

Stereotypies: a critical review

GEORGIA J. MASON

Sub-department of Animal Behaviour, University of Cambridge, Madingley, Cambridge CB3 8AA, U.K.

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Abstract. Stereotypies are repetitive, invariant behaviour patterns with no obvious goal or function. They seem to be restricted to captive animals, mentally ill or handicapped humans, and subjects given stimulant drugs. In this respect they are abnormal, although possibly the product of normal behavioural processes. Stereotypies are often associated with past or present sub-optimal aspects of the environment, and have been used as a welfare indicator. It has been hypothesized that stereotypies have beneficial consequences which reinforce their performance, although other means, such as positive feedback, may equally explain their persistence. Empirical evidence links them with lowered awareness of external events, and reduced arousal and distress. However, as most of this evidence is correlational it remains uncertain that the stereotypies are themselves the cause of coping. Furthermore, they are heterogeneous in source of origin, proximate causation and physical characteristics, and they change over time in important respects, becoming more readily elicited by a wider range of circumstances. Therefore the properties of one stereotypy are not necessarily those of another.

A stereotypy is a behaviour pattern that is repetitive, invariant and has no obvious goal or function (e.g. Fox 1965; Hutt & Hutt 1970; Ödberg 1978; Wiepkema et al. 1983). A bout of recurring movements may be remarkably sustained (e.g. Ödberg 1986), and the animal may appear to have difficulty in stopping (Feldman & Green 1967; Cronin et al. 1984). Bouts of stereotypy are themselves repeated (e.g. Stolba et al. 1983), and may be as predictable in time and place of performance as they are in morphology (e.g. Hediger 1950; Berkson 1967; Meyer-Holzappel 1968; Hinde 1970, page 556). The organization of a stereotypy appears only partially dependent on external stimuli (e.g. Berkson 1967), particularly when performed at high speeds (e.g. Fentress 1977). With time, a stereotypy may become independent of the stimulus that originally elicited its performance (e.g. Levy 1944; Hinde 1970, pp. 556–557).

Stereotypies often develop in animals faced with insoluble problems (Stolba et al. 1983; Wiepkema 1983). They are not all induced by the environment, however. Some result from brain damage or psychiatric conditions (reviewed by Robbins & Sahakian 1981; Ridley & Baker 1982), and others from drugs such as d-amphetamine (e.g. Robbins 1976).

Stereotypies are diverse in nature. Form and timing depend on the species and the eliciting situation, and may differ between individuals. Stereotypies also differ in repetitiveness and inflexibility.

Examples include rocking movements and repetitive vocalizations in institutionalized humans (e.g. Stone 1964; Berkson 1967), bar-chewing in stalled sows, *Sus scrofa domestica* (e.g. Wiepkema et al. 1983), head-swinging in zoo-housed bears and elephants (Dittrich 1984), pacing in captive fennec foxes, *Vulpes zerda* (Ödberg 1984a), eye-rolling in veal calves, *Bos primogenius taurus* (Fraser & Broom 1990), and jumping in caged bank voles, *Clethrionomys glareolus* (Fentress 1977; Ödberg 1986).

In this review I address three questions. (1) Are stereotypies 'abnormal'? (2) Do stereotypies indicate a welfare problem? (3) Does performing a stereotypy reward the animal? I then consider the differences in how authors characterize stereotypies, and the problems raised by treating the activities covered by the term as though all are equivalent.

STEREOTYPIES AS ABNORMAL BEHAVIOUR

In this section, I discuss the two meanings of abnormality and the way the word is applied to stereotypy. I then describe the ways in which stereotypies resemble normal behaviour patterns, and the implications these have for hypotheses concerning the biological significance of stereotypies.

Stereotypy is often labelled an 'abnormal' behaviour, with the meaning of 'abnormal' left unspecified (e.g. Ödberg 1978, 1987a; Cronin et al. 1984, 1985; Hughes & Duncan 1988). This is a source of confusion, since the word can be used in two distinct ways. It can mean literally 'away from the norm', in the sense of being statistically rare or different from a chosen population (e.g. Meyer-Holzappel 1968; McMahon & McMahon 1983, page 29; Houpt 1987; Fraser & Broom 1990). It can also mean lacking in function (e.g. Fraser 1968; McMahon & McMahon 1983, page 37) or causing harm to the animal (e.g. Schmidt 1982; McMahon & McMahon 1983, page 37), perhaps because it is the product of underlying pathology (e.g. McFarland 1981; McMahon & McMahon 1983, page 39). A behaviour pattern may be abnormal in one or both senses.

Whether a stereotypy is abnormal in the first sense depends on what is selected as 'normal'. For example, stereotypies may be the norm for a captive population. When Harlow & Suomi (1971) wrote of 'normal' stereotypy levels, they meant those of laboratory monkeys that had been reared in a group rather than in isolation. However, the majority of authors (e.g. Fox 1968; Luescher & Hurnik 1987; Fraser & Broom 1990) take as the norm the animal living free or in naturalistic conditions in captivity. In this case stereotypies are abnormal, in the context and frequency of their performance (Broom 1983), and often in the form of the movements involved.

Are stereotypies also abnormal in the second, maladaptive sense? They have been described as 'pathological' by, for example, Ödberg (1984b), and are sometimes the expression of central nervous system dysfunction (e.g. Ridley & Baker 1982; Broom 1983). However, except in cases involving stereotypic drug self-administration (Ellinwood & Kilbey 1975), self-mutilation or severe weight loss, it is not clear that stereotypies are maladaptive in themselves.

Some assume that if stereotypies are abnormal in the first sense, they must also be abnormal in the second. The argument is that stereotypies cannot be the product of natural selection (they seem to be absent in the wild), nor of selective breeding for captivity (they are not unique to domesticated species). Hence stereotypies cannot possibly be of any benefit and, because they involve time and energy, can only represent a net cost to the animal. However, a learnt behaviour pattern, for example,

may be adaptive even when uncommon or unique. Furthermore, in some respects even the most bizarre stereotypy resembles behaviour patterns seen in the normal, healthy, free-living animal (Hinde 1962). Such similarities mean that although stereotypies might be pathological, they cannot be prejudged as such solely on the grounds of their unusual appearance.

Stereotypies and Normal Behaviour

Stereotypies resemble normal behaviour patterns in three respects. First, to be invariant and resistant to change, i.e. stereotyped, is not unique to stereotypies. The same is true of, for example, grooming, drinking and displays (Hinde 1970; Fentress 1977; Dawkins 1986; Groothuis 1989a). The rigidity of stereotypies may in part be explained by the unvarying nature of those environmental factors that would otherwise modulate and control the behaviour (Morris 1966; Ridley & Baker 1982). However, inflexibility in behaviour also results from repetition. This has been observed in stereotypies (e.g. Meyer-Holzappel 1968; Fentress 1976; Cronin et al. 1984), and in normal behaviour (e.g. Lashley 1921; Miller et al. 1960, pp. 81–93; Morris 1966; Stolba et al. 1983; Groothuis 1989a). The process underlying the progressive decrease in variability is that extrinsic factors become less important in the control of the behaviour pattern and although an external stimulus may remain the trigger, the pattern comes to be self-organizing (Fentress 1977; Carpenter 1984). With the involvement of information-processing systems minimized, the animal is free to direct its attention elsewhere (Lashley 1921; Fentress 1976) and the action pattern can be performed faster than would be possible if guided by sensory feedback (Lashley 1917, 1951; Miller et al. 1960; Fentress 1976; Carpenter 1984). Fixity of performance is therefore particularly evident in a state of high arousal (Fentress 1976, 1977), when selectivity of attention (Warburton 1987) and speed of behavioural response (Dantzer 1986; Warburton 1987) increase.

A second feature that a stereotypy shares with normal behaviour is that, once developed, it may become independent of its original eliciting stimulus. It may then be displayed in a range of different situations (Hinde 1962, 1970, pp. 556–558; Ödberg 1978, 1987a; Dantzer 1986). For example, a captive dingo, *Canis dingo*, would perform a stereotyped head movement when pacing, with every change in

direction. In time, this head-swing came to be shown whenever the animal made any turning-away movement (Fox 1971). With repetition, functional behaviour, too, can show ease of elicitation (Hinde 1970, page 557; Dantzer 1986, 1989) and autonomy from the original context (e.g. Baerends 1975). For example, the display of the young black-headed gull, *Larus ridibundus*, develops during agonistic encounters, but by adulthood it is no longer exclusively coupled with aggressive behaviour, and is shown in a range of circumstances (Groothuis 1989b).

A third important, and apparently 'abnormal', characteristic of stereotypy is that it has no obvious goal, end-point or function. This need not, however, indicate that the behaviour is pathological, as normal behaviour, too, can persist when apparently devoid of functional consequences. Habits, for example, are actions that are relatively independent of the current value of their original goal (Dickinson 1985). Foraging behaviour (Duncan & Hughes 1972; Wood-Gush et al. 1983; Anderson & Chamove 1984) and operant responses (Neuringer 1969; Singh 1970; Duncan & Hughes 1972; Markowitz 1982) may be performed even when food is supplied freely, and behaviour used in avoiding aversive stimuli will persist even when punishment stops (Hinde 1962; Solomon 1967). One suggested explanation is that the behaviour pattern is reinforcing in its own right (e.g. Wood-Gush 1963; Hinde & Steel 1972; Roper 1976; reviewed by Hughes & Duncan 1988). Alternatively, the apparently inconsequential behaviour may result in benefits that have not been identified, perhaps because they are evident only over a longer timescale (this tends to be assumed for play and sleep, for example; see reviews by Martin & Caro 1985 and McFarland 1989).

Conclusion

If one takes the free-living healthy animal as the norm, then stereotypies are in one sense abnormal: they seem restricted to captive or psychologically impaired individuals. However, one cannot infer from this that stereotypies are necessarily functionless or pathological, particularly as even the strangest of stereotypies may result from perfectly normal phenomena. Specific behaviour patterns are often elicited by situations of stress, conflict, frustration and the imminent arrival of food, and if these are repeated (for whatever mysterious, but

not necessarily pathological, reason) they may become inflexible, particularly in a highly aroused animal. Only if the costs of their performance demonstrably outweigh any benefits, or if they are shown to result from a pathological condition, can one say for sure that stereotypies are abnormal in the maladaptive sense.

STEREOTYPIES AND POOR WELFARE

Stereotypies have long been thought to indicate that an animal's environment is sub-optimal (e.g. Hediger 1950; Broom 1983; Luescher & Hurnik 1987; Ödberg 1987a), and that the animal is suffering from a welfare problem (e.g. Broom 1983; Wiepkema 1983 reviewed by Ödberg 1987a; Fraser & Broom 1990), such as stress (e.g. Vestergaard 1981; Anonymous 1989).

This view is based on several features of stereotypies: the contexts in which they develop; the behaviour patterns from which they arise; the factors that influence their development and subsequent performance; and the fact that some stereotypies involve self-damage. This evidence is outlined below.

The Contexts of Stereotypy Development

Stereotypies are often physically and temporally linked to sub-optimal features of the environment. Specifically, they develop in the following types of situation (types that are not mutually exclusive; fear may involve frustration if the animal cannot escape, and so on).

Frustration

Situations in which an animal is motivated to perform a behaviour pattern but is unable to do so, are frustrating (Hinde 1970, page 414; Duncan & Wood-Gush 1972). They tend to result in displacement or redirected activities (see McFarland 1985, page 384, for an account of displacement activities), or, if the problem is repeated or chronic, stereotypies (Duncan & Wood-Gush 1972; Broom 1983; Wiepkema 1983, 1987; Salzen 1990). Frustration is aversive (Duncan & Wood-Gush 1974; Dawkins 1990).

Examples include the stereotypic pacing developed by laying hens, *Gallus gallus domesticus*, with

no access to a suitable nest-site (Duncan 1970; Wood-Gush 1972), and in association with intense food frustration (Duncan & Wood-Gush 1972). Stereotypy can sometimes be reduced by providing the appropriate extrinsic factors (e.g. Meyer-Holzapfel 1968; Stevenson 1983; Appleby & Lawrence 1987), or artificial substitutes to which the behaviour can be redirected (e.g. Schmidt 1982).

Unavoidable stress or fear

Examples of stereotypies associated with stressful or arousing situations include the leg-swinging of children doing abstract homework (Soussignan & Koch 1985); the stereotypic vomiting and swaying of a female sloth bear, *Melursus ursinus*, in the presence of an aggressive male (Meyer-Holzapfel 1968); and the stereotypies such as body-rocking shown by the mentally handicapped when distressed (e.g. Stone 1964). The location of stereotypy performance may sometimes reflect the stressful nature of the causal factors: deprivation-reared monkeys retreat to the same part of the cage to perform stereotypies as they do to sleep, or to hide (Berkson 1967). That a tranquillizer will inhibit the development of stereotypic pacing in the hen has been suggested as indicating the role of fear (Duncan & Wood-Gush 1974). However, the agent used, reserpine, is a major, or anti-psychotic, tranquillizer, and as such has many effects besides fear reduction (e.g. Rech & Moore 1971). Interpretation of these results is therefore problematic. Interestingly, Munkvad & Randrup (1966) found major tranquillizers to block amphetamine-induced stereotypies, but minor tranquillizers (sedative, anxiolytic agents) to have no effect.

Restraint and lack of stimulation

Stereotypies have been associated with barren and restrictive conditions by, for example, Levy (1944), Hediger (1955), Morris (1964), Meyer-Holzapfel (1968) and Hinde (1970). This type of environment is thought to be sub-optimal (e.g. Stolba et al. 1983; Wood-Gush et al. 1983), perhaps because there is a need for sensory stimulation per se (e.g. Petric 1986, cited in Dellmeier 1989); because arousal needs to be kept within optimal limits (Ewbank 1973; Hennessy & Levine 1979; reviewed by Inglis 1983 and Toates 1983); because locomotor movement is constrained (Levy 1944;

Meyer-Holzapfel 1968; Dantzer 1986; Dellmeier 1989); or because it involves the lack of several specific factors (e.g. Keiper 1969), and hence the frustration of several motivations. Stereotypies that are more evident in barren than complex environments have been observed in a number of species (e.g. Levy 1944; Berkson 1967; Nørgaard-Nielsen 1984; Ödberg 1987b; Bryant et al. 1989), and rocking stereotypies are more common in blind than sighted mentally handicapped humans (Berkson & Davenport 1962, cited in Hinde 1970, page 557). The closer the confinement, the greater the stereotypy developed by sows, for example (Vestergaard 1981; Broom & Potter 1984), rhesus macaques, *Macacca mulatta* (Draper & Bernstein 1963) and bank voles (Ödberg 1987b). If an animal is isolation-reared in an impoverished environment (e.g. Berkson 1967), the stereotypies it develops resemble those of a range of clinical conditions, including autism, schizophrenia, mental retardation and organic brain damage (e.g. Stone 1964; Berkson 1967; reviewed by Robbins & Sahakian 1981). Such stereotypies are very persistent, and may indicate the initial challenge to have been so severe that the effects on the central nervous system are long-lasting, perhaps irreversible (Ridley & Baker 1982).

Behaviour Patterns from which Stereotypies Develop

Stereotypies develop from a range of behaviour patterns. The nature of its source behaviour pattern is often evident in the physical appearance of a stereotypy. These source behaviour patterns may themselves suggest that what causes the stereotypy is to the detriment of an animal's welfare. For example, they include displacement activities, adjunctive behaviour (i.e. the behaviour displayed by an intermittently reinforced animal whenever the probability of reinforcement is low; Falk 1971), and intention, vacuum and redirected movements (e.g. Levy 1944; Rushen 1984, 1985; Ödberg 1987a), behaviour that is classically associated with frustration, thwarting, or a conflict of motivations (see e.g. McFarland 1985). The stereotypies of some captive animals develop from what appear to be intention movements of escape (Hinde 1962; Meyer-Holzapfel 1968; Duncan & Wood-Gush 1972; Ödberg 1986). Pacing may also arise from thwarted intention movements of approach to conspecifics (Meyer-Holzapfel 1968; Ödberg 1978) or

prey species (Stevenson 1983). 'Yawning' and head-shaking stereotypies in hens develop from displacement activities shown in conflict situations (Nørgaard-Nielsen 1984), or alerting activities performed in the presence of disturbing stimuli (Hughes 1983). Stevenson (1983) explained the form of some stereotypies, such as pacing in a circle or figure-of-eight, as arising from two conflicting motivations, the animal alternately approaching, then retreating.

Factors Affecting Stereotypy Development

Stereotypies elicited by one aspect of the environment may have their development enhanced by another. Potentiating factors involve, in general, frustration, stress, or lack of control. For example, stereotypy is greater in single-housed than in group-housed sheep, *Ovis aries*, and is increased by a restriction in dietary intake (Marsden & Wood-Gush 1986). Isolation-rearing (Sahakian et al. 1975; Jones et al. 1988), uncontrollable footshock (MacLennan & Maier 1983), food deprivation (reported MacLennan & Maier 1983) and repeated restraint-stress (Cabib et al. 1984) can potentiate the stereotypy-inducing effects of psychomotor stimulant drugs. Heightened susceptibility to stress may predispose an individual to stereotypy; reactive, sensitive horses, *Equus caballus*, are more prone to the development of stereotypy than 'phlegmatic' breeds (although a major confounding factor here is that the former are often stabled more intensively; Kiley-Worthington 1983), and stress levels may be behind the great individual differences in human response to amphetamine (MacLennan & Maier 1983).

Factors Affecting Stereotypy Performance

Factors other than the original causal stimuli can trigger, prolong or increase the rate of repetition of an established stereotypy. Again, these eliciting or enhancing events are often stressful or frustrating (e.g. Fox 1984). For example caged mink, *Mustela vison*, perform their stereotypies when paired and wanting to flee (de Jonge & Carlstead 1987). Stress can reinstate the symptoms of amphetamine-intoxication in abstinent humans (reported MacLennan & Maier 1983). In the laboratory-housed chimpanzee, *Pan troglodytes*, stereotypy is potentiated by hunger (Berkson & Mason 1964) and low levels of stimulation (Berkson 1967). In a range of species, stereotypies increase in rate and

frequency on exposure to a novel object or loud noise, or disturbance by a human (e.g. Berkson et al. 1963; Meyer-Holzapfel 1968; Fentress 1976; Hughes 1980; Kiley-Worthington 1983). If the stimulus is very intense the stereotypy may be interrupted, the animal performing instead an appropriate orientation or flight response. However, the stereotypy may be performed at a greater intensity when resumed (Fentress 1977).

Factors that slow, reduce or eliminate stereotypy are those that, in contrast, give the animal the opportunity to perform other behaviour patterns (e.g. Berkson 1967; Keiper 1970) or that decrease arousal (Berkson 1967). For example, bank voles perform less stereotypy if moved from a small cage to a bigger and more enriched enclosure (Ödberg 1987b). The stereotypies of isolation-reared chimpanzees decrease with arousal-reducing drugs (Fitz-Gerald 1964, cited in Berkson 1967), and in a novel environment stereotypy performance falls as the animal habituates (Berkson & Mason 1964).

Stereotypies and Self-damage

Examples of stereotypies involving self-damage include self-biting (Berkson 1968; Broom 1983) and eye-poking by autistics (reported Ridley & Baker 1982). Stereotyped weaving and stall-walking by horses can cause weight loss and painful back conditions (Fraser 1980; Fraser & Broom 1990). Wind-sucking and crib-biting also reduce the condition of stabled horses (Fraser 1980; Kiley-Worthington 1983); wind-sucking can lead to gastro-intestinal catarrh, colic and reduced food intake (Dodman et al. 1987; Houpt 1987; Fraser & Broom 1990), and crib-biting to tooth-wear (Broom 1983; Dodman et al. 1987; Houpt 1987) and the ingestion of splinters (Dellmeier 1989). Repeated contact of the body with cage walls or bars during stereotypy may cause sores (Morris 1964; Meyer-Holzapfel 1968; Ödberg 1986), or impact injury (Fraser & Broom 1990). The detrimental effects of stereotypy are not exclusively physical: the stereotypies of autistic children may prevent learning and social interaction (Lovaas et al. 1971).

Conclusion

Overall, stereotypies are often seen in environments that seem sub-optimal (though this must be demonstrated independently of the presence of stereotypy, to avoid circularity). They are physically or temporally associated with lack of stimulation, or events such as acute stressors or the

expected arrival of food. All these environments may involve chronic conflict and frustration (Ödberg 1978, 1987b) and hence stress (e.g. Falk 1971; Duncan & Wood-Gush 1974; Brett & Levine 1979), particularly if uncontrollable or unpredictable (e.g. Weiss 1971; Reynolds 1978; Dantzer et al. 1983; Herbert 1987). Other stereotypies are relatively independent of the current environment, but reflect a past challenge severe enough to have traumatic effects on the central nervous system.

Thus the acquisition of stereotypies indicates an environment that is probably inadequate, and as such, presumably aversive. Does current performance therefore also indicate current suffering? It is certainly possible (e.g. Fraser 1990), but not all agree (e.g. Dantzer 1986, 1989). Without knowing what the consequences of performance are, for example, one cannot infer that this is necessarily the case.

STEREOTYPY AS A REINFORCER

It has been argued that performing a stereotypy rewards or reinforces the animal (e.g. Fox 1965, 1971). This is despite the behaviour's lack of apparent goal or function. The idea has arisen for two reasons. First, features of stereotypies suggest reinforcement. Second, empirical evidence associates stereotypy with states that the animal might find rewarding. The evidence for the reinforcing nature of stereotypy, the hypothesized reinforcers for stereotypy and the evidence supporting some of these hypotheses, are discussed in the following sections. Adjunctive behaviour is included in this discussion because it gives rise to some stereotypies (e.g. Rushen 1984). I conclude by discussing the implications of a reinforcing stereotypy for the long-term benefit of the animal.

Evidence for Reinforcement

That stereotypies develop over a period of time (e.g. Meyer-Holzzapfel 1968; Palya & Zacny 1980; Cronin & Wiepkema 1984), rather than being immediate responses to the eliciting situation, has been taken by some (Blackshaw & McVeigh 1984; Cronin et al. 1986a) as indicating that they are learnt, reinforced, behaviour patterns. For similar developmental reasons adjunctive behaviour has also been suggested as a learnt response (Roper 1980; Rushen 1984). However, sensitization, or some other progressive change in the central nervous system, is an alternative explanation.

Once developed, stereotypies are remarkably persistent, and this could indicate that performance has some reinforcing value (e.g. Duncan & Wood-Gush 1972; Ödberg 1987a). Stereotypies can remain unextinguished over long periods of time, e.g. blind, retarded children may spend their days engaged in the same stereotypies at 15 as at the age of 2 (Stone 1964). Stereotypy levels may even increase in performance over time, as they do, for example, in repeatedly tethered sows (e.g. Wood-Gush et al. 1983) and long-term inmates of mental institutions (Berkson 1967). Stereotypies that animals appear to have copied from others, for example, the spot-pecking of pigeons, *Columba livia*, placed adjacent to birds already showing this stereotypy, can persist even when the original 'tutors' are absent (Palya & Zacny 1980). Some stereotypies persist despite an energy cost. Stereotypic sows, for example, use more energy than non-stereotypic animals (Cronin et al. 1986a). Also consistent with reinforcement (see the argument of Warden et al. 1935, cited by Dawkins 1990) is the difficulty of deterring an animal from performing a stereotypy. For example, aversive conditioning will not cure horses of pawing (Fraser & Broom 1990). Some horses continue to wind-suck even if they have to work against a strap fitted around the throat, and may give themselves pressure sores in the process (Fraser & Broom 1990). The many cases of individuals persisting in stereotypy even when the behaviour results in self-damage have prompted suggestions that stereotypy is a 'need' (Ödberg 1986). Similarly, adjunctive polydipsia (excessive drinking) is difficult to discourage with punishment, even more so than deprivation-induced drinking (Falk 1971). Stereotypies may be so persistent that rewarding alternative behaviour patterns has little effect. For example, rats, *Rattus norvegicus*, on a schedule of random reward and punishment develop a jumping movement that persists even when the regimen is changed so that the problem is soluble (Feldman & Green 1967; Liberson 1967). Unfortunately, persistence may be explained by means other than reinforcement.

A number of other processes could give rise to persistent behaviour. For example, a behaviour pattern may be maintained by the constant presence of releasing stimuli, combined with a lack of behavioural competition from other motivational systems (Hediger 1950; Morris 1964). The persistence of some environment-induced stereotypies has been further explained in terms of positive feedback

from appetitive behaviour patterns upon the motivational bases for their own performance (Dantzer 1986; Hughes & Duncan 1988). These patterns, such as biting movements in intensively housed pigs, therefore persist as long as the extrinsic factors necessary for consummation, food, for example, remain absent. Whatever the original reasons for repeating a behaviour pattern, repetition itself can strengthen performance, by sensitizing the neuronal pathways involved (as discussed above; Dantzer 1986, 1989). This decreases the ability to shift behavioural programmes (Dantzer 1989): the animal becomes locked into a repeated sequence of movements. Raised arousal is a fourth possible cause of persistence (see Fentress 1976). Finally, an explanation for the persistent stereotypies induced by stimulant drugs is that they are by-products of drug-induced neurological 'over-activation' (Lyon & Robbins 1975; Robbins 1982). Reinforcement need not always be invoked to account for the persistent nature of stereotypies, and therefore persistence alone is not sufficient evidence that the behaviour is reinforced.

More convincing evidence for the reinforcement of stereotypies is that animals sometimes appear to work in order to allow performance. For example a mental patient whose stereotypy involved swinging a certain toy constructed a replacement one when this was removed (Berkson 1964). A dominant animal may chase a subordinate away from the spot favoured for pacing in order to perform this stereotypy itself (Ödberg 1984a), or push another out of its way in order to complete a stereotypic movement (Horsmann 1986). Similarly, on an intermittent feeding regime, animals will work for the chance to perform adjunctive behaviour such as polydipsia or aggression (Falk 1971).

Overall, it would seem that some forms of stereotypy could be reinforced in some way, and that others develop and persist in a way that is at least consistent with reinforcement. Other mechanisms may well be involved, however.

Consequences of Stereotypy

Several hypotheses have been advanced to explain the possible reinforcing nature of stereotypy. They all propose, explicitly or implicitly, that the reward value of stereotypy is that it is a coping response, i.e. that it in some way keeps the animal within optimal physiological or psychological limits (Fraser & Broom 1990), without actually

removing the animal from the eliciting situation (Ödberg 1989). For example, stereotypy has been suggested as relieving anxiety (Fox 1965).

The hypothesized means of effecting coping fall into three main types, discussed in this section. Some of the hypotheses have empirical support. I survey this in the following section.

Implicit in the first type of hypothesis is that the original, source behaviour pattern is reinforcing, and so is repeated by the animal. The stereotyped nature of the resulting behaviour is no more than a by-product of this repetition. Among hypotheses of this type are that the performance per se is important: the behaviour is suggested to be reinforcing in its own right, perhaps by providing an outlet for a specific behavioural 'need'. Wiepkema (1985), for example, suggested that oral behaviour directed at the bars of a cage can substitute for normal, consummatory activity (although whether it is an adequate substitute is open to question). In thwarted hens, the pacing that develops next to the cage door, apparently from attempts to escape, will persist even after the door is opened. It has been suggested that the stereotypy might be an adequate substitute for real escape (Duncan & Wood-Gush 1972), although of course the persistence may be explained in other ways (as previously discussed).

Alternatively, it may be that the consequences of the behaviour are important. For example, stereotypic tongue-playing in calves might stimulate the production of saliva, or increase feelings of satiety (Wiepkema et al. 1987); bill-shaking in chicks might have a role in preparing the animal for another activity (Forrester 1980); and some stereotypies of autistics may be a means of non-verbal communication (Garrigues et al. 1982). The exteroceptive or proprioceptive sensory input generated might be an important, more general, consequence of performance (Hinde 1962; reviewed by Berkson 1967; Stolba et al. 1983; Wood-Gush et al. 1983). This could come from rubbing against solid objects, as well as from the movement itself. Some stereotypies, such as pacing next to parallel bars, may provide a stimulating flicker of light and shadow (Fox 1971; Lovaas et al. 1971), and some rocking stereotypies have been suggested as masturbatory (Potter 1927, cited in Berkson 1967). Sensory input may be rewarding in a dull, unstimulating environment (e.g. Hinde 1970, page 557; Bareham 1972; Broom 1983, 1987).

Behaviour can be used to inhibit as well as to facilitate central nervous system activity (Forrester

1980). Stereotypy shown in an unpredictable, uncontrollable or otherwise arousing environment might be a means of reducing arousal (e.g. Hines 1942, cited in Hinde 1970, page 558; Ödberg 1978; Dantzer & Mormède 1981; Cronin et al. 1986a). Stereotypy may lower responsiveness to external stimuli (e.g. Ödberg 1978; Broom 1987) or pain (de Lissavoy 1963), and focus attention away from the source of conflict (e.g. Kiley-Worthington 1977; Wiepkema 1982a, 1987). It might do this by activating sensory channels so that the processing of input from other sources is interfered with (e.g. Hutt et al. 1964; Lovaas et al. 1971; Rushen 1984; Dantzer 1986). Thus the sensory input from stereotypy might, paradoxically, be rewarding in both under- and over-stimulating environments (Stolba et al. 1983). Alternatively, endogenous opioids might be involved in a stereotypy-mediated reduction of responsiveness and arousal (e.g. Cronin et al. 1986b; Broom 1987; Dodman et al. 1987; Kennes et al. 1988).

The second type of hypothesis considers the predictable, repetitive nature of the behaviour to be reinforcing. Some have linked stereotypies with the calming effects of being rhythmically rocked, cradled or groomed (Fox 1984, page 184), and the sleep-inducing effects of rhythmic audio-visual stimulation and limb movement (Stone 1964). Rhythmical stereotypies have been suggested as mimicking passive intra-uterine movements (Levy 1944), a mother's heartbeats (Fitz-Herbert 1950, cited in Berkson 1967), or the movements of suckling (Freud 1905, cited in Thelen 1979). Stereotypy's repetitiveness and rigidity have been hypothesized to increase the average predictability of an otherwise unpredictable environment (Forrester 1980; Broom 1981, page 99, 1983). The predictable outcome of repeating the movement may mean that the behaviour is no longer associated with emotion (Wiepkema 1987), a state that, in the contexts associated with stereotypy, the animal might find rewarding.

In the third type of hypothesis, finally, the reinforcer is not a genuine consequence of the behaviour but a coincidental event, superstitiously associated with it by the animal. For example, the animal might repeat a pattern of behaviour superstitiously associated with the arrival of food (Hinde 1962), the low arousal that might follow moving to the 'sleeping area' of the cage (Berkson 1967), the performance of functional behaviour such as defaecation (Cronin et al. 1984), or the

endorphin-release that occurs in times of stress or conflict (Cronin et al. 1986a; Broom 1987). Such explanations, however, fall down in cases where the animal spontaneously changes the form of its stereotypy.

Evidence

In this section I review the circumstantial and empirical evidence for the hypotheses outlined above. I tackle first the specific hypotheses that stereotypy increases sensory input and arousal, rewarding the animal; that it decreases arousal, perhaps by lowering responsiveness to external stimuli; and that it results in a release of endogenous opioids. I then discuss the evidence for the general hypothesis that stereotypy is, by whatever means, a coping response. I attempt to resolve the apparent contradictions within the data, and discuss the difficulties in interpreting results that suggest that stereotypy is of no consequence at all.

Evidence that stereotypy has beneficial consequences is largely correlational. The studies either exploit natural variation within (or sometimes between) populations, or focus on the changes within individuals that accompany the development or performance of a stereotypy. Not all the hypotheses have empirical support, however.

The use of stereotypy to increase sensory input, for example, is a hypothesis unsupported by data. Although a plausible idea, given the performance of stereotypy in barren environments and the descriptions of, for example, the 'self-stimulation' behaviour of autistics (Lovaas et al. 1971), it has yet to be shown that, with stereotypy, there is an increase in arousal dependent on sensory input. Furthermore, the circumstances of the performance of stereotypy may simply indicate that it occurs when there is no over-riding tendency to do anything else (e.g. Hinde 1970).

However, some evidence supports the idea that stereotypy lowers arousal. For example, the stereotypies of autistics are accompanied by increased heart-rate variability, a response associated with REM sleep and other states of low stimulus input (Hutt & Hutt 1978). Leg-swinging is associated with reduced heart rate in normal children (Soussignan & Koch 1985), and brain waves typical of drowsiness accompany the stereotypies of blind, retarded children (Stone 1964). That the significance of a stereotypy may lie in its very persistence is suggested by this last study, which showed only

protracted or intense bouts to be accompanied by the slowed brain waves. A relationship with de-arousal has also been found for some adjunctive or displacement activities (Marler & Ellen 1951, cited in Ödberg 1989; Barnett 1955, cited in Fox 1965; Delius 1967). Lowered arousal may stem from lowered responsiveness to external stimuli.

The association between stereotypies and lowered responsiveness to the environment has been made by, for example, Ödberg (1978), Cronin et al. (1984) and Dantzer (1986). Lovaas et al. (1971) found that autistic children trained to approach a dispenser for a food reward at the sound of a tone, showed much longer response latencies if engaged in stereotypy. Nodding in horses is associated with what appears to be a 'light somnolent state' (Fraser & Broom 1990), and Stevenson (1983) describes the 'trance-like' state of an alarmed and pacing animal as making the behaviour almost impossible to interrupt. Similarly, the rocking stereotypies of institutionalized humans are accompanied by a lowered awareness of external stimuli (Stone 1964; Berkson 1967), and may even culminate in a coma-like condition (Stone 1964). Low responsiveness may be evident even when the subject is not currently engaged in stereotypy (e.g. Berkson 1967). For example, Wood-Gush et al. (1983) found that sows with high levels of stereotypy showed one-third the exploration of non-stereotypic sows, when presented with a novel object, and that this difference was maintained whatever the animals were doing immediately prior to the test. Stereotypies may even be associated with analgesia (e.g. Kravitz et al. 1960).

Analgesia and physiological signs of coping could be mediated by endogenous opioids (reviewed by Rushen et al. 1990). The association between some stereotypies and opioids has been made on the basis of work with opiate receptor antagonists such as naloxone (Cronin et al. 1986b). However, the hypothesis that stereotypy somehow causes opioid release would not explain why the abolition of stereotypy by naloxone is immediate (Cronin et al. 1985, 1986b; Dodman et al. 1987), rather than preceded by a temporary attempt at compensation, as is usually the case in extinction (see e.g. Richardson & Zaleski 1986). This is also a problem for the hypothesis that the animal superstitiously associates the behaviour with an opioid release.

A general problem with the evidence considered so far is its correlational nature; stereotypies and

signs of lowered arousal may be independent and simply coincidental. For example, stereotypies and opioid-mediated analgesia both occur in the post-feeding period in sows, but there is no evidence that the reduced sensitivity is caused by the behaviour (Rushen et al. 1990). Similarly, where a stereotypy is linked with decreased attention to external factors, the former need not cause the latter: stereotypies and reduced attention may arise independently from exposure to an environment that the animal learns is unlikely to provide it with stimulation (Wood-Gush et al. 1983); from high arousal (Fentress 1976; Warburton 1987); or from a strong but frustrated motivation, the animal being uninterested in anything save food, for example (Wiepkema 1982b) and performing, in its frustration, repetitive adjunctive behaviour. An alternative interpretation of the correlational data is that stereotypy is dependent on the processes involved in coping.

Thus it is important to distinguish between the consequences of the stereotypy itself, and those of the processes underlying it: a stereotypy could be a symptom rather than a cause (e.g. Broom 1983). For example, restriction of attention could be the cause of stereotypies (Fentress 1976; see also McFarland 1966, on displacement activities). Similarly, endogenous opioids could be the cause of stereotypies. Injected opioids will cause or potentiate stereotyped behaviour (reported by Ödberg 1978; reviewed by Robbins & Sahakian 1981), endogenous opioids are involved in general persistence (e.g. reviewed by Rushen et al. 1990), and opioids are released at times of stress (Miczek et al. 1982; Akil et al. 1984). There is one problem with the hypothesis that stereotypy is nothing but the by-product of some other response: it explains why behaviour patterns in general may become stereotyped in a stressed or aroused animal, but it does not account for the specificity of the patterns elicited.

Overall, the data supporting hypotheses concerning the specific consequences of stereotypy seems impossible to interpret with certainty.

There is, finally, evidence supporting the general 'umbrella' hypothesis that stereotypy, by means unspecified, is a coping response. This evidence is the association between stereotypies and reduced physiological stress, and reduced negative emotion.

Examples of correlations between stereotypies and physiological signs of coping include some behaviour patterns of domestic fowl: pacing is

associated with a fall in corticosteroid levels (Duncan 1970), and head-flicking correlates negatively with adrenal weight (Bareham 1972, cf. Dawkins 1980, page 71 and Ödberg 1987a, who misquoted this paper). Cronin (1985) reported that young tethered sows often show no stereotypies and a chronic rise in corticosteroids; older sows, on the other hand, tend to perform stereotypies and have no hormonal response. In veal calves there is a significant negative relationship between stereotypic tongue-playing and the severity of abomasal lesions (Wiepkema et al. 1984, 1987). Similar results are found for the type of behaviour patterns from which some stereotypies may develop. For example, the gastric ulceration developed by rats when forcibly restrained is significantly lower in animals that perform the apparently irrelevant displacement activity of biting an object (Vincent et al. 1984). Adjunctive behaviour such as polydipsia (Brett & Levine 1979; Tazi et al. 1986; Dantzer et al. 1987) and chain-chewing by sows (Dantzer & Mormède 1981) may also be accompanied by physiological signs of coping.

Behavioural studies have also associated stereotypies with coping, by revealing, for example, reduced distress, anxiety or aggression. Children performing head-banging stereotypies do not cry (Kravitz et al. 1960) and may even enjoy the behaviour (Levy 1944); the alarm-calling of frustrated hens disappears once they develop a high frequency of stereotyped pacing (Duncan & Wood-Gush 1972); and aggressive, frustrated acts decrease in frequency as tethered sows' stereotypies develop (Cronin 1985). Schizophrenics and amphetamine addicts experience anxiety-reduction and even pleasure when performing stereotypies (Fox 1971; Rylander 1971, cited by Robbins & Sahakian 1981). Adjunctive or displacement activities, too, may be associated with behavioural signs of calming or reduced distress (Duncan & Wood-Gush 1972; Hutchinson 1977).

Again, a problem with such data is the interpretation of correlations. Further investigation of the association between adjunctive polydipsia and lowered corticosteroids, for example, has revealed the hormones to influence the behaviour, rather than the other way around (Mittleman et al. 1988; Levine & Levine 1989). Furthermore, in cases of anxiety-reduction, the effect must be shown to be specific to the stereotypy itself, rather than a general result of increased exercise (see Morgan & Goldston 1987).

More convincing as evidence that stereotypy is a coping response are the results of a study of stereotypic jumping in voles (Kennes & de Rycke 1988; Ödberg 1989). Stereotypy was selectively prevented by lowering the cage ceiling. In all animals this resulted in raised corticosteroid levels. However, the levels were significantly higher and more sustained in stereotypic than non-stereotypic individuals. The three voles that then developed a new form of stereotypy had a significantly accelerated fall to normal corticosteroid levels. In another elegant study, this time of amphetamine-treated rats, the selective pharmacological blocking of the drug-induced stereotypy was associated with a prolonging of the corticosterone elevation also produced by the stimulant (Jones et al. 1989a).

Stereotypy is no panacea, however. Some stressors, such as cold and inescapable electric shock, seem never to be linked with stereotypy (Robbins et al. 1990). Furthermore, stereotypy can be reduced or disrupted by very high arousal (e.g. Hutt & Hutt 1965; Sahakian & Robbins 1975; reviewed by Robbins & Sahakian 1981), and stressors may sometimes depress, rather than potentiate, the stereotypies induced by stimulant drugs (e.g. Cabib et al. 1985). This is a problem for the arousal-reducing hypothesis (Robbins & Sahakian 1983). Nor is stereotypy always accompanied by calming or stress-reduction.

There are several cases where stereotypy does not seem to result in coping. For example, the biting and licking stereotypies of veal calves seem to have no influence on abomasal lesions (Wiepkema et al. 1984, 1987), and chain-manipulation by sows has no influence on the pituitary-adrenal response to an aversive extinction condition (Dantzer & Mormède 1983). Amongst caged bank voles it is the stereotypic rather than the non-stereotypic individuals that seem most fearful, tending to flee on exposure to a loud noise (Ödberg 1987b). Similarly, adjunctive polydipsia is not always associated with lowered corticosteroids (Brett et al. 1982; Jones et al. 1989b), and indeed is associated with raised levels of prolactin (Dantzer et al. 1988). Thus there is no predictable relationship between stereotypy, or its source behaviour patterns, and coping.

The probable reason for the contradictions in the data is that, as will become evident below, stereotypies differ in many ways. The properties of one form of stereotypy are not necessarily those of another. The role of any one stereotypy may also depend on the situation in which it is performed. As

Falk (1971) pointed out for adjunctive behaviour, a form may be maladaptive in one environment, but beneficial in another. Thus it may well be that, in some cases at least, stereotypy does not have consequences that reward the animal.

Unfortunately, evidence that stereotypies have no function needs as much caution in interpretation as data suggesting that they have. For example, the appropriate measures may not have been made, especially if beneficial consequences are evident only in the long-term. Alternatively, it may be that there is some threshold effect. For example, if stereotypy has effects on the animal only if sustained for a certain length of performance, say, this would obscure the apparent relationship between stereotypy and benefit. Two further problems are, first, individual differences in 'starting point' prior to the development of stereotypy, and, second, that stereotypy may be just one of several means of reaching the same steady state.

There are often considerable differences between individuals in the extent to which they will respond to a situation with stereotypy. This is true of infant (Thelen 1979) and institutionalized (Berkson 1967) humans, and a number of farm, zoo and laboratory-housed animals (e.g. Draper & Bernstein 1963; Staddon & Ayres 1975; Palya & Zacny 1980; Wood-Gush et al. 1983; de Jonge et al. 1986; Ödberg 1986). If a stereotypy is a coping response, the extent to which it is performed will be influenced by the extent to which an animal perceives, and is affected by, sub-optimal aspects of the environment (Ödberg 1987a). For example, individuals may differ in their optimal levels of arousal (Kiley-Worthington 1983; Stevenson 1983; Wood-Gush et al. 1983), or in the extent to which they can predict stressors (Dantzer 1989), or in how frustrating they find the captive life (Ödberg 1986, 1987b). Therefore, before assessing the effectiveness of stereotypy as a coping response by comparing individuals, one must take into account the animals' differing sensitivities to the stereotypy's causal factors (Ödberg 1987a, 1989). As Rushen (1984) pointed out, it is not clear whether animals that show no stereotypies, for example, are not coping or are simply not stressed.

To understand the role of stereotypy, one must also realise that individuals may take alternative routes to the same end point. This is the problem of equifinality (Bateson 1976). Therefore, in the case of stereotypy, one must assess the use of alternative coping mechanisms (Broom 1985; Ödberg 1987a,

1989). Candidates for the latter include the pituitary-adrenal system (Dawkins 1980, pp. 62-63; Broom 1987); behavioural 'apathy' (Cronin et al. 1985; Broom 1987); and the performance of other behaviour patterns (Broom 1983) such as polydipsia (Rushen 1984; Cronin et al. 1985; Dantzer et al. 1988). If there is equifinality, stereotypies may be readily replaced by other phenomena in some coping animals. This does not mean that the stereotypy itself has no function.

Immediate Reward and Long-term Benefit

Let us suppose that further research does demonstrate that stereotypy has emotional or physiological consequences that appear to benefit the animal. An important question would still remain at issue: does repeated self-administration of this reward benefit the animal in the long-term? Stereotypy could be of immediate use only, ultimately unimportant or even detrimental to the animal's fitness (Dawkins 1980, page 96; Hinde 1982, page 81).

So far, evidence for an ultimate function is sparse. For example, Cronin (1985) compared tethered sows who showed little stereotypy with those who showed high levels, and found that 'high stereotypy' sows produced significantly larger second and third litters, but smaller fifth and sixth litters. A problem in pursuing this line of investigation is that fitness is generally estimated as the cumulative lifetime reproductive success of an animal (e.g. Trivers 1985). It is not enough to compare animals at just one stage of life, or before the end of their reproductive lifespan. In addition there is more to 'reproductive success' than number of surviving offspring: the fecundity of the next generations should be assessed too. Other problems accompany interpreting the data. For example, a fit and stereotypic animal may be stereotypic because it is fit, rather than the other way round; a poor animal may not have the energy reserves to allow performance of what may be no more than costly 'comfort' behaviour; and again, the effects of exercise in general should be taken into account. In female mink, for example, being lean and muscular improves reproductive success (reviewed by de Jonge et al. 1986).

Conclusion

Stereotypies are defined as being without obvious goal or function, but closer study suggests

that they could be reinforced and that they might be used to ameliorate a sub-optimal environment. However, although intriguing, this evidence is not always strong. Persistence may be explained by processes other than reinforcement, and much of the evidence for coping is based on correlations rather than an understanding of underlying mechanisms. Clearer results might be obtained by accurately recording the relative time-courses of the behaviour and the relevant physiological parameters, and by further experiments in which stereotypy levels are selectively manipulated. Investigation of the factors that predispose individuals to stereotypy may also help in our understanding of this behaviour.

Even if stereotypies are coping mechanisms in the short term, it would remain to be seen whether they are associated with long-term benefit, such as improved fitness. Nor would it mean that we can be complacent about the welfare of stereotypic animals. This is for two reasons. First, the likelihood is that the animal has been in an aversive situation in the past. Second, it remains an open question whether an animal that spends a lot of time in a stereotypy really is better off than one that, say, develops a gastric ulcer (Wiepkema 1987). The animal's welfare, if defined in terms of the amount of coping it is having to do (Broom 1986; Fraser & Broom 1990), could be said still to be poor.

STEREOTYPIES ARE HETEROGENEOUS

So far, I have emphasized the similarities between different forms of stereotypy and discussed them as a group. However, there are two important considerations when discussing the biological significance of stereotypies. First, are stereotypies unambiguously identifiable in practice? And second, are they really equivalent in source of origin, mode of development and potential function? I discuss each of these points in turn.

Identifying Stereotypies

Stereotypies are not, unfortunately, unambiguous to identify. There are two main problems: the morphological criteria used in identifying a stereotypy, and the problem of distinguishing a behaviour pattern with a function from one without.

The first problem is that authors differ as to just how rigid or repetitive a behaviour pattern has to be before they will call it a stereotypy. Because stereotypies become progressively more stereotyped with repetition, speed of performance and arousal, there is no rigid dividing line between what is 'truly' stereotypic and what is not; a continuum exists (for a similar problem see Hinde 1970, page 21; and Dawkins 1986 on 'fixed action patterns').

This continuum is reflected in a range of variations on the basic definition of stereotypy. Dantzer (1986) reserved the term for fixed sequences of behaviour, and Kiley-Worthington (1977) defined stereotypy as 'fixed in all details', a very restrictive definition if by this she means fixed in location and timing as well as morphology. In contrast, Forrester's (1980) stereotypies are not completely inflexible, and Fraser & Broom (Broom 1983; Fraser & Broom 1990) define a stereotypy as being only 'relatively' invariant. Tics and mannerisms are sometimes called 'stereotypies' in human psychiatric literature (reported by Ödberg 1984a), and to confuse the picture further, Berkson and co-workers (1963; Berkson 1967) even described some behaviour patterns, such as abnormal limb-postures and eye-poking, as 'non-repetitive stereotypies'.

A consequence of this confusion is that studies often differ in the ways in which they classify behaviour. There may even be differences within the work of the same authors. Ödberg (1989) pointed out that Dantzer & Mormède (1981, 1983) described chain-chewing as a stereotypy in one paper, and an adjunctive behaviour in another. De Jonge et al. (1986), in their studies of farmed mink, chose to divide repetitive, apparently purposeless locomotion into two categories, only one of which, on the basis of its greater rigidity and persistence, did they call 'stereotypy'. However, when I observed mink I found this classification over simple, excluding complex patterns even when highly predictable. One way around the problem of detecting repetitiveness in complex behaviour, which might otherwise not be classed as stereotyped, is to use informational redundancy to quantify the repetition within behavioural sequences (Stolba et al. 1983).

The morphological criteria used in identifying a 'genuine' stereotypy is not the only problem. The second major problem is that stereotypies are defined as being without obvious function. However, when stereotypies are exaggerated forms of normal behaviour (Kiley-Worthington 1977), it is

difficult to say at what point they stop being adaptive. For example, are the body-rocking and thumb-sucking, shown by normal primates at a certain stage of infancy (Berkson 1967; Thelen 1979), examples of stereotypy? Hutt & Hutt (1965) showed that, when familiar with a new toy, the stereotypy of autistic children would decrease, with a concomitant rise in play. However, as Robbins & Sahakian (1981) point out, the play was not normal; it involved stereotyped, repetitive patterns of movement, and perhaps could have been classified as a stereotypy itself. The close parallels between headshakes in jungle-fowl, *Gallus gallus spadiceus*, and those made by intensively housed hens, along with their possible role in attentional mechanisms, suggest that the behaviour might have a function when shown 'occasionally', but perhaps should be regarded as a stereotypy when shown 'often' (Fraser & Broom 1990). A similar problem was considered by Rushen et al. (1990). They chose not to call post-food rooting a stereotypy, even though repetitive and seemingly unconsummatory, because it closely resembles the normal post-feeding behaviour of free-living pigs. This was even though, in some individuals, the rooting appeared unusually persistent. As they conclude, 'which behaviours to include as "stereotypies" is not a simple issue'.

The Equivalence of Stereotypies

There are many differences between stereotypies. They are heterogeneous in form and rigidity, temporal organization, eliciting stimuli, and degree of variability between individuals. They are also heterogeneous in ontogeny: stereotypies are derived from a range of source behaviour patterns, and probably represent a range of motivational states (Dawkins 1980; Duncan & Dawkins 1983).

In an effort to clarify the situation various attempts have been made to classify stereotypies. Distinctions have been drawn between the following types: (1) deprivation and cage; (2) terminal and interim; (3) abbreviated and non-abbreviated; (4) developing and established; and (5) stimulant-induced and environment-induced.

These schemes overlap, and the distinctions they make between different forms may in some cases be artificial. However, I examine each in some detail. This is partly to discuss the limitations of each scheme, partly to emphasize the many differences between stereotypies, and partly to highlight the features of stereotypies that may be of particular

developmental or functional significance, and hence of particular importance when assessing the equivalence of different forms.

Deprivation and cage stereotypies

Deprivation stereotypies appear in animals that have been socially isolated or subjected to sensory deprivation since birth or infancy (Draper & Bernstein 1963; Berkson 1967; Ridley & Baker 1982). These include institutionalized children (e.g. Mason & Green 1962). They may also appear in animals chronically deprived of the opportunity to perform specific behaviour patterns, for example in buntings prevented from making the intention movements of flight by a low cage ceiling (Andrew 1956, cited in Hinde 1970). They tend to be non-locomotory, and may involve self-mutilation. They are exacerbated by amphetamines (e.g. Berkson & Mason 1964; Fitz-Gerald 1967, cited in Lyon & Robbins 1975). They are very difficult to disrupt (Ridley & Baker 1982), and may persist even when the animal is put into a normal environment (e.g. Davenport & Menzel 1963; Meyer-Holzappel 1968).

Cage stereotypies, in contrast (Draper & Bernstein 1963; Berkson 1967; Ridley & Baker 1982), tend to be locomotory, and are not increased (Ödberg 1984b), indeed are sometimes abolished (Ridley & Baker 1982), by amphetamines. They are typical of small or barren cages, but can be altered by changes in the environment. Ridley & Baker (1982) suggested that they are the response of a normal central nervous system to a sub-optimal environment.

This scheme is not without its problems. For example, the division between deprivation and cage stereotypy is not always clearcut in practice, probably because the effects of caging are more profound on a young than on a mature animal (Berkson 1968), and cage environments are often likely to involve a degree of sensory deprivation. Self-mutilation is not unique to monkeys with a deprived infancy (Erwin & Deni 1979; Ridley & Baker 1982), and other stereotypies that seem to be of the irreversible, 'deprivation' type can be produced in animals that are adult rather than young at the time of treatment, as Andrew's work with buntings (*ibid.*) and Hinde (1958) have shown. Conversely, deprivation stereotypies are not always irreversible; deprived rhesus monkeys have been cured through the use of infant 'therapists' (e.g. Harlow & Suomi 1971), and the stereotypies of

isolation-reared chimpanzees are reduced, at least in the short-term, by the provision of objects to manipulate (Berkson et al. 1963).

Another similarity blurs the division between the two categories: both increase with arousal (Berkson & Mason 1964). For example, both are exhibited in response to a novel environment (Mason & Green 1962; Berkson & Mason 1964) and increase in small cages (Draper & Bernstein 1963). This could suggest some common mechanisms (Berkson 1967).

Finally, the scheme is a little simplistic. Some cage stereotypies are elicited by one aspect of the environment, others by another. For example, Keiper (1969) found some stereotypies in canaries, *Serinus canaria*, to be abolished by enlarging the cage, others by increasing the foraging necessary to obtain food. Similarly, the cage stereotypies produced by a schedule of fixed feeding are of at least two different types (see Terminal and interim stereotypies). Deprivation stereotypies are also heterogeneous. For example, some mental defectives show mainly rhythmic body movements, others, complex hand movements. Both are associated with lowered reactivity to external stimuli. However, in the former, responsiveness is generally higher than in individuals who show no stereotypy; in the latter, responsiveness remains low even when the individual is not actively engaged in the behaviour (Berkson 1967).

Terminal and interim stereotypies

On a regime of periodic feeding, stereotypies develop both as the time of food delivery approaches and during the period after feeding. From their timing within the inter-food interval, these are called 'terminal' and 'interim' stereotypies, respectively (Staddon & Simmelhag 1971).

Interim behaviour is the more idiosyncratic and may represent adjunctive behaviour (Staddon & Simmelhag 1971; Rushen 1984), escape attempts (Staddon & Simmelhag 1971), or be due to disinhibition (Anderson & Shettleworth 1977). Terminal behaviour, in contrast, is subject to little or no individual variation on a given regime, and when the reinforcer is food it appears related to appetitive behaviour (Staddon & Simmelhag 1971; Anderson & Shettleworth 1977). The behaviour's lack of idiosyncrasy, and occurrence even if it reduces the rate of food-delivery by interfering with an operant response, suggests that it is not merely superstitious (Staddon & Simmelhag 1971).

Stereotypy is not only organized in this way in the laboratory. In farmed mink (de Jonge et al. 1986; de Jonge & Carlstead 1987) and some zoo animals (e.g. Ödberg 1984a), pacing reaches a maximum just before feeding. Pigs root (Dantzer & Mormède 1982; Cronin 1985), bar-bite and head-weave (Dantzer & Mormède 1982; Rushen 1984, 1985; Cronin 1985) predominantly in the pre-feeding period, while most of their stereotypy, in the form of sham-chewing (Dantzer & Mormède 1982; Rushen 1984, 1985; Cronin 1985), chain-manipulation (Dantzer & Mormède 1982), drinker-playing and polydipsia (Rushen 1984) peaks after feeding.

There are some problems with this classification, however. Again, not all stereotypies fit readily into one or other class. For example, the interim running behaviour of one intermittently fed rat appeared to have such 'momentum' that its persistence left no time for a terminal response (Staddon & Ayres 1975). Sow drinker-pressing and manipulation (Broom & Potter 1984; Rushen et al. 1990), chain-playing (Rushen 1984; Rushen et al. 1990) and vacuum chewing (Rushen 1984, 1985), and the stereotypies of captive mink (de Jonge et al. 1986) can be shown by animals at all times of day, in both terminal and interim periods. Neither are stereotypies restricted to the interval between intermittent stimuli: some may occur during stimulus presentation, e.g. pigeons pecking during an electric shock (Sterritt 1962, cited in Hinde 1970, page 208); and stereotypies occur in animals that are not on a schedule at all (e.g. Keiper 1969; Ödberg 1986).

Furthermore, one cannot assume that within each category all stereotypies are equivalent. For example, Anderson & Shettleworth (1977) found that when the expected food did not arrive, the various interim patterns of hamsters, *Mesocricetus auratus*, changed in different ways. Similarly, some animals have initial, temporary idiosyncrasies of terminal stereotypy, which then change to the species-typical form (Staddon & Simmelhag 1971), and it could be that these differ from the latter in being superstitious. Also, the terminal patterns seen when the regular stimulus is aversive, e.g. an electric shock (Hutchinson 1977), is presumably not equivalent to those seen during intermittent food reward. Even within schedules using the same reinforcer (food), there are disagreements as to what is represented by the stereotypies. For example, it may be the interim rather than the

terminal stereotypies that develop from appetitive behaviour (Palya & Zacny 1980; Rushen 1984). Rushen (1984, 1985) suggested that, in sows, pre-feeding (terminal) stereotypies represent frustration. Interpretation may depend on the species under study.

Abbreviated and non-abbreviated stereotypies

Some stereotypies closely resemble normal behaviour in form. Examples include pacing (Morris 1964; Broom 1983), and self-sucking in infant primates (Berkson 1967). Other stereotypies differ from their original source behaviour in that they have lost elements of the original action pattern. Such stereotypies are sometimes known as 'incomplete' (van Putten 1982; Broom 1983). The distinction between abbreviated and non-abbreviated forms of stereotypy is discussed for two reasons. First, it has been contended that a behaviour pattern that appears 'complete', i.e. to have an equivalent pattern in the animal's normal behavioural repertoire, should never be called a stereotypy (van Putten 1982), even though invariant and of no apparent function. Second, the process of abbreviation may have functional significance.

Dantzer (1986) suggested that the loss of elements might be responsible for the transition between environment-directed stereotypies, such as bar-biting, and the self-directed stereotypies, such as sham-chewing, more common in older sows. A similar change can be seen in horse stereotypies, crib-chewing sometimes progressing to air-sucking (Fraser 1980). Dantzer attributed no functional significance to this transition, explaining it in terms of repetition and rapidity of performance. Cronin (1985), in contrast, suggested that the frustrations of being restrained, prompt environment-directed stereotypies. He suggested that these are derived from redirected aggressive behaviour, the younger sows, with less experience of tethering, finding restraint the most stressful. Self-directed activities, such as oral stereotypies, are more common when all is quiet on the farm, and in the older, more experienced sows. They may represent some kind of compensatory self-stimulation.

One problem with this classification is that authors can differ in what they consider has an equivalent in the normal behavioural repertoire. For example, Berkson & Mason (1964) considered the rocking and swaying of deprivation-reared

chimpanzees to have no normal equivalent, but Mason & Green (1962) suggested that rocking, especially when accompanied by self-clasping, mimics the way that an infant rocks and rubs up against its mother when distressed. Similarly, self-biting may have an equivalent in play-fighting, stereotypies with the hands may originate in the normal hand movements of infant monkeys, and so on. However, detailed longitudinal studies would be necessary to establish homology reliably (Berkson 1967).

Furthermore, not all stereotypies fit neatly into this scheme. For example, sow stereotypies grow longer with continued restraint, new components being added (Cronin et al. 1984). Similarly, the complexity of mink stereotypies increases with age (de Jonge et al. 1986). In some cases this may be the result of increased maturity and muscular coordination (Bernstein & Mason 1962). Also, a stereotypy may become more, rather than less, environment-directed with age. For example, head-banging may develop in infants who previously had shown head-rolling or body-swaying (Kravitz et al. 1960). Nor is abbreviation exclusively the side-effect of long-term repetition; a stereotypy may also simplify if causal factors are less intense. For example, the somersaulting of one rhesus monkey was reduced to mere hints in a larger cage (Draper & Bernstein 1963).

Developing and established stereotypies

There are qualitative differences between developing and established stereotypies in the following respects: in the apparent emotional, motivational correlates of the behaviour; in the neural substrates involved; in the fixity of performance; and in the degree to which the stereotypies are emancipated from their original eliciting stimuli (Duncan & Wood-Gush 1974; Kiley-Worthington 1977; Ödberg 1978).

Developing stereotypies are inhibited by tranquillizers (Feldman & Green 1967; Duncan & Wood-Gush 1974), which could suggest that their elicitation depends on emotional, limbic systems (e.g. reported by Kennes & Ödberg 1987; Ödberg 1989). Tranquillizers had no effect on these stereotypies once fully established (Feldman & Green 1967; Duncan & Wood-Gush 1974), leading to suggestions that established stereotypies are emotionally neutral (e.g. Duncan & Wood-Gush 1974), 'pure motor automatisms' (Kennes &

Ödberg 1987; Ödberg 1989). Kennes et al. (1988) found that the opiate receptor antagonist naloxone did not inhibit stereotypies in bank voles over a certain age. Cronin et al. (1985, 1986b) have also found an inverse relationship between age of stereotypy and the latency with which it was suppressed by naloxone, in sows. It has been hypothesized that stereotypies depend on brain opioids in their early stages (e.g. Kennes et al. 1988). Established stereotypies, however, seem to be essentially under dopaminergic control (Cronin et al. 1985; Kennes et al. 1988).

Established stereotypies also differ from developing ones in being much more difficult to discourage or interrupt (Kiley-Worthington 1977; Cronin et al. 1984). For example, once firmly established, the pacing shown by food-deprived hens faced with a covered food-dish does not disappear even when food is made available (Duncan & Wood-Gush 1972). Established stereotypies may even be facilitated by stimuli that would have interrupted them earlier in their development (Fentress 1977). Furthermore, they are performed outside the original eliciting situation (Ödberg 1978), sometimes even in the absence of any apparent conflict (Kennes et al. 1988).

It is unclear whether the changes involved in this transition occur synchronously (Kennes et al. 1988). It is possible that the change in emotional involvement does not coincide with emancipation: Cronin et al. (1984, 1985) described the post-feeding stereotypies of tethered sows as changing from short bursts of apparently aggressive activity to prolonged bouts of much less aggressive behaviour. Only if restraint continued did this behaviour come to be performed at all times of day. Nor is it clear exactly how this categorization overlaps with the schemes classifying stereotypy as complete/incomplete, or abbreviated/non-abbreviated. Also, note that one individual may perform both developing and established forms of stereotypy. For example, Dodman et al. (1987) found that opiate receptor antagonists abolished crib-chewing in horses, but did not affect their weaving.

Although probably a spectrum rather than a dichotomy, it would appear that the distinction between developing and established stereotypies is valid and important, and might help to explain why different studies sometimes yield contradictory results. For example, the emancipation of stereotypy from its original post-meal context, as described by Cronin et al. (1984, 1985), would

account for the failure of some stereotypies to fit neatly into the terminal/interim classification, and perhaps for the differences in how authors describe the distribution of, for example, drinker-manipulation by sows (see Terminal and interim stereotypies). Kiley-Worthington (1977) suggested that the developmental change in the nature of a stereotypy explains the discrepancy between the results of Levy (1944) and Hutt & Hutt (1965). Environmental complexity, in the former study, increased the stereotypy shown by autistic children, while in the latter study, it decreased performance in children whose stereotypies were not so well established. The difference between developing and fully developed stereotypies may also explain the confusing relationship between stereotypy and litter size in sows of different ages (Cronin 1985); why Cronin (1985) found that, in contrast to the results of Wood-Gush et al. (1983), sows with high levels of stereotypy were more attentive to external stimuli and faster to react than sows with low levels; and why barbiturates reduced the deprivation stereotypies of chimpanzees in one study (Fitz-Gerald 1964, cited in Berkson 1967), but not those of mentally handicapped humans in another (Berkson 1967).

Stimulant-induced and environment-induced stereotypies

Stereotypies are induced by psychomotor stimulant drugs such as amphetamine and apomorphine (Lyon & Robbins 1975; Robbins & Sahakian 1981). The stereotypy develops from behaviour that was predominant prior to treatment, for example from eating in hungry animals (Ellinwood & Kilbey 1975; Robbins 1982; Dantzer 1986; reviewed by Robbins et al. 1990). It is usually idiosyncratic (e.g. Sahakian & Robbins 1975) and an individual's characteristic stereotypy will be shown on successive amphetamine trials even if these are months apart (Lyon & Robbins 1975). Locomotor activity also increases on treatment with a stimulant, and this is also stereotyped in a sense, the animal following a limited number of fixed routes (Robbins & Sahakian 1981). There is also a corresponding stereotypy of routine and thought similar to that of schizophrenics (Robbins 1976; Robbins & Sahakian 1981; Ridley & Baker 1982). There is some disagreement as to what the drug-induced stereotypies represent. As already mentioned, some believe they are the functionless side-effects of over-

stimulation (Lyon & Robbins 1975; Robbins 1982), while others present evidence that they are associated with coping (Jones et al. 1989a).

Stereotypy becomes more intense with increasing doses of stimulant (e.g. Lyon & Robbins 1975), and with repetition of the treatment, the animal becoming sensitized to the drug (e.g. Robbins & Sahakian 1981). As the stereotypy intensifies, the movements become more and more dissociated from their original context, in timing and in orientation (Robbins 1976, 1982; Robbins & Sahakian 1981). Rate of repetition increases, the movements become increasingly abbreviated, and the stereotypy becomes species-typical instead of idiosyncratic (e.g. as reviewed by Lyon & Robbins 1975). It typically involves oro-facial movements, or isolated limbs (e.g. Robbins & Sahakian 1981), but at extreme doses the animal can do little more than twitch.

This transition perhaps parallels the simplification seen during the development of other forms of stereotyped behaviour (Dantzer 1986). Drug-induced behaviour has further similarities with environment-induced stereotypy. For example, it seems very compulsive and will persist even when punished (Lyon & Robbins 1975; Robbins & Sahakian 1981). Robbins & Sahakian (1981) suggested that the subject may have restricted attention. Dopaminergic systems are involved (Robbins & Sahakian 1981), as they are in some environment stereotypies (Ödberg 1984b; Kennes et al. 1988). In addition, the involvement of opioids in some cases (opiate receptor antagonists block the stereotyped gnawing produced by apomorphine, although they appear to have no effect on amphetamine stereotypies; Robbins & Sahakian 1981) parallels the involvement of opioids in some environment-induced stereotypies. A further similarity between drug- and environment-induced stereotypies is the effect of stress, which often potentiates the behaviour.

In general, stressors sensitize animals to the stereotypy-inducing effects of stimulants (as reviewed above) and seem to interact with the drug in an additive way (Robbins et al. 1990). The stimulants may be acting as stressors themselves (e.g. Mittleman et al. 1986). In some cases stressful treatments do not enhance the development of stereotypy, and may even inhibit or disrupt it (Sahakian & Robbins 1975; and e.g. Lyon & Randrup 1972, cited in Robbins & Sahakian 1981; and Cabib et al. 1985). This may be similar to the way in which very

intense stimuli can interfere with environment-induced stereotypy (Fentress 1977; Robbins & Sahakian 1981).

The involvement of isolated limbs is further reminiscent of the deprivation type of environment-induced stereotypy. Stimulant drugs may even increase the performance of an animal's existing deprivation stereotypies (e.g. Berkson & Mason 1964; Fitz-Gerald 1967, cited in Lyon & Robbins 1975), as discussed earlier. However, other, cage-type, forms of environment-induced stereotypy are not enhanced by the administration of stimulants (e.g. Ödberg 1984b).

A final important point is that, like stereotypies induced by the environment, stimulant-stereotypies are a heterogeneous group. Different drugs result in stereotypies that differ in typical appearance (reviewed by Robbins & Sahakian 1981), response to a dose increase (Fray et al. 1980), and the way in which they are affected by, for example, food-deprivation (see e.g. MacLennan & Maier 1983). They may also involve opioid systems to different extents (see Robbins & Sahakian 1981). Furthermore, the various stereotypies elicited by increased or repeated dosage of one drug show different patterns of sensitization (Eichler et al. 1980), and may, as they change from complex to more simple forms, have different neurophysiological bases (reviewed by Robbins & Sahakian 1981, 1983; see also Mittleman et al. 1986).

Conclusion

Stereotypy is not a category with a clearly defined border: the stereotypies described by some authors may be classed differently by others. Nor does the term apply to a group of behaviour patterns that are homogeneous: there are many differences between the various forms of stereotypy. Their stereotyped nature would not seem reason enough for assuming genuine equivalence, since a shared repetitive rigidity in no way implies that the behaviour patterns also share a common cause, goal or function; nor does the other characteristic of stereotypies, their lack of apparent function, for it is hardly biologically meaningful to group things on the basis of what we do not know about them.

GENERAL CONCLUSIONS

Stereotypies have some linking characteristics, but they differ in many others. Furthermore, their common features may be trivial. It is therefore not

reasonable to assume that all stereotypies are homogeneous. This should be taken into account when discussing their welfare implications or functional significance. Arousal reduction, say, or lowered responsiveness, could be associated with one stereotypy but not with another, even within the same individual (Lovaas et al. 1971; Cronin & Wiepkema 1984; Ödberg 1987), and a behaviour pattern might have a function in one context (Falk 1971), or at one stage of development (see Dantzer 1989, on adjunctive polydipsia), but not in another.

Because of this heterogeneity, care must be taken not to extrapolate without reason from one animal or from one situation to another. However, each stereotypy is not a unique, isolated case; some generalizations from one case to another are probably valid, if the stereotypies are equivalent in source behaviour pattern, current timing and age, and similar in current morphology. For example, the pre-feeding stereotypy of one carnivore species is probably homologous with that of another. A behaviour pattern classed as a stereotypy should always be clearly, ostensibly, and perhaps quantitatively (see Stolba et al. 1983) defined to avoid confusion, and some features of the stereotypy in question, such as whether or not it is emancipated from its original context, should always be recorded so that one can assess more reliably with which other examples it is comparable.

Together, stereotypies raise some fascinating questions. They are interesting for what they may reveal about motivation and the organization of behaviour (e.g. Fentress 1976; Rushen et al. 1990); they may shed light on human psychological disorders such as schizophrenia and neurosis (e.g. Hinde 1962; Wolpe 1967; Robbins 1976; Ridley & Baker 1982); and they may reveal fundamental differences between individuals in terms of dopamine systems, general tendencies to persist with behaviour, and styles of coping with adversity (e.g. Mittleman et al. 1986; Dantzer 1989). Furthermore, it is essential to understand stereotypies if we are to improve practices of husbandry in ways that abolish the causes, and not just the symptoms (Ödberg 1978; Ridley & Baker 1982; Dantzer 1990; cf. Dodman et al. 1987) of central nervous system dysfunction or poor welfare.

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