying this behaviour. Where data exist, most (approximately 68%) situations that cause/increase stereotypies also decrease welfare. Stereotypy-eliciting situations are thus likely to be poor for welfare, although exceptions exist. Within such an environment, however, most (approximately 60%) accounts link individual stereotypy performance with improved welfare (cf approximately 20% linking it with reduced welfare). Thus, in a sub-optimal environment, non-stereotyping or low-stereotyping individuals could well have the poorest welfare, although again exceptions exist. Examining the mechanisms underlying stereotypy performance, we discuss four processes that could account for these complex links between stereotypy and welfare. Beneficial consequences from performing the specific source-behaviour of the stereotypy ('do-it-yourself enrichment'), or arising from repetition per se *('mantra effects'), may ameliorate welfare in poor environments. In addition, stereotypies that have become centrally controlled (habit-like), or that arise from autistic-like changes in the control of all behaviour (perseveration), are likely to be unreliable indicators of current state because they can be elicited by, or persist in, circumstances that improve welfare. To refine the role of stereotypy in welfare assessment, we suggest the collection of specific additional data to reveal when any of these four processes is acting. Until such research increases our understanding, stereotypies should always be taken seriously as a warning sign of potential suffering, but never used as the sole index of welfare; non-stereotyping or low-stereotyping individuals should not be overlooked or assumed to be faring well; simple measures of frequency should not be used to compare stereotypies that differ in age, form, or the biological or experiential characteristics of the performing animal; enrichments that do not immediately reduce stereotypies should not be assumed failures with respect to welfare; and finally, stereotypies should not be reduced by means other than tackling their underlying motivations.*

Keywords: *animal welfare, central control, coping, crib-biting, perseveration, stereotypies*

Introduction

Stereotypies are repetitive, unvarying and apparently functionless behaviour patterns (eg Ödberg 1978; Mason 1991a) commonly suggested to indicate welfare problems (eg Lawrence & Rushen 1993; Appleby 1999). They have been used to assess animal welfare in a number of ways. Some authors suggest that *any* level of stereotypy indicates poor welfare (eg Broom & Johnson 1993; EC 1996; Laidlow 2001), others that increasing levels of stereotypy indicate decreasing levels of welfare (eg Fox 1984; Dawkins 1990; Broom & Johnson 1993), and others still, that welfare is unacceptable if stereotypies occur in more than 5% of a population (Wiepkema *et al* 1983), or for more than 10% of an animal's time (Broom 1983; Broom 1991). However it is unclear which, if any, of these suggestions is correct. This issue is important because we estimate that stereotypies are currently performed by over 85 million animals worldwide (see Table 1), which potentially means that a vast number of animals experience poor welfare. But is the welfare of *all* of these stereotypers equally impaired? Is it definitely worse than that of their non-stereotyping conspecifics? And are all methods of reducing stereotypy equally beneficial for welfare? At the moment, the answers to these questions are uncertain, but despite this, several practical initiatives aim to reduce stereotypies. Reducing stereotypy is, for example, the most common aim of environmental enrichment programmes in zoos (eg Shepherdson *et al* 1999; Young 2003). Animals' environments may also be altered to make stereotypies unpleasant or difficult. For example, crib-biting and 'wind-sucking' in horses is often tackled by smearing crib edges and other horizontal surfaces with greasy or hot-tasting substances (Kohnke 2000; Country Supplies 2003); by using anti-stereotypy devices, such as neck straps (eg McBride & Cuddeford 2001; Country Supplies 2003); or even by surgery (eg Kohnke 2000; Brouckaert *et al* 2002; Delacalle *et al* 2002). Other approaches target the animal's phenotype. For example, anti-depressants have been used to treat a variety of 'behavioural problems' in domesticated and zoo animals (Melman 1995), and have successfully reduced pacing in a zoo-housed polar bear (Poulsen *et al* 1995). Opiate antagonists have also been used to reduce crib-biting and weaving in horses (Kohnke 2000; Nicol 2000). Stereotypy has also been genetically selected against, for example in hens and mink (Mills *et al* 1985a,b;

Table 1 Estimated number of stereotyping animals worldwide. Here, estimated global population sizes and published stereotypy prevalence data are used to estimate the total number of stereotyping captive animals. Note, however, that some populations in which stereotypies occur (eg laying hens, veal/dairy calves, laboratory and zoo primates, beef cattle, caged pets and zoo birds) are not considered here because of a lack of data, and that some of the population sizes given are not global (eg being only for Europe and the USA). The total number of stereotypers calculated — around 87 million — is thus an underestimate of the true global sum. Totals here represent those occurring over a period of approximately 6 months; annual figures would be larger because of those animals generally kept for less than 12 months (eg laboratory mice).

Species (System)	Estimated total population size	Estimated stereotypy prevalence (% individuals)	Estimated total number of stereotypers	Sources of data	Notes
Pigs (Confined sows)	16 822 500	91.5%	15 393 000	EC (1997) and papers on stereotypy cited within it	Population size given for Europe and North and Central America only
Poultry (Broiler breeders)	68 400 000	82.6%	56 498 000	EC (2000) and papers on stereotypy cited within it	Population size given for Europe and North America only
Mice (Research and laboratory breeding establishments)	15 000 000	50.0%	7 500 000	National Association for Biomedical Research statistics, from the Humane Society of the United States; EC 1999; Australian and New Zealand Council for the Care of Animals in Research and Testing (ANZCCART) unpublished data	Population size estimated from annual figures and based on an estimated mouse lifespan of 6 months. Stereotypy prevalence is a conservative guessed estimate; prevalence data are published only for ICR and ICR-nu mice, and are 98% (eg Würbel *et al* 1996), but this strain is known for high stereotypy
American mink (Breeding females on fur farms)	5 850 000	80.0%	4 680 000	European Fur Breeder's production figures for 1997–1998. Stereotypy prevalence is a mean for two farms (de Jonge *et al* 1986; Mason 1993)	Population size estimated from pelt output, based on assumed production rate of 5 kits per female. Prevalence estimate ideally needs data from more sites
Wild carnivores (Zoos)	325 000	82.0%	246 000	International Species Information System (ISIS) database (http://www.isis.org) and Spedding (2000) cited in Clubb (2001)	Stereotypy prevalence is the median of species medians, from papers on 22 species, and probably an over-estimate, since non-stereotyping individuals/species are less likely to attract behavioural study
Elephants (Zoos and circuses)	1700	47.0%	800	Clubb & Mason (2002)	African and Asian elephant data pooled. Stereotypy prevalence is estimated at 41% for 1100 individuals in zoos, and 65% for 530 individuals in circuses
Horses (Stables)	14 770 000	18.4%	2 724 000	Waters (2002) and the Food and Agriculture Organisation of the United Nations (http://www.fao.org)	Population size is that of the 'Developed world'

Vinke *et al* 2002); indeed in the Netherlands, it is now national policy for fur farmers to breed out this behaviour (eg EC 2001; Vinke *et al* 2002). Zoos may also indirectly act similarly, in that they often do not replace or breed from highly stereotypic individuals (Ironmonger 1992; Irven 1993; Dollinger *et al* 1996). But do such approaches automatically improve welfare? Our aim here is to help answer this question by examining the relationship between stereotypies and suffering, and by using the current understanding of the causes of stereotypy to interpret the confusing picture that emerges. We then suggest how the use of stereotypy in welfare assessment might be refined, and highlight the unknowns still needing research.

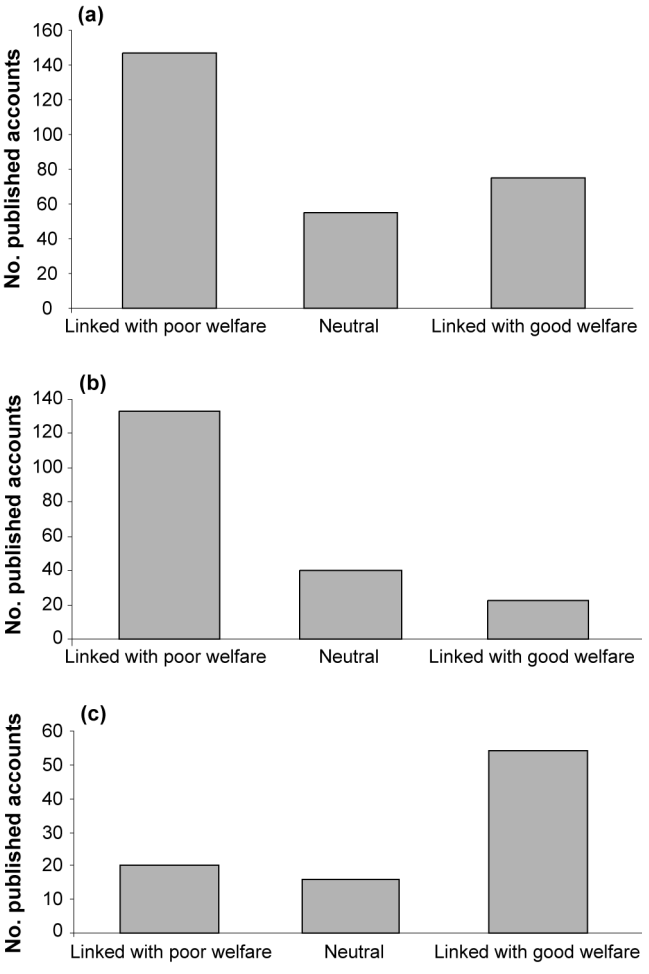
Stereotypies and welfare: what are the links?

The evidence linking stereotypies with poor welfare is diverse, and also well known. Extensively reviewed by many authors (eg Ödberg 1978; Mason 1991a,b; Lawrence & Rushen 1993; Garner & Mason 2002), it comprises the types of environment in which stereotypies often develop (eg restraint [Redbo 1992]); the cues that elicit them (eg hunger [Bildsoe *et al* 1991]); the source-behaviours from

which they tend to derive (eg escape attempts [Nevison *et al* 1999a,b]); and the correlates sometimes seen for the behaviour (eg raised corticosteroids [Wielebnowski *et al* 2002]). However, there is also ample evidence that stereotypies do *not* always indicate poor welfare. For example, normal human stereotypies, such as thumb-sucking and gum-chewing, are not generally associated with stress or restraint (eg Thelen 1981; Sroufe & Cooper 1988; Frith & Done 1990). Lourie (1949) even describes a girl who "rhythmically and audibly sucked her tongue only when happy". Some animal stereotypies similarly increase in response to changes that can be presumed positive for welfare. For example, increasing dietary bulk, and thence time spent eating, can increase sham-chewing in pigs (Broom & Potter 1984); stereotypy increases with increasing cage size in arctic foxes (Korhonen *et al* 2001); and providing mink with 'playballs' also increases their stereotypies (Jeppesen & Falkenberg 1990). Even when this does not occur, environmental enrichments may fail to reduce stereotypy, even when researchers believe that welfare has improved (eg Meyer-Holzapfel 1968; Ames 1994; Cooper *et al* 1996). Finally, stereotypies do not always positively correlate with other signs of poor welfare. For example, in farmed mink and several other animals, stereotypy is *negatively* correlated with corticosteroid levels (Redbo 1993; Vestergaard *et al* 1997; reviewed in EC 2001).

To clarify this puzzling picture, we totalled up accounts linking stereotypy either with good, bad or uncertain welfare. A comprehensive collection of several hundred publications on human and animal stereotypy (collated by GJ Mason since 1985) was analysed. Accounts of stereotypy, both from individual case studies and from research on groups of animals, were scored for their reported links with welfare. To be 'Linked with Poor Welfare', stereotypy had to be associated with likely signs of stress, fear or depression (eg alarm calling, raised corticosteroids) or performed in circumstances shown to be poor with other evidence (eg avoidance in preference tests). Where statistically analysed, this association had to be significant. Accounts were scored as 'Neutral' if stereotypy was shown in circumstances seemingly neutral with respect to welfare, or in conjunction with no apparent change in other recorded welfare measures. Stereotypies linked with putative positive welfare measures (eg lowered heart rate), or reported in any circumstance that independent evidence suggests to be good for welfare (eg preferred in choice tests), were scored as 'Linked with Good Welfare'. Again, where statistically analysed this association had to be significant. For simplicity, reported links with welfare were not weighted by their rates of occurrence within each publication (eg a paper describing an animal or population as stereotyping in several stressful circumstances and a single pleasurable one would yield one score in each of the categories 'Poor' and 'Good Welfare'), nor by the sample size involved in each publication (to avoid the problematic weighting of studies that use multiple non-independent replicates). Surveying these papers revealed 153 reports of links with poor welfare, but 133 reports of no such link (see Figure 1a). This is not significantly different from that expected by chance ($\chi^2 = 1.40$, $df = 1$, not significant). One reason for this lack of overall relationship emerged when the papers were sorted by the source of variance in stereotypy (ie by the nature of low-stereotyping or non-stereotyping controls). When studies that compared different environments or treatments (eg different feeding regimes or the addition/removal of environmental enrichments) were examined separately from those that focused on individual differences in stereotypy within a single treatment or population (see Figures 1b and 1c), most of the former studies linked stereotypies with poor welfare ($\chi^2 = 107.37$, $df = 2$, $P < 0.0001$), but most of the

Figure 1



The links between stereotypy and welfare: results of a literature survey (see text for survey details). Figure 1a shows the overall results in terms of the total number of papers in which stereotypy was linked with poor, neutral or good welfare. Reports were then categorised by the source of variation in stereotypy, ie whether or not high and low-/non-stereotyping subjects came from different treatment groups. Figure 1b summarises the results from accounts where variation in stereotypy stems from variation in treatment (eg enrichment studies; studies of different housing conditions or weaning ages). Figure 1c summarises the results from accounts that track changes within an individual as it switches between stereotypy and normal behaviour, or that compare differentially stereotyping individuals within a single population/housing condition.

latter studies found positive correlates of the behaviour (eg lowered corticosteroids or heart rate), thus linking stereotypies to relatively good welfare (χ^2 = 29.07, *df* = 2, $P < 0.0001$).

Thus environments that induce or increase stereotypy are indeed typically worse than those that do not, but within a stereotypy-inducing environment, the most stereotypic animals are likely to be the least welfare-compromised individuals. However, even this distinction is clearly not the whole story. Some treatments or housing conditions that cause good welfare also enhance stereotypy (see Figure 1b); while within a similarly treated group of animals, stereotyping animals do not always have better welfare (see Figure 1c). The relationship between stereotypies and welfare is thus still not straightforward. Type I or Type II statistical errors may play some role here, as well as interpretive issues raised by other 'welfare measures' (see eg Rushen 1991; Mason & Mendl 1993), but examining stereotypy in more detail is crucial too.

Why are stereotypies not a faithful signal of suffering?

For stereotypies to track suffering reliably (see eg Mason 1991b), the time an animal spent performing them would need to reliably signal the strength of the frustrated underlying motivation; and/or track general levels of stress; and/or indicate the boredom that could stem from the 'spare time' that many captive animals seem to fill with this activity. However, several factors could blur these potential relationships between stereotypy and suffering, and therefore account for the behaviour's complex relationship with welfare. We discuss the four most important here.

1) Stereotypies as 'do-it-yourself enrichments'

That artificial analogues can provide the feedback properties of a natural activity is not a new idea. It explains why we throw sticks for dogs, and pacify babies with dummies. It also underlies most forms of environmental enrichment, where objects such as 'boomer balls' and running wheels are used as outlets for behaviour patterns akin to natural activities (eg Shepherdson *et al* 1999; Young 2003). Perhaps it is not surprising, then, if captive animals devise their own ways of performing natural behaviours, albeit to unnatural substrates and in curtailed or unvarying forms.

So, can stereotypies substitute effectively for natural behaviour patterns? The largest body of evidence, although not the strongest because of its largely correlational nature, is the great number of papers linking stereotypy performance with apparent benefit (see eg Figure 1c). Recent evidence from cattle provides a particularly nice example. In very young, bucket-fed calves, post-feeding non-nutritive sucking is directed to objects such as artificial teats. This behaviour increases plasma insulin and cholecystokinin, which is thought to aid digestion (De Passille *et al* 1993). In older calves, grazing-like tongue-playing then commonly develops, and is associated with reduced gastric ulceration both in young and in adult cattle (Wiepkema *et al* 1987; Sato *et al* 1992; Canali *et al* 2001). A probable mechanism is that the stereotypy generates saliva, which when swallowed buffers the stomach from excess acid, a risk for concentrate-fed animals (Wiepkema *et al* 1987; Nicol 2000; Nicol *et al* 2002). The success of such tactics is further suggested by negative correlations between bovine oral stereotypies and adrenocorticotrophic hormone (ACTH) responsiveness (Redbo 1993; Redbo 1998; Van Reenen *et al* 2001), and a link between tongue-playing and lowered heart rate (eg Seo *et al* 1998). Thus, by performing these foraging-like movements, cattle may help to improve their own welfare by minimising the potentially adverse effects of artificial diets. Additional evidence consistent with reward comes from a few cases in which animals have apparently worked to perform stereotypies. For example, anecdotal reports portray animals competing for locations where stereotypies are displayed (reviewed in Mason 1991a), while empirical data show that wheel-running (a repetitive, apparently functionless activity, which in carnivores, at least, is predicted by the daily distance a species would travel in the wild [Clubb 2001]) is an effective reinforcer for several taxa (reviewed in Sherwin 1998).

However, not all stereotypies can be assumed to be satisfying ways of expressing natural behaviour, especially those that develop from unsuccessful attempts to reach a goal. For example, some develop from intention movements to approach conspecifics (eg Meyer-Holzapfel 1968; Ödberg 1978; Stevenson 1983), and it seems highly unlikely that they even remotely substitute for true access. Likewise, the stereotypic digging of captive gerbils in the corners of their cages (Wiedenmayer 1997) is not prevented by giving substrates that allow more naturalistic digging, but is prevented by the creation or provision of a tunnel; thus the ability to dig *per se* seems no substitute at all for the animals' desired endpoint, a suitable den. Even the oral stereotypies that seem beneficial in some species may not be effective in others. For example, horses' oral stereotypies are not linked with low ulceration, but rather the opposite (Nicol 2000; Nicol *et al* 2002). Furthermore, stereotyping horses tend to have higher baseline heart rates (Minero *et al* 1999) and higher cortisol levels (McGreevy & Nicol 1998; but see Pell & McGreevy 1999). Thus, in this species it would seem that when animals with acidosis use oral movements to try to self-buffer, they fail (Nicol 2000; Nicol *et al* 2002).

Implications of 'do-it-yourself enrichment' for stereotypy as a welfare indicator

If some stereotypies are 'do-it-yourself enrichments', then one source of variance in the welfare correlates of stereotypy will be the abilities of different stereotypies to effectively surrogate for natural behaviour. For stereotypies that do have beneficial feedback, it would also be clearly highly counter-productive to physically prevent them, or to use selective breeding programmes or drug regimes which might only tackle the expression of the behaviour without reducing underlying motivations. Furthermore, within a given housing system, it would make sense to be just as concerned, if not more, about the welfare of the least stereotypic animals.

2) The mantra effect: calm through repetition

It has long been known that rocking soothes human babies (eg Lourie 1949), and rhythmic behaviour also calms normal human adults. Chanting and mantras, for example, lower reported stress levels (Janowiak & Hackman 1994; Lee *et al* 1997; Wolf & Abell 2003) and induce alpha brain waves and altered cardiovascular responses (Lee *et al* 1997; Bernardi *et al* 2001). Repetition is also involved in the pleasure we get from music (eg Sakakibara 1996), while voluntary walking, running and similar forms of exercise all improve mood (eg Murphy *et al* 2002; Hicks *et al* 2003). If mere repetition can have beneficial effects, could this also account for the apparently positive properties of some animal stereotypies?

That stereotypies may serve as general 'coping mechanisms', increasing or decreasing arousal, has been considered by many authors (eg reviewed in Mason 1991a; see also Guess & Carr 1991). The best evidence comes from the verbal reports of human stereotypers. For example, Kathy Carlstead corresponded with a prisoner about his stereotypy, with fascinating results (K Carlstead 1999, personal communication). "Pacing translates the mind away from the present situation …", he wrote, " … a means of tranquillising and sedating". Autistics also sometimes report that their stereotypies ('stims') are pleasurable. For example Temple Grandin (Grandin & Scariano 1986) reports: "I enjoyed twirling myself around or spinning coins or lids round and round and round", while Bee (2002) describes some as "fun". They can even act as effective positive reinforcers, the opportunity to 'stim' sometimes being used as a reward for completing desired tasks (Gillberg 2003). There is no specific evidence of such effects for animals, aside from anecdotal accounts of stereotyping animals becoming 'glazed-looking' and less responsive to external stimuli (see eg Mason 1991a), but the apparent positive correlates and reinforcing properties of some stereotypies would be consistent with this hypothesis as well as that of the previous section.

Implications of 'mantra effects' for stereotypy as a welfare indicator

These properties could, just as in the previous section, help explain the variation in the correlates of stereotypy, with some being effective 'mantras', and others not. They again suggest that within any population of stereotypy-susceptible individuals, ignoring the welfare of non-stereotyping animals may be ill-advised; and they argue against preventing stereotypy performance without tackling its underlying causes. As one autistic website put it, "These behaviours are necessary" (Kalen 2000), and another, "if you do not allow [your child] to stim ... the need to stim will build up until it becomes unbearable" (Dana 2001).

3) When stereotypies become habits: the role of central control

Stereotypies may become dissociated from welfare (good or bad) as a result of changes that naturally occur in the neural control of repeated behavioural outputs. As this topic has been previously extensively reviewed (see eg Dantzer 1986; Mason 1991a; Lawrence & Terlouw 1993; Mason & Turner 1993; Toates 2000), we shall just summarise it here. With repetition, behaviour may shift into a form of automatic processing (Mason & Turner 1993; Toates 2001) known as 'central control' (Fentress 1976; Martiniuk 1976). This enables individuals to execute regularly performed or fast movements with minimal cognitive processing or need for sensory feedback (Fentress 1973; Fentress 1976) (speed touch-typers provide a good example). Such behavioural sequences may then also become more readily triggered by a range of cues (Toates 2001) (for example, one of us — GJ Mason — cannot type the word 'monkey' without starting it 'mink', because she has worked with the latter and so has typed this word thousands of times). Stereotypies that have reached this developmental stage should thus be performed in a more diverse set of situations, and also should be harder to interrupt or modulate with changes in the environment. This has been proposed to explain why environmental enrichment becomes less effective in reducing bank voles' stereotypies with age (Cooper *et al* 1996; see also eg Cosyns & Ödberg 2000), and why sow stereotypies seem to occur in a range of situations of high arousal (eg Lawrence & Terlouw 1993; Haskell *et al* 2000).

Note that the possible role of central control seems to vary greatly between stereotypies. For example, several rodent studies provide convincing evidence of a change in control over time (eg Kennes & Ödberg 1987; Cooper *et al* 1996), but in other cases, no such effects have been found — for instance, some horse stereotypies up to seven years of age have been rapidly cured by improvements to the environment (eg Cooper *et al* 2000). This difference could perhaps be because animals vary in their tendencies to form routines (see eg Benus *et al* 1987, 1990).

Implications of central control for stereotypy as a welfare indicator

Because central control would make a stereotypy easier to perform and harder to interrupt, it is likely to increase bout length and thence overall stereotypy levels — but without any concomitant change in welfare. If it also increased the range of situations that elicit the behaviour, this too would increase overall stereotypy levels without signalling a change in welfare. The development of central control thus potentially dissociates stereotypy and welfare (eg Mason 1991b). The varying role of central control is thus another potential source of variability in stereotypies' properties, as it is probably involved in some instances but not in others. For instance, this could even perhaps explain why stereotypy and corticosteroids were found to be uncorrelated in high-stereotyping groups of mice, but (negatively) correlated in low-stereotyping groups (Nevison 1999b), and why stereotypies did not seem linked with signs of poor welfare in one population of adult mink, but were so in younger animals (Mason 1992). Finally, central control means that we should not automatically take a failure to alleviate stereotypy as a failure to improve welfare. As Ames (1994) advises for bears, environmental enrichments should be persevered with because "stereotypies can persist long after the initial cause has been removed."

4) Perseverative behaviour: stereotypies as a symptom of altered behavioural control

The final issue that may dissociate stereotypy from suffering is a link with general 'perseveration' — "the continuation or recurrence of an … activity without the appropriate stimulus" (Sandson & Albert 1984, 1987). In the section above, the properties of particular stereotypies were argued to change, but here, we propose that the animal itself is altered, such that *all* of its behaviour becomes less appropriately coupled to internal state and external circumstance.

In humans, excessive perseveration is associated with disorders such as schizophrenia, autism, and some types of brain injury. Perseverative individuals have forms of central nervous system dysfunction that impair the proper regulation of behaviour. They therefore tend to produce behavioural responses to environmental cues or instructions that may be unnecessary or inappropriate; for example, a perseverative person walking down a corridor may knock at any door with a sign saying "Please Knock" (Sacks 1986). They are also prone to inappropriate repetition. For example, a perseverative individual may repeatedly draw a quadrangle, when asked to first draw a quadrangle but then a series of other shapes (eg Luria 1965); or may be poor at generating random sequences in gambling tasks, instead repeatedly producing the same response, or alternating responses in a stereotyped manner (eg Frith 1970, 1972; Frith & Done 1983). Could such failures to inhibit 'old' or inappropriate responses contribute to stereotypy? In individuals with schizophrenia and autism, perseverative tendencies do indeed correlate with levels of spontaneous stereotypy (eg Frith & Done 1983; Turner 1997), and similar deficits may also occur in captive animals. Isolation-reared primates have long been known to be both stereotypic and perseverative (eg Gluck & Sackett 1976; Beauchamp & Gluck 1988; Sanchez *et al* 2001). More recently, in captive species as diverse as voles, songbirds and bears, stereotypy has been found to correlate with impaired performance in tasks used to assess perseverative behaviour, such as gambling and extinction tasks (eg Garner 1999; Garner & Mason 2002; Garner *et al* 2003; Vickery & Mason 2003). Thus, perseveration is likely to play a role in at least some captive animals' stereotypies.

The relationship between perseveration and welfare is complex. On the one hand, perseverative rituals and stereotypies can increase autistics' awareness of being different from other people (eg Kalen 2000; Dana 2001), and such self-consciousness may well explain why some individuals report distress or embarrassment when making perseverative errors during psychological tests (Milner 1963; Hudson 1969; Turner 1997). Perseveration may also become a welfare problem when the subject is in a demanding, constantly changing environment (Turner 1999b; Loftin 2003). It may also sometimes be a product of stress (see Francis *et al* 1995; Lopatto *et al* 1998; Watkins & Brown 2002). However, freed from social concerns or challenging levels of environmental complexity, autistics' accounts of everyday life do not portray perseveration as either the cause, or the result, of stress (Kalen 2000; Bee 2002; M Turner 2003, personal communication). Many even report their perseveration, and/or their stereotypies (see above), as a source of pleasure (eg Handley 2001; Loftin 2003). Furthermore, other results from human studies suggest that perseverative individuals may sometimes be quite unaware of their repetitive tendencies (Milner 1963; Luria 1965; Hudson 1969; Sandson & Albert 1984), and indeed some autistics report being unaware even of performing stereotypies unless they consciously attend to them (Neral 2002). Thus, overall, in the types of undemanding environments that most captive animals live in, perseverative tendencies *per se* are probably neutral with respect to welfare.

Implications of perseveration for stereotypy as a welfare indicator

The main implications of perseveration for the welfare significance of stereotypy resemble those of central control. First, perseveration is a factor largely neutral with respect to welfare that nevertheless can influence stereotypy levels. Second, the extent to which perseveration is involved varies from stereotypy to stereotypy (NR Latham unpublished data); thus, it is yet another factor that could help account for the variation in stereotypies' correlates. Third, stereotypies that are due to severe perseveration may be hard to cure with enrichments, but this need not mean that welfare has been unaffected.

There is, however, one important way in which perseverative stereotypies differ from centrally controlled ones, and that is in the changes seen in other aspects of behaviour. The psychological literature reveals that perseveration and its accompanying stereotypy can be linked with reduced abilities to respond appropriately to novel stimuli, and even with tendencies to find environmental change stressful (eg Turner 1999a,b; NAS 2002; Loftin 2003). This suggests that in such instances we may need to be both gentler and more patient with our use of environmental enrichments. Perhaps such effects could explain why some stereotypies can take many months to reduce when the environment is enriched (eg Novak & Harlow 1975; Meehan *et al* 2001), and why some enrichments even cause stress and fear (Di Giovanni & Valente 2001).

Discussion: stereotypies and welfare assessment

Stereotypies are very common in captive animals, and undoubtedly have a role in welfare assessment. Our literature survey shows that where data are available, environments that elicit or enhance stereotypies are typically sub-optimal, and thus the great prevalence of stereotypies suggests that many millions of animals currently experience poor welfare. However, our survey also shows that stereotypies can appear or increase in situations that seem neutral, or even beneficial, with respect to welfare, and other studies reveal that some aversive environments do not elicit stereotypies. For example, tethering and exposure to cold or electric shock do not always increase stereotypy (Archer 1979; Broom 1986; Robbins *et al* 1990); and being moved between cages can even temporarily reduce stereotypy in mink (Mason 1991b, 1992). Furthermore, our analyses

Table 2 A summary of four factors affecting the relationship between stereotypy and poor welfare. For any single stereotypy, four main properties affect its relationship with welfare (each is given in a separate row here). For each of these independent factors, a stereotypy may have the property described at the left hand side of the arrow, that described at the right hand side of the arrow, or be somewhere on the continuum in between. See text for more details. Table 3 gives some suggestions as to how such properties may be identified empirically.

Relationship between stereotypy and poor welfare		
Stereotypy is a sensitive index of poor welfare (eg frustration)	⟷	**Stereotypy is not tightly linked with poor welfare**
Properties of stereotypy		
No substitute for normal behaviour	⟷	Full substitute for normal behaviour
Repetition *per se* has no effects	⟷	Repetition has 'mantra effects'
Flexible; form is responsive to changes in the environment	⟷	Centrally controlled
Switched on and off appropriately	⟷	Product of perseveration

show that when animals are compared *within* housing systems, individual stereotypies are linked with improved welfare nearly three times as often as with poor.

This overview has three main implications for the use of stereotypy in welfare assessment. First, it corroborates its general use: systems that lead to stereotypy are indeed likely to be worse than systems that do not. Second, it shows that despite this likelihood, simple stereotypy scores should never be used as the sole index of welfare (although how stereotypy assessment might be improved, we come to later). This is an important point, as stereotypy is often focused upon to the exclusion of other indices (surveying the proceedings of recent Environmental Enrichment conferences, for example, shows that in the zoo world, stereotypy is assessed twice as often as all other welfare measures put together). Third, it is clearly vital not to overlook the potential problems of animals with low or absent stereotypies: in stereotypy-eliciting circumstances, these individuals quite possibly have the worst welfare.

So why are stereotypies' relationships with welfare not clearer? As we have discussed, four processes in particular may obscure links between stereotypies and poor welfare. Some stereotypies may function as 'do-it-yourself enrichments', or have mantra-like calming effects. To allude to our paper's title, these would fall into the 'won't stop' category, and may ameliorate, at least partially, welfare in a sub-optimal environment. Stereotypies may also be caused or enhanced by changes in behavioural regulation, either because specific behaviour patterns have become centrally controlled, or because the animal itself is generally perseverative. These stereotypies would fall into the 'can't stop' category, and are arguably more 'scars' of past welfare than indicators of present (cf Mason 1991b). Each of these processes may play anything from no role to a major role in different forms of stereotypy. Table 2 summarises how these processes would then contribute to a stereotypy's properties as a welfare indicator, and also how they could potentially combine. The left-hand side of this Table illustrates the 'worst case scenario' for a stereotypy (though the best situation for those hoping to use it in welfare assessment). Here, the behaviour sensitively and accurately reflects the animal's motivation to perform frustrated natural activities, and it also has no beneficial consequences. In such a case, any housing system that increases stereotypy is reliably decreasing welfare, and within any single system, high stereotypers are also the worst off. On the right-hand side, however, we see the loosest potential relationship between stereotypy and current poor welfare. Here, all four of the processes that we have discussed are acting. Thus, the hypothetical stereotypy is a habit, and also performed by a generally perseverative individual; furthermore it has beneficial consequences. Such a stereotypy is little use in welfare assessment on its own: it would be performed in diverse circumstances (eg whenever the animal was aroused), and in long bouts that persist after their causal stimuli have ceased; it would be slow to respond to environmental enrichments, even ones that increase welfare; and its performance would improve an individual's welfare over that of a non-stereotyper in the same situation.

Considering the mechanisms of stereotypy thus helps us to understand its complex relationship with welfare, but it can also help us further refine the behaviour's use as a welfare indicator. For one thing, it highlights how there is only one circumstance in which reduced stereotypy means improved welfare, and that is when the motivation to perform the source-behaviour is diminished. Many previous authors have warned of the potential dangers of simply physically preventing a stereotypy (eg Schofield & Mulville 1998), or of using drugs that potentially only affect motor output (Garner 1999; J Garner 2002, personal communication), but it is sobering that stereotypy-preventing practices still continue today, especially in the equine world. Even genetically selecting against stereotypy needs to be done with care. Mills' work on poultry (Mills *et al* 1985a,b) provides a nice example of where selecting against stereotypy was achieved by selecting against the underlying motivation, and thus done in a manner likely to be beneficial for welfare. However, farmed Dutch mink (see eg EC 2001; Vinke *et al* 2002) provide a far more troubling example, as here stereotypy alone is used as a selection criterion, and furthermore,

mink stereotypies are linked with lower endocrine stress responses (reviewed in EC 2001). This suggests a potential risk of selecting against the ability to express behaviours, and, furthermore, behaviours which may help mink to cope.

A second insight from considering mechanism is that it suggests means by which environments that lead to stereotypy development could also lead to continued stereotypy performance even after improvements to welfare. Again, we are far from the first to make this observation, but we think it worth re-emphasising here. Eaton *et al* (1994), for example, found that housing isolation-reared rhesus macaques in pairs did not reduce stereotypy, and so concluded that pair-housing did not improve welfare. We would suggest that this is a dangerous conclusion to reach without further data, as the monkeys' welfare could well have been improved, but their perseverative tendencies simply left untouched. These sorts of behavioural changes are also potentially important for reasons other than welfare, as they may well be undesirable if animals are being reared for conservation purposes (Vickery & Mason 2003) or for behavioural or neuroscience research (Garner & Mason 2002; Garner *et al* 2003).

The third advantage of considering mechanism is that it highlights how seldom stereotypies are truly comparable with one another. Thus, even within individuals, stereotypies can differ in their relationship with welfare. For example, various zoo-housed ungulates exhibit both oral and locomotor stereotypies (Bashaw *et al* 2001). In these animals, oral stereotypies are thought to be linked with rumination and/or foraging (and thus may be 'do-it-yourself enrichments'), but the locomotor stereotypies are suggested to represent escape or approach-motivated behaviours (and thus may be associated with frustration) (Bashaw *et al* 2001). Even stereotypies of a broadly similar form and in the same population may be incomparable. For example, gastric ulceration is negatively correlated with tongue-playing in veal calves, but uncorrelated with biting and licking stereotypies in the same animals (Wiepkema *et al* 1987). Considering mechanism allows us to hypothesise as to why this might be so, and stops us assuming that all stereotypies are equivalent, or that '*X* amount of stereotypy always equals a *Y* level of welfare'.

Relatedly, the fourth and final consequence of thinking about mechanism is that it suggests additional data that could help us better understand stereotypies. For example, we *could* potentially compare different types of stereotypy if we could experimentally or statistically control for differences in the consequences of the behaviour and the relative contributions of central control and perseveration. Likewise we *could* use stereotypy as a valid, stand-alone welfare indicator, again if we could factor out or control for these other processes (NR Latham unpublished). This would be useful to those unable to use other techniques of assessing welfare or unwilling to use other measures which themselves do not have a clear-cut relationship with animal suffering. In Table 3, we therefore suggest data that could be used to assess the contribution of these other processes and to identify forms of stereotypy that differ in their welfare significance. The left-hand column illustrates the properties of a stereotypy that simply and sensitively track frustration, while the four columns to the right illustrate what happens when other processes act (and note that, just as in Table 2, these processes are independent and not mutually exclusive). The suggested additional data range from detailed ethological analyses of the behaviour itself to the effects on the stereotypy, and on the animal, of different types of environmental enrichment; and the '?'s in this table highlight how many gaps still exist in our understanding of these behaviour patterns. As well as helping stereotypy become a more useful welfare indicator, the knock-on advantages of collecting such data would be that these gaps would start to close, and also that we might, for the first time, start generating principles allowing us to *predict* a given stereotypy's relationship with frustration from its form, its age, and/or the biological and experiential background of the subject.

Conclusions and animal welfare implications

In this review, we have shown that stereotypy is linked with good or neutral welfare nearly as often as with poor. In part, this is because circumstances that lead to stereotypy tend to be linked with poor welfare, while individual expressions of stereotypy in such situations are often linked with relative improvements in welfare. However, in addition, we propose that this complex relationship also arises because not all stereotypies are sensitive indicators of current stress or frustration. Instead, other processes are likely to intervene and make the picture more complex. For example, beneficial consequences from performing the specific source-behaviour of the stereotypy ('do-it-yourself enrichment'), or arising from sheer repetition ('mantra effects'), may ameliorate welfare in poor environments. In addition, stereotypies that have become centrally controlled (habit-like), or that arise from autistic-like changes in the control of all behaviour (perseveration), are likely to be unreliable indicators of current state because they can be elicited by, or persist in, circumstances that improve welfare. There is still relatively little research into any of these fascinating processes but they could account for some of the stranger properties of stereotypies, as well as having practical implications, beyond welfare, for animal use. To refine stereotypies' use in welfare assessment, we suggest the collection of specific additional data to reveal when any of these four processes is acting. Such data might also help us generate principles for understanding why stereotypies differ between species and situations; we agree with Minero *et al* (1999) when they said, "The patient accumulation of [stereotypy] data in different species and in different circumstances should help to find the answer."

Until such research increases our understanding, stereotypies should always be taken seriously as a warning sign of potential suffering, but never used as the sole index of welfare; non-stereotyping or low-stereotyping individuals should not be overlooked or assumed to be faring well; simple measures of frequency should also not be used to compare stereotypies that differ in age or form, or in the biological or

Table 3 The properties of stereotypies that differ in their welfare significance. Here we suggest additional data that could be used to distinguish between stereotypies that differ in their underlying processes. Note that the processes represented in the four right-hand columns are not mutually exclusive; also that these four right-hand columns correspond to the right-hand extremes of each of the factors presented in Table 2.

Property	Type of stereotypy (for terms see text)				
	Stereotypy solely an index of frustration	Stereotypies involving other processes:			
		DIY enrichment	Mantra effects	Central control	Perseveration
Correlates with other signs of poor welfare?	Yes, positively*	Yes, negatively*	Yes, negatively† (and positively correlates with alpha brain waves?)	No relationship	Usually no relationship
Individual differences in stereotypy development predicted by …	Motivation to perform specific natural behaviour (Higher in wild-caught/enriched-reared animals?)	Motivation to perform specific natural behaviour (Higher in wild-caught/enriched-reared animals?)	?	Tendencies to form routines with repetition	Perseverative tendencies (Higher in abnormally reared animals?)
Elicited by few specific, or many general cues?	Specific	Specific	General	General	Specific
Resembles a specific natural activity in form and context?	Yes	Yes	Not necessarily (form is arbitrary)	No	Depends on nature of the source-behaviour
Behaviour is normal if animal is not stereotyping?	Yes	Yes	Yes	Yes	No, perseverative‡
Stereotypy a reinforcer?	No	Yes	Yes	No	No
Welfare decreases if stereotypy is prevented?	No	Yes	Yes§	No	No
Animal can attend to external stimuli while stereotyping?	Yes, but may pause	Yes, but may pause	No	Yes, and can do so easily without pausing	Yes
Form of the behaviour (degree to which it is unvarying)	Repeated elements and repeated bouts can vary	Repeated elements and repeated bouts can vary	Elements within a bout are very predictable, but successive bouts can vary	Elements and bouts are both very predictable#	Elements in a bout are very predictable, but successive bouts can vary
Likely response to environmental enrichment	Only decreased by enrichment which tackles underlying motivation; effect is then immediate and welfare is improved	Only decreased by enrichment very effectively tackling the underlying motivation (ie better substitute than stereotypy); effect is then immediate and welfare is improved	May be decreased by a range of enrichments, including rocking devices and/or repetitive stimuli? Welfare is not necessarily improved?	Resistant to enrichment, but welfare can be improved despite minimal changes in stereotypy	Resistant to enrichment; welfare may decrease, at least initially; welfare may then improve

*Especially if individual differences in the motivation to perform the frustrated natural behaviour are corrected for.

†Possibly only once the behaviour achieves a threshold rhythmicity?

‡Methods for assessing this are reviewed by eg Garner and Mason (2002) and Garner *et al* (2003).

§Unless a new stereotypy is developed (as form can be arbitrary); see eg Bumin *et al* (2002) on Rett's syndrome children prevented from stereotyping.

#The stereotypy may also have to be re-started from the beginning if interrupted (reviewed in Mason & Turner 1993).

experiential characteristics of the performing animal; enrichments that do not immediately reduce stereotypies should not be assumed failures with respect to welfare; and finally, stereotypies should not be reduced by means other than tackling their underlying motivations.

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