

The 'coping' hypothesis of stereotypic behaviour: a reply to Rushen

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We welcome Rushen's (1993) comments that our results (Cooper & Nicol 1991) have the potential to revitalize the debate over stereotypic function by focusing more directly on behavioural measures of aversion. This was our original intention as experiments in the area were becoming increasingly reductionist.

The 'coping' hypothesis maintains that stereotypic behaviour is a response to aversive or stressful conditions, and that in some way the performance of stereotypes reduces the level of stress or aversion experienced. Rushen's first general point is that not all recent studies appear to support this hypothesis. We agree with Mason's (1991) view that different forms of stereotypy have heterogeneous causes and, like Rushen (1993), see no reason to suppose that all stereotypes are a response to stress, or that the performance of all stereotypes will affect physiological systems associated with stress. Rushen primarily cites studies that investigated the short-term effects of stereotyping on heart rate (Schouten et al. 1991), pain perception (Rushen et al. 1990) and pituitary-adrenal output (Terlouw et al. 1991; von Borrel & Hurnik 1991). These studies have shown that high arousal is associated with the onset or development of stereotypes, but not that performance of stereotypes reduces this arousal. Preventing stereotypy, however, has been found to increase arousal. The prevention of environmentally induced stereotypes in voles, *Clethrionomys glareolus*, leads to changes in plasma corticosterone and white blood cell levels that are consistent with chronic stress (Kennes & De Rycke 1988). Unfortunately, in this study there was no examination of the effect of preventing non-stereotypic activities. Direct manipulation of the dopaminergic neural pathways by application of amphetamine or apomorphine elevates plasma corticosterone (Antelman & Chiodo 1983) and reliably produces stereotypic behaviour (Robbins et al. 1989). Preventing such drug-induced stereotypes by

neurotoxic lesions prolongs the elevation in plasma corticosterone (Jones et al. 1989), whereas lesions preventing non-stereotypic locomotion have no effect on corticosterone levels. The relationship between drug and environmentally induced stereotypes is, however, unclear. Dopamine agonists increase the level of captivity-induced jumping in voles (Odberg et al. 1987), whereas antagonists inhibit the jumping stereotypy (Odberg et al. 1987; Kennes et al. 1988). Furthermore, prior exposure to stressors such as social isolation (Jones et al. 1988; Lewis et al. 1990), immobilization (Cabib et al. 1984) or foot shock (Maclennan & Maier 1983) potentiates the performance of drug-induced stereotypes. These studies suggest a link between environment, dopaminergic activity and stereotypy, but the nature of this link is not clear.

Traditional support for the 'coping' hypothesis includes evidence that environmentally induced stereotypes are associated with reductions in both the long-term and short-term physiological signs of stress (see Mason 1991 for a review). Stereotypes are associated with reduced heart rate in children (Soussignan & Koch 1985), reduced corticosteroid in hens, *Gallus gallus domesticus* (Duncan 1970) and reduced abomasal damage in veal calves, *Bos taurus* (Wiepkema et al. 1987). These effects do not, however, hold for all stereotypes. For example, a tongue-playing stereotypy is associated with the reduction in abomasal damage in veal calves, whereas a biting/licking stereotypy is not (Wiepkema et al. 1987). So, overall, the physiological evidence for and against the 'coping' hypothesis is inconclusive (Robbins et al. 1989; Dantzer 1991).

Rushen's suggestion that oral stereotypes may affect digestion is an extrapolation of work indicating that non-nutritive sucking behaviour in calves affects the secretion of important digestive hormones (de Passillé et al. 1991). Movement stereotypes may have very different effects if

different behavioural or physiological systems are involved. Repetitive movements with short bout lengths such as grooming and yawning are a common response to acute stress in many mammals. Treatments such as transport, handling or water immersion (Jolles et al. 1979; Gispen & Isaacson 1981) all result in a subsequent lengthening of otherwise normal grooming bouts. During the performance of such behaviour the CNS activity that causes ACTH release is reduced, and a balance amongst dopaminergic systems is restored (Isaacson & Gispen 1989). The relationship between normal repetitive movements associated with stress recovery and the development of stereotypies is not clear, but these pre-existing responses may indicate that certain stereotypies are more likely to have de-arousing properties than others.

Rushen complains that in our experiments 'no measures were taken to determine whether or not the barren cage was in fact aversive'. We were, however, more interested in the ability to discriminate between the two cages, the relative aversion or attraction, than in the absolute aversion. Rushen states 'To indicate aversion, it would be necessary to show that the voles would be prepared to pay some "cost" to avoid the barren pen'. If some cost (e.g. lever pressing or food restriction) were imposed, we would only be able to demonstrate that a choice was less aversive than the cost. Behavioural data can only reveal how particular resources or environments are ranked in preference relative to each other, or to a third resource or environment (the cost). There is no sharp cut-off point at which one can infer that an animal subjectively experiences an environment as aversive or unpleasant. None the less, some measure of the degree of aversion or attraction to the two cages used in the choice test would be valuable, as further evidence of changes in the ability to discriminate as stereotypies develop. Rather than imposing a simple cost, we would suggest future experiments employed a calibration of attraction or aversion using demand curve analysis (Dawkins 1990).

We agree that our study was essentially correlational and recognized the difficulty of inferring a causal relationship when we wrote 'the performance of stereotypies may cause or be associated with a change in the vole's perception of its environment'. Rushen's alternative explanation of our results is not, however, equally plausible. Rushen suggests that voles that developed stereotypies may simply have found both environments more

aversive than voles that did not develop stereotypies. If so, the relative difference in preference for the cages, apparent at the start of the experiment, should have been preserved as stereotypies arose. However, we found the relative difference in preference decreased for voles that developed stereotypies. Rushen suggests stereotypic voles may have learnt not to choose between two unacceptable environments but, again, our data did not support this explanation. Voles that developed stereotypies did not cease to choose. The number of visits to the two cages did not vary with age and there was no difference in number of visits between voles that developed stereotypies and voles that did not at any age (Cooper 1992). Furthermore, at each age, each vole received a 2-h choice test on each of 4 successive days. There was no variation in preference between these 4 days at any age. There was, however, a marked decrease in preference for the enriched cage between each age, when the voles had gained no further experience of the choice apparatus, since the intervening weeks had been spent in the simple home cage. Hence, our data demonstrate that voles that developed stereotypies ceased to discriminate between environments when clear preferences had previously existed.

Such a reduction in discrimination may be due to the effects of stereotyping on both motivational and perceptual systems. The stereotypic vole is either less aware of differences between the two environments, or no longer motivated to avoid the less attractive choice. In both cases the vole would be better able to cope with an unavoidable aversive environment. Hence our results appear to support the 'coping' hypothesis of stereotypic behaviour, at least for locomotor stereotypies in bank voles.

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