Chapter 2

MECHANISMS INVOLVED IN THE DEVELOPMENT AND CONTROL OF STEREOTYPIES

Georgia J. Mason
Sub-department of Animal Behaviour
Madingley, Cambridge CB3 8AA
England

Michelle A. Turner
Department of Experimental Psychology
Downing Site, Cambridge CB2 3EB
England

I. ABSTRACT

Stereotypies are unvarying, repetitive behavior patterns that have no obvious function, and that are often performed by animals in captivity. They are a heterogeneous group of behavior patterns, differing in ways that suggest that their underlying mechanisms are very different. The development and control of normal behavior, together with the processes involved in the abnormal behavior seen in some psychological conditions, suggest a number of possible mechanisms that could give rise to stereotypies, some causing the behavior pattern to be repeated even when its performance would seem inappropriate, and others causing the movements involved to be very similar from one occasion to the next. We suggest that investigating the mechanisms behind stereotypies would help the construction of valid classification schemes for these behavior patterns, and increase the understanding of why stereotypies differ so much in such features as their sensitivity to environmental change and their consequences for the animal that performs them.

II. INTRODUCTION TO STEREOTYPIES

Many animals in captivity perform stereotypies, examples of which include the pacing of polar bears in zoos (e.g., Meyer-Holzapfel, 1968), the jumping of caged voles (Fentress, 1977; Öderberg, 1986), and the head-weaving of stabled horses (e.g., Kiley-Worthington, 1983). These remarkable behavior patterns have three defining characteristics: they are unvarying, repetitive, and have no apparent function or endpoint (e.g., Fox, 1965; Öderberg, 1978; Wiepkema et al., 1983). Stereotypies are unvarying in that they involve movements with a form that is highly predictable from one performance to the next. In addition, bouts of stereotypy may also be predictable in their timing and in where they are performed (reviewed by Mason, 1991a). Stereotypies are repetitive in that movements are repeated over and over again, in a more-or-less rhythmic manner within a bout. As for their function, why an animal should indulge in what are often prolonged bouts of energetic activity remains obscure. To illustrate, a stereotypy that develops in a bird from attempts to escape from a cage will persist even when the animal no longer seems frightened (Hinde, 1970, p. 556)—and for long after it must have learned that escape is impossible. Such persistence is particularly difficult to explain when the behavior involves obvious costs, such as self-damage (e.g., Morris, 1964).

Their defining characteristics are thus puzzling for the ethologist. Stereotypies are also interesting to applied ethologists who want to improve the welfare of animals housed in captivity, for they are often associated with what seem to be inadequate environments (e.g., Broom, 1983; Wiepkema et al., 1983; Mason, 1991a). Unfortunately, a unitary explanation for stereotypies has not emerged; the causes and correlates of the behavior differ from one example to the next. For instance, they are not restricted to captive animals; some are evident in free-living humans. In this chapter we shall discuss the variety of mechanisms that might underlie this heterogeneity.

III. THE HETEROGENEITY OF STEREOTYPIES

Stereotypies differ in ways that suggest that their causes, their neurological bases, and their significance as welfare indicators are all very different. For example, some stereotypies are abolished by naloxone, the opioid receptor antagonist, while others are not (Cronin et al., 1985, 1986; Dodman et al., 1987; Kennes et al., 1988). Some stereotypies are seen in cases where it is difficult to imagine a welfare problem, as exemplified by small children who, just before they fall asleep, perform rhythmic banging movements of their heads on the pillow (A. Chamove, personal communication). Stereotypies differ in how often the movements are performed; some are performed very frequently, even if the animal’s circumstances are quite barren or frustrating conditions, and others are performed less frequently. For example, pacing stereotypies developed in very small, barren enclosures (Meyer-Holzapfel, 1968) and intensively housed animals around the time of feeding (Wechsler, 1991); yet Stevenson (1983, 1985) showed whenever it made a turning movement, not even if the animal’s circumstances are quite barren or frustrating conditions, and others are performed less frequently.

Stereotypies differ in how often they may be short or long, and involve few movements or many movements. For example, the stereotypic head tossing of amphetamine addicts report reduced anxiety and self-damage (Fox, 1971; Rylander, 1971, cited in Mason, 1991a). Of these stereotypies, some are seen in free-living horses (Kiley-Worthington, 1983), while others are not. For example, head-weaving of stabled horses is associated with the size of their adrenal gland, and stereotypic tongue playing by veal calves is associated with the size of their adrenal gland. Stereotypies of these same veal calves have been linked with the size of their stomach ulceration; and stereotypy level correlates with their relative adrenal size (Mason, 1991a).

Stereotypies also differ in the extent to which the bouts then disappear if they are moved from a barren or frustrating conditions, and others are not. For example, head-weaving of stabled horses is associated with the size of their adrenal gland, and stereotypic tongue playing by veal calves is associated with the size of their adrenal gland. Stereotypies of these same veal calves have been linked with the size of their stomach ulceration; and stereotypy level correlates with their relative adrenal size (Mason, 1991a). Some stereotypies are so obvious that the environment be altered. For example, the stereotypic head tossing of amphetamine addicts report reduced anxiety and self-damage (Fox, 1971); yet Stevenson (1983, 1985) showed whenever it made a turning movement, not even if the animal’s circumstances are quite barren or frustrating conditions, and others are performed less frequently.

The extent to which the bouts then disappear if they are moved from a barren or frustrating conditions, and others are not. For example, head-weaving of stabled horses is associated with the size of their adrenal gland, and stereotypic tongue playing by veal calves is associated with the size of their adrenal gland. Stereotypies of these same veal calves have been linked with the size of their stomach ulceration; and stereotypy level correlates with their relative adrenal size (Mason, 1991a). Some stereotypies are so obvious that the environment be altered. For example, the stereotypic head tossing of amphetamine addicts report reduced anxiety and self-damage (Fox, 1971); yet Stevenson (1983, 1985) showed whenever it made a turning movement, not even if the animal’s circumstances are quite barren or frustrating conditions, and others are performed less frequently.

The extent to which the bouts then disappear if they are moved from a barren or frustrating conditions, and others are not. For example, head-weaving of stabled horses is associated with the size of their adrenal gland, and stereotypic tongue playing by veal calves is associated with the size of their adrenal gland. Stereotypies of these same veal calves have been linked with the size of their stomach ulceration; and stereotypy level correlates with their relative adrenal size (Mason, 1991a). Some stereotypies are so obvious that the environment be altered. For example, the stereotypic head tossing of amphetamine addicts report reduced anxiety and self-damage (Fox, 1971); yet Stevenson (1983, 1985) showed whenever it made a turning movement, not even if the animal’s circumstances are quite barren or frustrating conditions, and others are performed less frequently.
Mechanisms Involved in Stereotypies

pillow (A. Chamove, personal communication). Other forms, however, occur in barren or frustrating conditions, and at times of stress or fear (see Mason, 1991a). Of these stereotypies, some are associated with signs of reduced stress, while others are not. For example, head flicking in caged hens negatively correlates with the size of their adrenal glands (Bareham, 1972); schizophrenics and amphetamine addicts report reduced anxiety when performing their stereotypies (Fox, 1971; Rylander, 1971, cited in Robbins and Sahakian 1981); and stereotypic tongue playing by veal calves is associated with reduced severity of stomach lesions (Wiepkema et al., 1984, 1987). In contrast, the biting and licking stereotypies of these same veal calves have no relationship with their degree of stomach ulceration; and stereotypy levels in young caged mink positively correlate with their relative adrenal size (Mason, 1992).

Stereotypies also differ in the extent to which they meet the defining criteria. For one thing, stereotypies differ in just how unvarying they are. Some movements are performed in exactly the same way on each occasion, while other stereotypies, such as the oral sequences of stall-housed sows, are more variable (Cronin, 1985). Some stereotypies are so fixed in form that they remain unaltered even if the animal's circumstances are changed. For example, polar bears with pacing stereotypies developed in very small enclosures have been seen continuing to perform these movements, not even changing the number of paces, when rehoused in a far bigger enclosure (Meyer-Holzapfel, 1968). In contrast, other stereotypies change in form or orientation, and may even disappear altogether, should the environment be altered. For example, the stereotypies of young voles disappear if they are moved from a barren to an enriched environment (Cooper and Odberg, 1991).

Stereotypies differ in how often they are repeated, too. Bouts of stereotypy may be short or long, and involve few or many repetitions of a movement. In some cases, stereotypic movements may even occur singly, rather than in a series; for example, the stereotypic head-swing of a caged dingo came to be shown whenever it made a turning movement in the course of moving about its enclosure (Fox, 1971). To some extent the degree of repetition within a bout depends on how easy the behavior is to interrupt. For some stereotypies, this is very easy; for others, far more difficult. One pacing polar bear has been seen to break off from stereotyped pacing when a visitor dropped a leaf into its moat (Wechsler, 1991); yet Stevenson (1983) has described other pacing animals as being quite oblivious to potentially interrupting stimuli.

The extent to which the bouts themselves are repeated also differs between stereotypies. Some stereotypies may be returned to many times in a day, in a variety of different circumstances. For example, stabled horses (Meyer-Holzapfel, 1968) and intensively housed pigs (Cronin, 1985) perform stereotypies around the time of feeding and if they are alarmed, but also often just before they urinate or defecate. Other stereotypies are much more limited in the
circumstances in which they are performed. For instance the repetitive vomiting of a female sloth bear was shown exclusively when her male cagemate was monopolizing the food bowl (Meyer-Holzapfel, 1968). An individual’s stereotypies may be performed many times over years; Stone (1964) describes blind children with learning difficulties as showing the same stereotypies at the age of 15 as they did 13 years earlier. Alternatively, stereotypies may be transient. For example, some rocking movements are shown by normal children only at certain stages of their development (Berkson, 1967; Thelen, 1979). Stereotypies may even be one-off occurrences; consider the pacing of a fox caught in a box trap (White et al., 1991) or an expectant father in a hospital waiting room.

This highlights the problem of identifying whether or not something is a stereotypy, and the heterogeneous nature of the behavior patterns that are classified as such. That stereotypies are “rigid” and “repetitive” in such different ways, and to such different extents, suggests that the various mechanisms that underlie the development and control of these characteristics could be very different. Furthermore, as stereotypies may in practice be highly repetitive yet quite variable, or conversely, extremely unvarying yet repeated only infrequently, the mechanisms that are involved in these two aspects of the behavior may well be different, in any one example. The processes that could account for repetition and those that could account for low variability therefore need to be considered separately.

In this chapter, we investigate a range of possible mechanisms by which behavior patterns may be repeated again and again, despite their lack of any obvious benefit to the performer. We draw here on two main areas of research: first, ethological studies of the control and development of normal behavior patterns, such as displaying and territory patrolling; and second, psychologists’ studies of stereotypies and similar behavior in humans and experimentally manipulated animals.

IV. MECHANISMS THAT COULD UNDERLIE STEREOTYPIES

This section is organized in two parts. First, we consider the means by which certain behavior patterns may be repeated again and again, despite their lack of any obvious function. In the second section we consider the possible mechanisms behind the other diagnostic feature of stereotypies, their similarity from one occasion to the next.

Within each section, mechanisms are grouped according to their role in the control of behavior. These mechanisms act at a number of levels, from “high level,” that is, involving ideas, representations, memory, cognition, etc., to “lower level,” based on the stimulus–response-type nature of some motor systems. The lists of mechanisms below are not presented in any logical order; this may seem long and tortuous reading when we are trying to make a simple point. Instead, we have given a few examples for each mechanism described, using ethological or psychological evidence to illustrate the role of each mechanism in stereotypies in a particular species.

A. Factors that Could Result in Repetition

Several mechanisms will cause the recurrence of an activity in the absence of any obvious benefit. Some of these forms of stereotypy have been described by psychologists as perseverative. Perseveration involves the recurrence of an activity in the absence of any obvious benefit. It is sometimes seen in small animals (Sandson and Albert, 1984), sometimes in larger animals (Frith and Done, 1990), and sometimes in humans (Frith and Done, 1990). The two descriptions overlap, and indeed perseveration would probably be a case for many captive animals, or if the movements were repeatedly exposed to the same individual (as it is the case for many captive animals), or if the movements predominated for a long period of time. Movement or other forms of repetition may increase the regularity of the behavior, or increase the series of movements both. Some of these mechanisms may also apply to behavior patterns that are “executed blindly according to sequences or appropriateness” (Legge and Emery, 1989).

1. Repeated Initiation by External Stimuli

Aspects of the external environment may influence the behavior pattern, in the way that the eyes are used to mobbing behavior by small birds, for example. Sensory inputs that constantly expose animals to repetitive forms of stereotypies. One such case is the zebra dove (Geopelia striata) that developed a paw-raising stereotypy when it was presented with a brightly colored object. This movement was recognizable part of the animal’s repertoire. A second example also comes from a zebra dove. If the dove was given additional scent-marking stereotypy. In the wild, this involves locomotion into the confines of a cage, however, time and time again, and so it marked the area.

A number of factors could increase the
Mechanisms Involved in Stereotypies

A. Factors that Could Result in Repetition

Several mechanisms will cause the recurrence of a behavior pattern that has no obvious benefit. Some of these forms of inappropriate repetition are described by psychologists as perseverative. Perseveration is defined as the continuation or recurrence of an activity in the absence of the appropriate stimulus or reward (Sandson and Albert, 1984), sometimes in spite of the subject’s efforts to produce a new movement (Frith and Done, 1990). Perseveration differs from stereotypy in that it involves the repetition of a recent movement, in an almost echolike manner; it is thus transient, and dependent on the initial eliciting stimuli (Frith and Done, 1990). The two descriptive terms, however, undoubtedly overlap, and indeed perseveration would produce stereotypy like behavior if the subject were repeatedly exposed to the same initial eliciting stimulus (as may be the case for many captive animals), or if the memory of the original behavior pattern predominated for a long period of time. Mechanisms that act to cause perseveration or other forms of repetition may increase the frequency of initiation of bouts of the behavior, or increase the series of repetitions made within each bout, or both. Some of these mechanisms may also be involved in habits, normal behavior patterns that are “executed blindly and without reference to their consequences or appropriateness” (Legge and Barker, 1976, p. 12).

1. Repeated Initiation by External Stimuli

Aspects of the external environment may repeatedly elicit or release a behavior pattern, in the way that the eyes and speckled coloration of an owl elicit mobbing behavior by small birds, for example (Hinde, 1982, p. 35). Environments that constantly expose animals to releasers may be responsible for some forms of stereotypies. One such case is that of a male okapi in a zoo, which developed a paw-raising stereotypy when housed next to an inaccessible female. This movement was recognizably part of the courtship sequence (Odberg, 1978). A second example also comes from a zoo, where a pine marten developed a scent-marking stereotypy. In the wild, this species would re-mark old traces of its anal scent. In the confines of a cage, however, the animal came across old traces time and time again, and so it marked them repeatedly (Hediger, 1964, p. 75).

A number of factors could increase the tendency of external stimuli to elicit
a particular behavior pattern. For instance, the environment may be such that few other demands are made on the organism, allowing repeated expression of what would otherwise be low-priority behavior (Hinde, 1962; Duncan and Wood-Gush, 1974, interpreting the data of Keiper, 1970). High motivation could also result in an increased tendency for a behavior pattern to be elicited (Rushen et al., in press). In addition, practice and repetition of a movement can increase the ease with which it is elicited, if this increases central control (e.g., Fentress, 1976). Central control, or what psychologists term closed or closed-loop control (Martiniuk, 1976, p. 15), is where the organization of a behavior pattern comes from within the central nervous system (CNS), which issues a precise set of commands. Peripheral factors such as feedback are relatively unimportant (Hinde, 1970, p. 26). (Central control is discussed in more detail in Section B).

Learned behavior patterns may also become more readily elicited with experience in that they come to need fewer of their original external cues to be initiated (Bindra, 1959, cited in Hinde, 1970, p. 557). Frequent elicitation of behavior by external factors can also sometimes be explained by a specific alteration in brain functioning. This effect has been demonstrated in subjects with damage to the frontal cortex and with disrupted functioning of the basal ganglia.

The basal ganglia are the motor initiation centers of the brain. As Dantzer (1986) summarizes, dopamine in the nigrostriatal pathways modulates the system’s sensitivity to input and thus plays a key role in the initiation of movements. A decline in dopamine in the basal ganglia is responsible for Parkinson’s disease, a disabling condition in which sufferers find it difficult to begin or end any movement, no matter how great their will to do so (e.g., Sacks, 1990, p. 7). In contrast, activation of this system increases an individual’s responsiveness to sensory stimulation (Fentress, 1976, reporting Ungerstedt, 1974), making behavior more likely to be elicited by external factors. Enhanced activity of these dopaminergic systems underlies a number of forms of stereotypy and stereotypylike behavior.

Overactive initiation centers have been implicated in a number of examples of stereotypy, for example, those seen in subjects dosed with stimulant drugs such as amphetamine. Amphetamine increases the effect of forebrain dopamine systems on the basal ganglia (Lyon and Robbins, 1975; Robbins and Sahakian, 1983; Robbins et al., 1989, 1990). The stereotypy produced seems to result from the increased rate of induction of activities. Thus behavior that was predominant before treatment, for example, eating in hungry animals, is repeated at low levels of amphetamine (Ellinwood and Kilbey, 1975), while at higher doses simpler movements that are easier to repeat rapidly become more frequent. In rats, these are usually head and mouth movements (Lyon and Robbins, 1975).

Luria (1965) implicated the basal ganglia in some stereotypylike behavior. Patients with injury to the frontal lobes that also extended to the basal ganglia showed a form of perseveration in which a movement, once performed, would be immediately initiated again and again (experiments). Thus, a patient, once started, might continue for hours. An example. Such behavior suggests that the basal ganglia.

Frontal damage alone will also lead to stereotypy. The frontal cortex of the brain is involved in preceptive, anticipatory behavior (e.g., Soares and Pereira, 1980). Overactive impulses, reactive influence of frontal lobes are damaged, the absence of an anticipatory stereotype response to external stimuli. Patients with damage to the frontal cortex will show a stereotypylike response even when the ensuing behavior is internally driven. A patient will put things back into a pair of glasses, the patient will put them back again with a second pair, the subject will never get it right (Lhermitte, 1983, in Frith and Done, 1991) — a feature that differentiates them from other tendencies or stereotypies.

So what role do the basal ganglia play in intact and unmanipulated brains? Stressed animals show increased dopamine activity in the nigrostriatal pathway (Dantzer, 1989; Jones et al., 1989), and show higher basal and striatal dopamine levels after amphetamine (Robbins et al., 1989, 1990). Isolation-reared animals show similar increases in stereotypy levels in response to external stimuli (Robbins et al., 1989).

Dopaminergic, striatal systems seem to be at least partly responsible for stereotypies so typical of isolation-reared animals (e.g., Berkson, 1964). Isolation-reared animals, at least in part due to altered motivation, are certainly evidence that dopamine is involved. In caged animals, haloperidol, a dopamine antagonist, and its metabolite, increase basal ganglia dopamine activity in voles (Kennes et al., 1985; Mittleman et al., 1986; Robbins et al., 1989). Isolation-reared animals show increased stereotypy levels in response to external stimuli (Kennes et al., 1985; Mittleman et al., 1986; Robbins et al., 1989).
Mechanisms Involved in Stereotypies

immediately initiated again and again (especially the initial parts of these movements). Thus, a patient, once started, might be unable to stop drawing circles, for example. Such behavior suggests that the damage had a disinhibiting effect on the basal ganglia.

Frontal damage alone will also lead to the inappropriate repetition of behavior. The frontal cortex of the brain is involved in planning and forming sequences of preemptive, anticipatory behavior (e.g., Luria, 1973, pp. 89–90). It thus often overrides the impulsive, reactive influence of the basal ganglia. However, if the frontal lobes are damaged, the absence of their inhibitory role is often manifest in a stereotypylike response to external stimuli. This is evident in the way that patients with damage to the frontal cortex seem unable to resist responding to stimuli even when the ensuing behavior is quite inappropriate. If presented with a pair of glasses, the patient will put them on, as if compelled to do so. Presented with a second pair, the subject will unhesitatingly put these on, too, on top of the first (Lhermitte, 1983, in Frith and Done, 1990). In some cases frontal lobe damage results in stereotypylike behavior. For example, a dog may constantly, without purpose, shift between two bowls of food (Luria, 1973, pp. 89–90). The inability of these subjects to suppress inappropriate responses means that they are also, paradoxically, very easily distracted (Stuss and Benson, 1984; Robbins, 1991)—a feature that distinguishes them from other subjects with perseverative tendencies or stereotypies.

So what role do the basal ganglia play in the stereotypies of animals with intact and unmanipulated brains? Stressed and isolation-reared animals have high dopamine activity in the nigrostriatal pathways (Robbins and Sahakian, 1981; Dantzer, 1989; Jones et al., 1989), and show enhanced striatal rises in dopamine and greater stereotypy levels after amphetamine (Sahakian et al., 1979, in Robbins et al., 1989, 1990). Isolation-reared rats also have an enhanced reactivity to external stimuli (Robbins et al., 1989). It is thus tempting to speculate that the stereotypies so typical of isolation-reared animals, such as the body-rocking of isolated primates (e.g., Berkson, 1967), and those of animals exposed to stressors, are at least in part due to altered functioning of the basal ganglia. There is certainly evidence that dopamine is involved in some of the stereotypies of caged animals. Haloperidol, a dopamine antagonist, reduces the stereotypy levels of captive voles, and to a greater extent the older the animal. Thus dopaminergic, striatal systems seem to be involved in the more well-established stereotypies of voles (Kennes et al., 1988).

Other experiments could be performed to investigate this hypothesis. Individual laboratory rats with naturally high activity in certain dopamine pathways to the basal ganglia are predisposed to the development of tail-pinches induced oral behavior patterns, behavior evoked by electrical stimulation of the lateral hypothalamus, and schedule-induced behavior (e.g., Mittleman and Valenstein, 1985; Mittleman et al., 1986; Robbins et al., 1990). Schedule-induced behavior is seen
when an animal is put onto a regimen of food delivery where very small amounts of food are delivered at frequent intervals, and it includes excessive drinking. It resembles stereotypies in a number of ways, typically being rather unvarying in form, and seemingly unaffected by the factors that would normally control it [e.g., rats will drink bitter quinine (Roper, 1983)]. It would be interesting to see if the farm or zoo animals that develop stereotypies are also particularly prone to these forms of experimentally induced dopamine-related behavior.

The dopamine systems of the basal ganglia, however, do not seem important for other stereotypies. In the experiments of Kennes et al. (1988), the stereotypies of the youngest voles were not significantly affected by treatment with the dopamine antagonist. A dopamine agonist does not increase the stereotypy levels of caged voles (Ödberg, 1984a). Likewise, the dopamine agonists amphetamine and apomorphine will not elicit the stereotypic chain-chewing and head-weeping previously developed by pigs in their captive environment (Terlouw et al., in press).

2. Reduced Specificity of Eliciting Stimuli

Behavior may be performed more often and in more inappropriate contexts if it comes to be elicited by a wider range of stimuli or situations. In humans, behavior patterns may also become divorced from their usual contexts if they are repeatedly elicited by recurring thoughts, rather than by specific external stimuli. For example, subjects with obsessive–compulsive disorders feel themselves compelled to perform particular actions, such as hand washing.

Behavior patterns that recur because of repetitive ideas are heterogeneous in a way that would not be evident in animals. For example, subjects with obsessive–compulsive disorder feel, along with the sense of compulsion, an awareness of the pointlessness of the behavior, and hence, fear or embarrassment. Moreover, the idea that they should try and resist performing it (Rachman, 1985). In other cases, however, compulsions have a delusional basis, the subject feeling that outside causes, such as God, or genuine contamination on their hands, are responsible for the behavior. Such behavior may resemble a stereotypy in appearance; for example, one schizophrenic patient repeatedly touched his ear in the belief that doing so made his blood pump round (Jones, 1965). The cognitive correlates of the behavior patterns initiated for these different reasons are quite distinctive and distinguish from stereotypies resulting from organic dysfunction (Rachman, 1985); yet in animals the different cognitions would be inaccessible, and manifestations of such behavior would therefore all be classed simply as stereotypies.

The tendency of the external environment to elicit behavior can also be increased in a number of ways. In both humans and animals, practice may increase the ease with which a behavior pattern can be elicited, as discussed in Section IV-A-1), and to the extent that an increase of stimulus effectiveness in elicitation. This will occur if the subject's behavior is under central control (Hinde, 1970, p. 26; Fentress, 1971) and they are not then able to invoke to explain a similar phenomenon, a "Copernican slip." In some situations a familiar, habitual activity not related to the accident, if the context seems superficially related, can be performed. Thus a wide range of stimuli can elicit the same stereotypies, and these patterns have to have been so common in the animal's past, that is, sensorimotor organized.

To what extent might these processes influence behavior in captive animals? Some stereotypies can be thought of as parts of the animal's normal behavior, separate from the original eliciting situation. For example, the stereotypy being well established rather than being performed in the animal's environment (Mason, 1991a,b). In some cases the increase in behavior may also be because the animal is responding to a wider range of stimuli. They may be performing them in the presence of a variety of stimuli, whereas in the animal's environment, they were performed with the establishment of central control, that is, with the establishment of central control, the animal may perform a variety of different but related behavior patterns, all of which are elicited by internal cues. As Norman (1981) puts it, illustrating a situation in which a behavior occurs in the absence of a specific external stimulus, such as a subject going to their bedroom to change their bed linen: "pass too near a well-formed habit and there is little chance the behavior will be inhibited." Instead, the behavior sequence is performed in the absence of any particular external stimulus. The same idea is as if a stereotypy is substituting for a non-specific external stimulus. For example, Fox’s pacing dingo (Fox, 1971), whose pacing was developed during stereotypic pacing, came to repeat pacing movements in the absence of any specific external stimulus.

3. Behavior Not Terminated

Normal behavioral control mechanisms are usually repeated in a sequence of behavior, where one behavior is elicited or replaced by another, and the latter replaces the first. Behavior could recur to a higher degree of arousal increases (Fentress, 1973, 1976; Rice et al., 1976). In some cases it is as if a stereotypy is substituting for a more specific external stimulus. For example, Fox’s pacing dingo (Fox, 1971), whose pacing was developed during stereotypic pacing, came to repeat pacing movements in the absence of any specific external stimulus.

Normal behavioral control mechanisms are usually repeated in a sequence of behavior, where one behavior is elicited or replaced by another, and the latter replaces the first. Behavior could recur to a higher degree of arousal increases (Fentress, 1973, 1976; Rice et al., 1976). In some cases it is as if a stereotypy is substituting for a more specific external stimulus. For example, Fox’s pacing dingo (Fox, 1971), whose pacing was developed during stereotypic pacing, came to repeat pacing movements in the absence of any specific external stimulus.
Mechanisms Involved in Stereotypies

Section IV-A-1), and to the extent that an increasing number of stimuli are effective in elicitation. This will occur if repetition results in the establishment of central control (Hinde, 1970, p. 26; Fentress, 1976). Higher-level processes are invoked to explain a similar phenomenon, that of a particular kind of “action slip.” In some situations a familiar, habitual behavior pattern can be elicited by accident, if the context seems superficially appropriate or if another, similar, act was intended. Thus a wide range of stimuli, including those that should elicit different but related behavior patterns, might come to elicit a particular movement. As Norman (1981) puts it, illustrating this with the wonderful case of someone going to their bedroom to change for dinner and finding themselves in bed: “pass too near a well-formed habit and it will capture your behavior.” As with the establishment of central control, the unintentionally activated behavior patterns have to have been so common in the past that they have become stored as schemas, that is, sensorimotor organized memory units (Norman, 1981).

To what extent might these processes be involved in their stereotypies of captive animals? Some stereotypies can be performed in circumstances quite separate from the original eliciting situation. This does indeed seem to depend on the stereotypy being well established rather than recently developed (reviewed by Mason, 1991a,b). In some cases the increase in the number of contexts in which they are performed seems to be because the stereotypies are elicited by a widening range of stimuli. They may be performed, for example, whenever general arousal increases (Fentress, 1973, 1976; Ridley and Baker, 1982). In other cases it is as if a stereotypy is substituting for normal, similar behavior patterns, for example, Fox’s pacing dingo (Fox, 1971). Here its distinctive head-toss, developed during stereotypic pacing, came to replace all normal turning movements.

3. Behavior Not Terminated

Normal behavioral control mechanisms (e.g., habituation) ensure that behavior is not usually repeated in a stereotypylike series if functional consequences are not forthcoming. The factors that usually act to terminate behavior are consummation, that is, the reaching of the goal of the behavior; an accumulation of the costs of the behavior, such as fatigue; and behavioral competition, where a second behavior is elicited or becomes higher in priority, so that it replaces the first. Behavior could recur to an unusual extent if any of these factors failed to have their usual effect.

a. Lack of Consummation. In captivity, it is sometimes the case that consummation of behavior simply is not possible. An animal may pace against the fence that separates it from conspecifics, for example, yet never succeed in getting through it. This has been observed as the source of a pacing stereotypy in a dingo isolated from its pack (Meyer-Holzapfel, 1968). Similarly, appetitive behavior may not be terminated if insufficient food is provided to satiate the
animal. This may well be the case for many food-restricted, intensively farmed animals (Rushen et al., in press).

Alternatively, consummatory stimuli may be present, but may not be treated as such, leading to delayed termination. For instance, the displacement eating of the thirsty pigeon frustrated of water does not involve ingestion, even though it increases if the bird is hungry. McFarland (1965) explains this in terms of the mutual inhibition between eating and drinking systems. The frustrated, thirsty bird will therefore not make the consummatory movements for feeding even if it has the appetite to do so. Another example of the reduced effectiveness of consummatory stimuli is that of isolation-reared rats. These animals are greatly resistant to satiation (reviewed by Fagen, 1982), as if they do not notice the consummatory consequences of eating. The failure of the normal consummatory stimuli to terminate behavior has been observed in several examples of stereotypy, as though this was at least a contributory factor in their continued performance. Examples include caged hens pacing against a door that is now open so that they can escape (Duncan and Wood-Gush, 1972); young mink continuing briefly with a prefeeding stereotypy even after food has been delivered (Mason, 1992); and rats dosed with amphetamine, pressing operant levers without stopping to pick up the rewarding food pellet (Evenden and Robbins, 1983).

b. Reduced Perception of Costs. A bout of behavior may persist to an unusual extent if the costs associated with it are disregarded, for instance, if a subject is unusually insensitive to fatigue, or to being thought socially odd. Being relatively oblivious to social norms may encourage the unusual repetition of pointless behavior and hence the performance of stereotypies. This may be the case in retarded and autistic people; and stereotypies such as foot tapping are also displayed by normal people who think that they are unobserved (Frith and Done, 1990). Physical costs, on the other hand, may be ignored by animals with high levels of testosterone, for example. One short-latency effect of this hormone is to increase the effort an animal will put into overcoming obstacles (Andrew, 1976, 1991) and the persistence with which behavior is repeated in the extinction condition (Andrew, 1989). Testosterone-treated chicks demonstrate this persistence when in an open field or faced with a novel object, performing escape jumps in a repetitive series, rather than singly. Another hormone, adrenocorticotropic hormone (ACTH), has been implicated in the reduction of mental fatigue and in aiding sustained attention in human performance (Gaillard, 1981). The role that these hormones may play in stereotypies is unknown, and experiments to investigate this must consider that these effects of testosterone on behavior are quite different in kind from their effects on aggression and on sexual behavior. Strains of mice that differ in their tendency to develop routines and stereotypies (Benus et al., 1991) also differ in their testosterone levels (van Oortmerssen et al., 1985). However, the short-latency effects of the hormone cannot be responsible for these differences in behavior, for castration had no effect on the behavior of the more unvalued (Koe, 1985).

c. Lack of Behavioral Competition. Behavioral selection processes that occur in the brain may be influenced by a number of reasons, both intrinsic and extrinsic to the organism. Sometimes associated with restricted attention, factors in its environment may elicit few other behaviors, thus compelling the organism to continue behavior. Attention may be restricted so that the animal is focusing on one task, with little to no feedback upon feeding motivation (Dantzker and Perri, 1991), as if changing to another behavior was incompatible with the learning task (Koegel, 1985). The likelihood of an organism changing from one behavior to another is often governed by factors such as the learning task (Koegel, 1985).

The endocrine state of the animal may also contribute to the performance of stereotypies. ACTH also acts to focus attention and performance if slight variants of a behavior pattern are changed and the organism is rewarded for other reasons, too. The endocrine state of the animal may also contribute to the performance of stereotypies.
Mechanisms Involved in Stereotypies

effect on the behavior of the more unvarying strain (van Oortmerssen et al., 1985).

c. Lack of Behavioral Competition. Behavioral competition can be low for a number of reasons, both intrinsic and extrinsic. Behavioral competition may be low if the environment elicits few other behavior patterns (Hinde, 1962). This would seem likely to be true for many captive animals, and in several cases providing opportunities for alternative behavior patterns has reduced the incidence of stereotypies. For example, providing fennec foxes with sand in which they could dig reduced their stereotypic pacing (Öberg, 1984b, 1987). Alternatively some property of the individual may make the environment functionally low in eliciting stimuli. One such case is that of two learning-disabled infants who were very shortsighted. They persisted with hand-waving stereotypies until they were provided with glasses, whereupon they sat up, took notice of things in their environment, and significantly reduced the time they spent in this behavior (Gallagher and Berkson, 1986).

The likelihood of an organism changing its behavior is also affected by behavioral selection processes that occur in the CNS at a number of levels. Attention may be restricted so that the animal does not respond to competing, potentially eliciting, factors in its environment. Evidence that stereotypies are sometimes associated with restricted attention comes from studies of autistic children. Autistic children do not learn an associative task when they are engaged in stereotypies, even though the behavior they are performing is not physically incompatible with the learning task (Koegel and Covert, 1972). Attention may be restricted because the subject’s motivation to perform the first behavior is very high. For example, rats trained to press a lever for food pellets maintain the behavior for longer periods in the extinction condition if they are hungry (Dickinson, 1989), as if changing to another behavior is rendered less likely by the high priority of the first. This may well be why stereotypies are often associated with high motivation in association with frustration (reviewed by Mason, 1991a), and may be why many stereotypies are oral movements that could exert positive feedback upon feeding motivation (Dantzer, 1991). An animal’s attention may be restricted for other reasons, too.

The endocrine state of the animal may affect the attention it pays to external stimuli while engaged in a behavior. For instance, a second short-latency effect of testosterone is to reduce distractability, so that animals are less likely to break off from a behavior pattern to look at a novel stimulus, for example. This it does in mice (Archer, 1977), rats (Thompson and Wright, 1979), chicks (Andrew, 1991), and humans (reviewed by Andrew, 1976).

ACTH also acts to focus attention, in both rats and humans. It improves performance if slight variants of a behavior are required, but worsens it if stimulus parameters are changed a great deal or if a different type of behavior is required (reviewed by Andrew 1991). Similar results are seen in subjects given
stimulants. For example, after amphetamine, marmosets make “stuck in set” perseverative errors in a learning task, finding it difficult to change their behavior when the reverse becomes the rewarded response (Ridley and Baker, 1982). A similar result has been found in children. Dyne et al. (1982) gave small doses of amphetamine to hyperactive children. Although they showed some superficial improvements in their general behavior, when faced with a complex Wisconsin card-sorting task, the children showed errors of the type described above, tending to continue sorting cards according to an old category. Here, then, is a case where a treatment that reduced the general ability of the subject to change its behavior is also associated with stereotypy. These studies suggest that the stereotypy produced at higher doses of these drugs may involve more than just the increased rate of behavioral initiation; the compounds may have effects on attentional processes too.

Behavioral competition may also be low if the subject is limited in the number of alternative behavior patterns that it can perform. Thus, a behavior pattern may be resorted to time and time again, even in inappropriate contexts, not because of anything special about that behavior per se, but because the generation of alternative behavior patterns is limited. A number of factors may reduce an organism’s behavioral repertoire and its generation of new behavior patterns.

Humans with autism, schizophrenia, or damage to the frontal lobes of the cerebral cortex all seem limited in their ability to generate novel responses. Their reduced ability to generate behavioral variety has been demonstrated in a number of experiments. For example, patients with damage to the frontal lobes cannot spontaneously generate lists of animal names, coming to a halt after only a few examples (Frith and Done, 1990); and schizophrenics are impaired in their ability to generate random numbers (Horne et al., 1982). Similarly, autistic children seem limited in their ability to generate a series of drawings that are each different from the next, even if they are asked to do so (Lewis and Boucher, 1991), or to make novel or variable patterns when printing patterns on paper or playing a xylophone (Frith, 1972). They tend to use only a subset of the available colors or musical notes, which they then repeat in set patterns. Note how this poverty of behavior is not just a question of getting stuck in one well-practiced type of behavior; it is evident, de novo, at each new test. Subjects with this limited ability tend to default to old responses (Frith and Done, 1983) or underlying tendencies to repetition, even when this is quite inappropriate (Frith and Done, 1990). As autism and schizophrenia are also associated with stereotypy, it may be that this inability also plays a role in their long-term, idiosyncratic stereotypic behavior. Low behavioral competition perhaps explains, too, the finding of Frances (1966) that Down’s syndrome individuals with stereotypies generally have small behavioral repertoires.

But how would one test for the relevance of such processes in the etiology and control of the stereotypies of captive animals? Could the hypothesis that stereotypies are linked with the reduced behavioral competition explain the results of Wood-Gush et al. (1987)? Stereotypies were generally much less easy to test this for sure. Schwartz (1982) used a conditioned place preference test to develop variable responses by rewarding the birds tended to adopt a “win-stay” strategy. One would have to devise a task that one could generate many novel responses (and fail) that would also influence success and thus behavior.

4. Repetition Due to Reward

Behavior may persist, not because it is rewarded or because of some stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolish, because their reinforcing properties are low. Other stereotypies, at least, may be rewarding. Some stereotypies are difficult to abolis...
Mechanisms Involved in Stereotypies

Stereotypies are linked with the reduced ability to generate new behavior patterns. Explain the results of Wood-Gush et al. (1983), who found that sows with stereotypies were generally much less exploratory than those without. It is difficult to test this for sure. Schwartz (1982a) had great difficulty in training pigeons to develop variable responses by rewarding the development of novel responses; the birds tended to adopt a "win-stay" strategy, each time they were rewarded! One would have to devise a task that could only be done if the animals could generate many novel responses (and factors such as persistence and neophilia would influence success and thus confound the results).

4. Repetition Due to Reward

Behavior may persist not because aspects of its control have been disrupted, but because its performance rewards the animal. In the learning of behavior patterns, reinforcers selectively increase the repetition of contingent behavior (e.g., Schwartz, 1980). Endogenous opioids may be the means by which the expression of certain behavior patterns is enhanced. Beta-endorphins are released in rewarding situations and they increase positive emotions. This change in affect may increase the search for these rewards and maintain the behavior patterns involved. For example, morphine, an exogenous opioid, has an anti-extinction effect in food-rewarded situations (Panksepp, 1981; Dum and Herz, 1987).

Thus an explanation for the recurrent nature of stereotypies is that, despite their lack of obvious goal or function, they are in fact rewarding. Evidence that some stereotypies, at least, may be rewarding can be summarized as follows. Some stereotypies are difficult to abolish by means of punishment or by reinforcing alternatives (e.g., Fraser and Broom, 1990). Second, individuals will work to perform some stereotypies (e.g., Berkson, 1964). Third, if stopped from performing a particular stereotypy, individuals will sometimes develop an alternative one. This has been found both in children with learning difficulties (Young and Clements, 1979), and in caged voles (Kennes and de Rycke, 1988; Odberg, 1989). Finally, opioids are involved in some stereotypies. This would be consistent with the behavior being rewarding (although opioids are involved in so many other systems (e.g., Rushen et al., 1990; Keverne, 1992) one perhaps should not jump to conclusions). For example, in several cases stereotypies are blocked by opioid antagonists such as naloxone (e.g., Odberg, 1984a; Kennes et al., 1988; reviewed by Rushen et al., 1990; Kars et al., 1989). Stereotypies may also increase if exogenous opioid agonists are given (e.g., Panksepp, 1981; Dantzer, 1986; Panksepp (1981) speculates that overactive brain opioid systems might be responsible for the symptoms of autism, since, if left alone and unchallenged, autistics sometimes appear remarkably serene and self-sufficient, without the desire for social interaction seen in normal children.

A variety of properties have been suggested to reinforce stereotypies (e.g.,
Stereotypies may represent normal behavior that is intrinsically rewarding, for instance (see review by Hughes and Duncan, 1988), or they may provide stimulation in a barren environment. Indeed, the rhythmicity of this repetitive stimulation may be what the organism finds rewarding. De Lissavoy (1962, cited in Mitchell and Etches, 1977) reported that normal children who showed head-banging behavior were described by their mothers as prone to other forms of rhythmic activity and as very responsive to music.

Alternatively, stereotypies may persist because they have been reinforced in the past. Past reinforcement can lead to very persistent behavior. This is evident in operant conditioning, where abolition of the response contingency (e.g., by periodically presenting food, irrespective of the behavior performed, to an animal that has been trained on fixed-interval schedule) often has little effect on changing the animal’s behavior. It will continue to respond, habitually, even though responding is now unnecessary (Staddon, 1987). The degree to which the reinforced behavior persists, in extinction and other conditions, depends on a number of things.

The degree of repetition in the past may be important. When a behavior pattern is reinforced, cues associated with the reward can, as a result of repeated performance, become substitute, secondary cues that elicit the response in their own right, even in the absence of the reinforcer itself and its associated signals (e.g., Bindra, 1959, cited in Hinde, 1970, p. 557; Hall and Halliday, 1992, p. 153). The past consequences of the behavior are also important—some behavior may be too important to risk ceasing or changing! Thus, avoidance reactions are particularly resistant to extinction, even if the trained animal is temporarily prevented from performing them and so is forced to experience that its response is no longer necessary (Hinde, 1962). Finally, the past relationship between the behavior and delivery of the reinforcer is also important, as intermittently reinforced behavior is particularly hard to extinguish (Berlyne, 1960; Dickinson, 1985, 1989; McFarland, 1985, p. 388), and is particularly resistant to satiation (reviewed by Morgan, 1973). Whatever the precise explanation, the effects of intermittent reinforcement can be seen graphically in human gambling (e.g., Berlyne, 1960, p. 207). Intermittent reinforcement in the form of unpredictable arrival of food (Mason, 1992) or sporadic exposure to aversive stimuli (Hinde, 1962) may well contribute to the persistent nature of the stereotypies of some captive animals.

Finally, reinforcement that increases the expression of stereotypies may be superstitious, the behavior reinforced by adventitious events (Hinde, 1970, pp. 448–449). For example, Hinde (1962) suggested that the arrival of food may reinforce stereotypies. How one could investigate the role of superstitious reinforcement is suggested by Roper (1983), who studied schedule-induced behavior. Schedule-induced polydipsia in the rat was demonstrated not to be maintained by the superstitiously reinforcing effect of the arrival of food, for if the

Mechanisms Involved in Stereotypies

behavior was explicitly rewarded with water, it looked quite different in morphology, with the waterspout.

However, in many cases stereotypies are present. They may be abolished fairly easily by their control (e.g., Dodman et al., 1986; Kennes et al., 1988).

6. Discussion

Some of the processes considered above, captive environments may encourage behavior pattern both through repeatedly eliciting few other competing behaviors, one mechanism has to be invoked in order to find different subjects. Subjects with schizophrenia (Robbins, 1991), or autism, reduced ability to plan, generate alternatives and change their problem-solving strategies. The frontal lobes is evidently diminished, and perseveration means that the subjects have a high level of indistractibility, acting on impulse or calligraphy (and Done, 1990). However, this high-level explanation for these subjects’ stereotypies do not show long-term stereotypy, only a tendency to distractability. Autistics, in contrast, indistractibility and a general desire for stereotypies of people with autism or schizotypic forms, autism being typified by a wide range of movements (e.g., Frith and Done, 1990). However, this high-level explanation does not entirely explain the mechanisms must be involved.

B. Factors that Could Reduce Variability

The mechanisms described above would not result in a stereotypy. Further mechanisms of extreme invariance and limitation of movement...
behavior was explicitly rewarded with food, then the drinking that developed looked quite different in morphology, with the rats often gnawing and pawing at the waterspout.

However, in many cases stereotypies show no sign of reinforcement, past or present. They may be abolished fairly easily, and opioids may not be involved in their control (e.g., Dodman et al., 1987). Opioid antagonists are particularly ineffective in blocking older, more established stereotypies (Cronin et al., 1985, 1986; Kennes et al., 1988).

6. Discussion

Some of the processes considered here may act in combination. For example, captive environments may encourage the development of a repeated behavior pattern both through repeatedly eliciting its performance and through demanding few other competing behavior patterns. Indeed, sometimes more than one mechanism has to be invoked in order to explain the different stereotypies of different subjects. Subjects with schizophrenia, frontal lesions (Stuss and Benson, 1984; Robbins, 1991), or autism (Ozonoff, in press) all seem to have a reduced ability to plan, generate alternative behavior patterns, or use feedback to change their problem-solving strategies. The supervising of behavior by the frontal lobes is evidently diminished, and the reduced executive functioning that ensues means that the subjects have a tendency to fall back on repetition and perseveration, acting on impulse or calling up old behavior patterns (e.g., Frith and Done, 1990). However, this high-level dysfunction cannot be the complete explanation for these subjects’ stereotypies. For one thing, frontal patients do not show long-term stereotypy, only short-term perseveration along with a tendency to distractability. Autistics, in contrast, combine their stereotypies with indistractibility and a general desire for sameness (see Section B). In addition, the stereotypies of people with autism or schizophrenia differ in their characteristic forms, autism being typified by arm flapping and object twiddling, and schizophrenia by the face and mouth movements known as tardive dyskinesia, amongst other movements (e.g., Frith and Done, 1990). Thus, the “high-level” explanation does not entirely explain the stereotypies of each group: additional mechanisms must be involved.

B. Factors that Could Reduce Variability

The mechanisms described above would result in an organism repeatedly turning to a particular class of behavior pattern, but this tendency alone would not result in a stereotypy. Further mechanisms are needed to account for the extreme invariance and limitation of morphology seen in stereotypies. Thus, a
captive carnivore that paces is not only stuck in appetitive behavior, like a fox in a bountiful chicken coop that kills repeatedly without eating; it is performing only a limited number of the movements possible, and often in highly predictable cycles (always taking the same number of steps, for example). Similarly, the autistic child who draws similar types of pictures again and again is not performing a stereotypy. A number of factors reduce the variability of behavior patterns, and could therefore be behind the predictable morphology so characteristic of stereotypies.

1. External Influences Unimportant for a Specific Behavior Pattern

A specific behavior pattern will become very fixed in form if central control comes to predominate, as information from the environment will then not be used to modify the movements involved (e.g., Hinde, 1970, p. 26). Central control is important in both learned and unlearned behavior patterns, and its relative importance may be affected by the general predisposition of the organism, the degree of past repetition of the movement, and the demands of the current situation. These factors are considered below.

Some behavior patterns are performed in an unvarying way without prior practice or the opportunity for learning. These are sometimes known as “fixed action patterns,” and include courtship displays by birds (e.g., Hinde, 1982, pp. 43–46), mammalian swallowing (Doty, 1976), and the species-specific characteristics of song, which, in some birds (e.g., the canary), will develop even in juvenile individuals prevented from hearing adults and the noise that they make themselves (reviewed by Marler, 1991).

In addition, once-flexible patterns that have been often repeated can become less and less variable through the establishment of central control (e.g., Lashley, 1921; Miller et al., 1960, pp. 81–93; Fentress, 1976; Martinuk, 1976, pp. 142–150). Eventually one movement in a sequence comes to follow another without conscious, volitional control or prompting by environmental cues, and the form of each movement becomes very predictable from one occasion to the next. In addition, in humans the “automatized” nature of such responses can be seen in the way that verbal tasks can easily be engaged in at the same time (Lashley, 1921). Examples of centrally controlled learned movements include signing one’s name (Legge and Barker, 1976, pp. 50–51), and swinging a golf club, which a practiced golfer can perform unaltered even if suddenly plunged into darkness and hence denied visual feedback (McFarland, 1987a,b). One model for this developmental process is that neurons come to be sensitized in particular paths; such pathways are “opened” or “deepened” with repeated activation (Stolba et al., 1983; Dantzer, 1986). The cerebellum is involved in this process (e.g., Lashley, 1921; Miller et al., 1960; Carpenter, 1989).

The ease with which central control becomes established differs between species and between strains. For one thing, it is never seen in some organisms. In the flexible-limbed, joint-receptors means that the animal has the sequence, the parts of the brain concerned feedback on how any act has been carried of skilled movements through practice in the behavior of the “SAL” strain of more of the behavior patterns. These mice do not lose to small changes in the physical environment. They therefore become less aggressive, less sensitive to the stereotypy-inducing effects.

Various short-term effects can also alter central and peripheral control upon a behavior high, sensory input will be less effective; if behavior is too fast it cannot be guided; if behavior is too slow it cannot be guided; if the behavior of the “SAL” strain of house mouse rapidly establishes slow and persistent behavior patterns. These mice do not lose their use of environmental cues. Rather, they just tend readily to build up several times, instead of staying exploratory. They therefore become less aggressive, even to small changes in the physical environment. They become less sensitive to the stereotypy-inducing effects.

Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241). Control reduces central with speed; it may quantitatively reduce the speed at which skilled movements of the cockroach are less impaired by local anesthesia. The slow walking movements of its relative, the roach (McFarland, 1985, p. 241).
species and between strains. For one thing, such a process simply is not possible in some organisms. In the flexible-limbed octopus, the lack of joints and hence joint-receptors means that the animal has no proprioceptive sense. As a consequence, the parts of the brain concerned with learning never receive detailed feedback on how any act has been carried out. This means that the development of skilled movements through practice is impossible (Wells, 1979). Research into the behavior of the “SAL” strain of mouse, in contrast, suggests that this aggressive strain of house mouse rapidly establishes central control over repeated behavior patterns. These mice do not learn tasks particularly slowly, that is, it is not that their use of environmental cues is poor in general (Benus et al., 1990). Rather, they just tend readily to build routines after repeating the same behavior several times, instead of staying exploratory and alert to stimuli in the environment. They therefore become less able to adapt their current behavior rapidly even to small changes in the physical or social environment (Benus et al., 1987, 1988, 1990; Koolhaas, 1989). This strain is also more prone than a similar but less aggressive strain to the development of stereotypies, showing stereotypic gnawing and licking not seen in the more passive strain, and being much more sensitive to the stereotypy-inducing effects of apomorphine (Benus et al., 1991).

Various short-term effects can also influence the relative influences of central and peripheral control upon a behavior pattern. If the speed of performance is high, sensory input will be less effective in influencing the behavior, for if the behavior is too fast it cannot be guided by sensory feedback (Lashley, 1917, 1951; Miller et al., 1960; Fentress, 1976; Carpenter, 1989). Hence, the rapid phases of grooming in mice are relatively difficult to interrupt with a noise, and are relatively unimpaired by local anesthesia (Fentress, 1976). Likewise, the fast movements of the cockroach are less influenced by peripheral stimuli than are the slow walking movements of its relative, the stick insect (Wendler, 1966, cited in McFarland, 1985, p. 241). Control may not only become qualitatively more central with speed; it may quantitatively change from peripheral to central as speed increases. For example, Fentress (1976) housed voles in a complex environment in which they came to establish preferred paths. The environment was then rearranged, and the voles given plenty of time in which to explore it, become familiarized with the changes, and establish new paths. However, when scared, some individuals (and it would be interesting to know which, and why) would flee along previously established pathways, jumping over objects no longer there and repeatedly bumping into new obstacles.

If attention is being directed elsewhere, behavior will be less influenced by other information from the periphery, since the capacity of information-processing systems is limited (e.g., Berlyne, 1960, p. 45). Stimuli with a strong affective value, such as pain or food, are particularly good at gaining attention (Berlyne, 1960, pp. 52–66). Thus, mice in a novel environment have attentional demands that reduce the effectiveness of the control of grooming by external
stimuli, and therefore their grooming is stereotyped (Fentress, 1976). Peripheral factors may also play a little role in behavioral control if attention is focused on consummation-related stimuli because of high motivation. This decreases the likelihood that the behavior will be varied, as demonstrated by Andrew (1991). Hungry chicks trained to travel a runway to reach a food dish were less distracted by local novelty than less hungry chicks, and their speed and the path they traveled were therefore relatively unaffected. Testosterone can also reduce variability in movements by reducing distractability, as discussed previously in Section A.

Central control may well be involved in some stereotypies, either because the stereotypies derive from fixed action patterns, or because the movements have been repeated often enough for central control to become established. The decrease in variability of stereotypies with age has been recorded, for instance by Meyer-Holzapfel (1968) and Stolba et al. (1983). The role of central control could be demonstrated in a number of other ways:

(a) Selectively reducing input, through deafferentation for instance, should not disrupt the behavior. Sherrington [1931 (in Hinde, 1970, p. 46)] revealed the central control of the scratch reflex of the dog by deafferenting a leg and stimulating the cut end of the nerve. The correct rhythmic pattern of contraction occurred in the leg muscles, despite the lack of sensory input. Several examples of stereotypy suggest that external factors that should be important in the control of the behavior are not in fact being attended to. One such case is that of a pacing hunting dog, which tripped over a rope that was stretched across its path (Fentress, 1976, 1977).

(b) Electrical stimulation of the CNS might elicit the behavior. This is a characteristic of central control. For example, intracranial stimulation of the pigeon results in the expression of a variety of well-integrated behavior patterns very similar to those seen in normal social contexts, such as the bowing and cooing seen during courtship (Hinde, 1970, p. 26, citing Akerman, 1966). Similar results have been obtained for at least one stereotypy. Fentress (1976) elicited the stereotypies of laboratory squirrel monkeys through electrical stimulation of the mesencephalic reticular system.

(c) What happens to the pattern after a brief interruption? Centrally controlled behavior patterns tend to be restarted from the beginning if interrupted. This is true of automatized skills in humans, and likewise, rats trained to choose an alleyway for food on the basis of a signaling light will wheel about and return to their starting compartment, before running back down the alley, if distracted on the way by a noise or jolt (Lashley, 1921). A similar tendency has been observed in an unlearned behavior pattern of the greylag goose. This species rolls wayward eggs back into its nest with a characteristic bill movement. Should the egg roll out from under the bill while the bird is doing this, it will complete the movement, pulling its bill into its body, before delivering food (Mason, 1992). In addition, the stereotypy should become context-conditioned, as long as the discriminative variable is present. This is illustrated by the behavior of a Capuchin monkey whose pacifier was unaltered when moved to a new and large unvarying environment, after a certain age (Fraser, 1975).

Some stereotypies, however, do not appear to be context-conditioned. For example, described a Capuchin monkey whose pacifier was unaltered when moved to a new and large unvarying environment, after a certain age. Intrinsic features of an organism may not modify their stereotypies (Cooper and Shettleworth, 1991).
movement, pulling its bill into its body, before reaching out to start again (Doty, 1976, citing Lorenz and Tinbergen, 1938). An “interruption” test has not to our knowledge ever been conducted on a stereotypy.

2. External Factors that Are Generally Uninfluential

External factors often influence the strength and orientation of behavior patterns and therefore cause them to vary. If the environment is unvarying, then behavior patterns in general may themselves be correspondingly unvarying. As an illustration, consider the regular, unvarying movements made by a person while walking along a smooth pavement, compared with the movements made by the legs, arms, and body when walking over rough ground.

An unvarying environment could therefore be responsible for the predictability of movements that make up stereotypies. For example, one can surmise that a fetus sucking one of its digits (Sroufe and Cooper, 1988), a behavior considered a stereotypy by Levy (1944), would have little cause to vary these movements in the stable environment of the uterus. The environments of captive animals similarly often demand little variation in behavior. A captive predatory animal performing appetitive behavior will probably have neither changes in terrain nor prey movement to respond to, for example. The importance for stereotypies of the unvarying nature of external factors that would otherwise modulate and control the behavior has been suggested by Hediger (1950), and Morris (1964, 1966), and more recently by Rushen et al. (in press).

To be consistent with this hypothesis, a stereotypy should immediately alter, in an appropriate way, should the environment change. Some stereotypies do indeed respond in this way. The locomotory stereotypies of young mink, for example, alter in form so that paired cagemates do not collide, and are performed on whatever side of the cage is nearest the current position of the machine that delivers food (Mason, 1992). In addition, if the environment is made more variable, the stereotypy should become correspondingly more variable. A possible example here is that the stereotyped oral behavior of stall-house pigs changes to the less stereotyped oral manipulation of straw, when this substrate is provided (Fraser, 1975).

Some stereotypies, however, do not change in this way. Morris (1964) described a Capuchin monkey whose pace-and-twist stereotypy remained almost unaltered when moved to a new and larger cage, and similarly, if voles are reared in a barren environment, after a certain age moving them to an enriched cage will not modify their stereotypies (Cooper and Odberg, 1991).

Intrinsic features of an organism may also make the environment generally unable to effect behavioral change. For example, a small child who rocks in an unvarying way may not have the coordination to do much else. Thelen (1979) discusses how these rhythmic movements may be an infant substitute for com-
plex behavior that is not yet possible. Also, the environment might be effectively unchanging to an organism that has some impairment of sensory input or processing. A number of characteristics may decrease the extent to which an organism reacts to change. An animal that is drowsy has a reduced capacity to process information (Fentress, 1976; see also Martiniuk, 1976, pp. 39–43, and Berlyne, 1960, p. 45). Also, if arousal is very high, the processing of information may be poor (Berlyne, 1960, p. 45). So, does this contribute to stereotypy? In several cases, stereotypies are associated with states that, at a variety of levels, reduce effective input. For example, accompanying blindness may contribute to the development of stereotypies in learning disabled children (Thompson and Berksen, 1985). Frith and Done (1983) suggest that the stereotyped sequences generated by people with schizophrenia during a card-guessing game are the secondary consequence of an abnormality of information processing such that they cannot “construct meaningful events from sensory inflow”; and Frith and Done (1990) suggest that the unresponsiveness of the stereotypies of the severely learning disabled to environmental changes is a result of the subjects’ low IQ, rendering them incapable of detecting a change in environmental stimulation.

In many cases, however, stereotypies cannot be the product of a general reduction in effective input. Many animals and humans with stereotypies respond appropriately to complex and varying stimuli, when they are not engaged in the stereotypy itself. Autistic children, for example, can often learn, play, and communicate (e.g., Koegel and Covert, 1972; Boucher, 1977), and likewise, zoo animals often appear quite normal when not performing their stereotypies.

### 3. Reduced Variability Due to Reinforcement

Reinforcement may lead to the strict adherence to certain set patterns of movements. The development of daily routines, for instance, is a common response to an environment in which some activities are more profitable at some times than at others (McFarland, 1985, pp. 305–307). Thus, kestrels that have found food at a particular place at a particular time tend to repeat the same search pattern the next day (Daan, 1981). The low variability of behavior patterns resulting from reinforcement can be seen when adventitious reward results in the development of superstitious rituals. For example, pigeons may develop stereotyped superstitious behavior from patterns temporally correlated with the delivery of food, performing bizarre movements such as turning quickly in small circles (Skinner, 1948).

Opioids may be involved in this process. Their role in reinforcement has already been discussed in Section A, but they may do more than just increase the probability of certain types of behavior. Panksepp (1981) speculates that “endogenous opioids may help mold stable behavior sequences which facilitate an organism’s progressions through its daily affairs,” and writes of such habits being based on stable underlying structures that result (rather than memories of the informational consequence).

Unvarying, inflexible behavior is part of reinforcement if some organic dysfunction modifies the environment to suppress previously reinforced behavior patterns. This occurs in subjects with frontal lobe damage and isolation-reared rats (reviewed in McFarland, 1985). If rats are group-housed but reared in physically barren cages, instead of large, enriched cages, they come to show a greater tendency to solve a maze, even when more direct solutions are available (Evenden and Robbins, 1984).

Reinforcement also results in unvarying behavior so as to minimize losses, perhaps because of stereotyped “win–stay” sequences developing in unpredictable, flexible sequences seen in problem-solving situations, such as when the consequences of reinforcement are low, rats are more likely to become stereotyped (Luchins, 1942; Schwartz, 1960). For example, when the chances of success are slight, rats are more likely to reinforce is low, rats are more likely to become stereotyped (Luchins, 1942; Schwartz, 1960).

So, what role might reinforcement play in stereotypies of sows? The evidence for this has been discussed in Section A-4.

Examples such as these suggest that stereotypies are the product of a general reduction in effective input. Many animals and humans with stereotypies respond appropriately to complex and varying stimuli, when they are not engaged in the stereotypy itself. Autistic children, for example, can often learn, play, and communicate (e.g., Koegel and Covert, 1972; Boucher, 1977), and likewise, zoo animals often appear quite normal when not performing their stereotypies.

### 4. Fixity of Goal or Internal Representation

The mechanisms described above work to suppress previously reinforced behavior patterns (McFarland, 1985, cited in McFarland, 1985). For example, sometimes animals fail to solve a maze, even when more direct solutions are available (Evenden and Robbins, 1984).

Examples such as these suggest that stereotypies of sows are the product of a general reduction in effective input. Many animals and humans with stereotypies respond appropriately to complex and varying stimuli, when they are not engaged in the stereotypy itself. Autistic children, for example, can often learn, play, and communicate (e.g., Koegel and Covert, 1972; Boucher, 1977), and likewise, zoo animals often appear quite normal when not performing their stereotypies.
based on stable underlying structures that represent internalized behavioral rules (rather than memories of the informational aspects of the environment).

Unvarying, inflexible behavior is particularly likely to develop with reinforcement if some organic dysfunction means that the organism is unable to suppress previously reinforced behavior patterns when confronted with a new situation. This occurs in subjects with frontal lesions (Stuss and Benson, 1984) and isolation-reared rats (reviewed in Morgan, 1973), and may explain why, if rats are group-housed but reared in physically impoverished surroundings (small, barren cages, instead of large, enriched cages with much gentle human contact), they come to show a greater tendency to adhere to an oft-repeated mode of solving a maze, even when more direct solutions are then made available (Luchins andForgus, 1955).

Reinforcement also results in unvarying movements if the subject is acting so as to minimize losses, perhaps because the risks of failure are great. Hence, stereotyped "win-stay" sequences develop in gambling, in contrast to the inventive, flexible sequences seen in problem-solving games where failure is of less consequence (Luchins, 1942; Schwartz, 1982b; Frith and Done, 1990). It also occurs if the chances of success are slight. For example, if the probability of reinforcement is low, rats are more likely to adopt a stereotyped win-stay strategy (Evenden and Robins, 1984).

So, what role might reinforcement play in stereotypy? Cronin (1985), for one, claimed that the fixity of performance was evidence of learning and reward, in the stereotypies of sows. The evidence that some stereotypies are reinforcing has been discussed in Section A-4.

Examples such as these suggest that animals may form procedural rules when they are reinforced. This means that they learn a set of instructions that, if followed, will automatically take them to their goal (McFarland, 1985, pp. 354–356). For example, sometimes animals fail to integrate information from different contexts, suggesting that procedural rules do indeed underlie their learned behavior patterns (McFarland, 1985, citing Dickinson, 1980). However, very often animals act in a rather more flexible, goal-oriented way, as will be discussed in the next section.

4. Fixity of Goal or Internal Representation of Behavior

The mechanisms described above would reduce the variability of the instructions sent to the muscles, and thereby the variability of the movements involved in a behavior pattern. However, animals may achieve low variability of behavior by other means, by conforming to a sensory template or goal of how the behavior should be. The actual muscle involvement may be versatile, differing on each occasion according to the demands of the situation, but the behavioral end product will be similar in final appearance from one performance to the next.
For example, the head-up threat posture of the great tit may be equally recognizable, whether the bird is perched on a twig, clinging to a vertical trunk, or standing on flat ground. The controlling system may be producing as close an approximation as possible to a required pattern of sensory feedback (Hinde, 1970, p. 47).

The development of this "required pattern" or idea of a goal may sometimes be the result of reinforcement. In the case of operants and other reinforced behavior, animals may achieve reward via a variety of behavior patterns that have the same end result. For example, guinea pigs that have learned to press a button to reach food will each use their right paw, left paw, or teeth interchangeably and at random (Tolman, 1932, pp. 170–171). Likewise, Tolman (1932, pp. 166–170) demonstrated that a rat in a familiar maze will always take the shortest route to the site of food, but if its path is blocked, it will immediately proceed to the food via an alternative route. Note how this contrasts with central control, where a movement may not be changed even when it would seem productive to do so. For example, egg rolling by the graylag goose always involves the bill, and although it would sometimes seem more efficient for a goose to use its wing or its foot, no bird has been known to develop a new movement for retrieving its eggs (Lorenz and Tinbergen, 1939 and Tinbergen, 1953, in Hinde, 1970, p. 22). These cases of learned and flexible behavior suggest that the animal is using a declarative representation rather than a procedural rule—that it has a mental image of its desired goal, but it is not committed to using this knowledge to behave in any particular set way (McFarland, 1985, pp. 354–356).

Bleuler (1950) described how adhering to an internal representation of a behavior pattern might play a role in the rigidity of one abnormal form of behavior. In the catalepsy sometimes evident in schizophrenia, patients can assume certain positions for months at a time, and they resist all passive attempts to move their limbs. Bleuler writes: "If one observes such a case more closely, one can always see that the muscular contraction adjusts to any external force applied and that the muscles flex exactly as much as is needed to maintain the assumed position." But to what extent does adhering to a goal result in the unvarying nature of stereotypies? To test for this, one would have to show that feedback is necessary for continued performance. For instance, in some songbirds, deafening, but not isolation, will remove the bird's ability to generate species-specific song, revealing that is does not need a tutor but that without monitoring its own vocalizations it cannot match its auditory song template (reviewed by Marler, 1991). One could also measure the electrical impulses that give rise to seemingly exactly reproducible movements, since Hoyle (1964, cited by Fentress, 1991) demonstrated that while the stepping movements of the locust are very regular in form, they are not accompanied by fixed patterns of excitation in the motor neurons. Such tests have not as yet been performed on any stereotypies. One could also see if the animal adjusts to environmental changes in such a way as to always produce a similar behavior pattern. For example, a guinea pig gnawed the coat of a cagemate in a one particular spot only. This stereotypy involved the animal had to follow its cagemate every time (Sahakian and Robbins, 1975). If the second animal still, the nature of the stereotypy's control would fact that the gnawer acted flexibly in order to always have that high-level, goal-directed processes was any.

5. Preference for Predictability

An alternative source of the low generation wanting to alter its behavior. Humans may have a need for predictability, which reduces their behavioral variation. For example, order and feelings of control seems to be involved in rituals (such as having favorite bedtime stories) and behavior (such as repeatedly checking things) (Leopold, 1991). These have been hypothesized to explain the performance in circumstances, where the behavior could increase under otherwise unpredictable environment (e.g., Brown, 1964). The stereotypies performed by autistics

Subjects with autism are remarkable for their wanting to alter its behavior. Humans may have a need for predictability, which reduces their behavioral variation. For example, order and feelings of control seems to be involved in rituals (such as having favorite bedtime stories) and behavior (such as repeatedly checking things) (Leopold, 1991). These have been hypothesized to explain the performance in circumstances, where the behavior could increase under otherwise unpredictable environment (e.g., Brown, 1964). The stereotypies performed by autistics

6. Discussion

In previous accounts of stereotypies (e.g., Baron-Cohen, 1989), rigidity with age and repetition has been emphasized. Central control considered the major reason for the stereotypies performed by autistics. Some of the processes discussed in this section may be associated with some of the processes discussed in behavioral competition and the reduced influence...
Mechanisms Involved in Stereotypies

always produce a similar behavior pattern. For example, an amphetamine-treated
guinea pig gnawed the coat of a cagemate in a stereotyped manner, chewing on
one particular spot only. This stereotypy involved changes in posture, for the
animal had to follow its cagemate every time this second animal moved
(Sahakian and Robbins, 1975). If the second animal had remained completely
still, the nature of the stereotypy’s control would not have been apparent, but the
fact that the gnawer acted flexibly in order to act inflexibly, as it were, reveals
that high-level, goal-directed processes were at work.

5. Preference for Predictability

An alternative source of the low generation of variability is the subject’s not
wanting to alter its behavior. Humans may have a cognitive desire for predictabil-
ity, which reduces their behavioral variation. For example, a desire for maintain-
ing order and feelings of control seems to be behind both normal childhood
rituals (such a having favorite bedtime stories) and obsessive–compulsive behavior
(such as repeatedly checking things) (Leonard et al., 1990). Such feelings
have been hypothesized to explain the performance of stereotypies in arousing
circumstances, where the behavior could increase the average predictability of an
otherwise unpredictable environment (e.g., Broom, 1983). It could also explain
the stereotypies performed by autistics.

Subjects with autism are remarkable for their insistence on sameness. They
may ask the same question again and again, arrange objects in ordered patterns,
insist on routines and become very upset if these are not adhered to, and have
obsessive interests in a narrow range of topics, which often involve complex yet
ordered, predictable things such as machinery or timetables (e.g., Prior and
Baron-Cohen, 1989). Their stereotypies may be another way of imposing order
on a world they find chaotic and unpredictable (e.g., Wing, 1966 and Rutter,
1966, as cited by Prior and Macmillan, 1973). Of course it is difficult to say the
extent to which these intentional stances can be used to interpret animal exam-
pies.

6. Discussion

In previous accounts of stereotypies (e.g., Mason, 1991b) their increasing
rigidity with age and repetition has been emphasized, and the establishment
of central control considered the major reason for their low variability. However,
Section B discusses several other possible explanations for this phenomenon.

Some of the processes discussed in this section are more likely than others
to be associated with some of the processes discussed in Section A. Reduced
behavioral competition and the reduced influence of peripheral control could
both be the product of high motivation to perform the behavior pattern, for instance, while reward may account for both the recurrence and the low variability of a behavior pattern, particularly if the consequences are so important to the animal that it will not risk altering its behavior. In other cases, however, the processes that underlie repetition and those that underlie low variability may be quite independent.

V. CONCLUSIONS

In this review we demonstrate that a range of quite different phenomena could be involved in the development and control of rigid, repetitive behavior patterns that have no apparent goal or function. As discussed above, some might influence repetitiveness and rigidity alike, while in other cases separate processes may act concurrently to give rise independently to these two attributes. Some of these mechanisms are more likely than others to be important at certain stages in the development of a stereotypy. Some will be involved only during the development of the behavior, while others will be involved only in the control of the developed form—perhaps in the way that eating peanuts at a party may be initiated out of nervousness and a lack of behavioral competition, and then maintained by the appetizing effect of consuming small amounts of food. To illustrate this with a stereotypy example, when a hen in a cage develops a pacing stereotypy, it may do so originally out of attempts to escape, but after a time, the behavioral control mechanisms are such that the behavior is not terminated when escape is made possible (Duncan and Wood-Gush, 1972). Another distinction to be drawn among the mechanisms we discuss is that some of them are aspects of normal behavioral control, "tricked" by unusual environments into yielding bizarre forms of behavior. These include processes important in the development and control of habits, daily routines, skills, fixed action patterns, and the maintenance of feelings of predictability and control. Other processes, in contrast, are pathological, the product of natural or experimentally induced dysfunctioning of the CNS.

The heterogeneity of possible mechanisms reveals that a unitary explanation for the stereotypies of captive animals is unlikely, if not impossible, since different mechanisms will predominate in different circumstances, and to different extents depending on the functioning of the CNS. In addition, some processes are more likely than others to have particular correlates or consequences. Rewarding behavior, for instance, might be more likely to help an animal to cope in captivity, by satisfying it in some opioid-mediated way, than an unrewarding behavior pattern that is repeatedly elicited by external stimuli. Similarly, it is easy to see that a fixed action pattern will be far less than behavior that looks superficially similar environment so barren that it is never varied for stereotypies makes the heterogeneity in one stereotypy suggests why only some stereotypies appear to some are changed by environmental enrichment to poor welfare.

So, why investigate mechanisms further heterogeneity of stereotypies, but are they those interested in this behavior? We believe.

One reason for considering possible features that may predispose individuals to stereotypy. For example, individuals with a limited array of patterns spontaneously, or who readily rest high testosterone levels, might be more impulsively movements. Such features may differ among vertebrates and yet be common to other, cognitive, traits perhaps being expressed in different in their propensities to develop or control welfare implications, for it suggests that a stereotypy is just a product of how aversive it finds and is influenced by the readiness with which it can be maintained (see Mason, 1991b).

A second reason is that knowledge gives rise to testable questions that may stereotypes and behavior associated with them should be collected in order to cast light interesting and suggestive correlations. Syndrome patients (Frances, 1966), and isolation-reared animals (Morgan, 1973), are prone both to forming unvarying routines, and that what the stereotypies? One could investigate whether it is insensitive to environmental stimuli [this would reared mice, for example, as their ability (Morgan 1973), or whether they are inclined re-d these phenomena related, and what do the stereotypies? One could investigate whether it is insensitive to environmental stimuli [this would reared mice, for example, as their ability (Morgan 1973), or whether they are inclined to poor welfare. As well as being interesting from behavior, for instance, might be more likely to help an animal to cope in captivity, by satisfying it in some opioid-mediated way, than an unrewarding behavior pattern that is repeatedly elicited by external stimuli. Similarly, it is easy to see
that a fixed action pattern will be far less responsive to environmental changes than behavior that looks superficially similar merely because it is performed in an environment so barren that it is never varied. The variety of possible mechanisms for stereotypies makes the heterogeneity at other levels rather less puzzling, for it suggests why only some stereotypies appear to have beneficial correlates, only some are changed by environmental enrichment, and not all seem closely related to poor welfare.

So, why investigate mechanisms further? They may reveal (or confirm) the heterogeneity of stereotypies, but are they a useful area of future research for those interested in this behavior? We believe that they are, for several reasons.

One reason for considering possible mechanisms is that they suggest features that may predispose individuals toward developing various stereotypies. For example, individuals with a limited ability to generate a range of behavior patterns spontaneously, or who readily restrict their attention, perhaps because of high testosterone levels, might be more inclined than others to develop stereotypic movements. Such features may differ between species, some being common to all vertebrates but denied unjointed animals such as the octopus, and other, cognitive, traits perhaps being exclusive to humans. That animals may differ in their propensities to develop or control behavior in particular ways has welfare implications, for it suggests that an individual’s stereotypy levels are not just a product of how aversive it finds its current environment, but are also influenced by the readiness with which certain behavioral control mechanisms come into play (see Mason, 1991b).

A second reason is that knowledge of the possible mechanisms involved gives rise to testable questions that may increase our understanding of stereotypies and behavior associated with them. For example, it indicates what data should be collected in order to cast light on what are at present no more than interesting and suggestive correlations. Consider the way that older Down’s syndrome patients (Frances, 1966), and older pigs (Stolba et al., 1983), and isolation-reared animals (Morgan, 1973; reviewed by Fagen, 1982) all seem prone both to forming unvarying routines and to showing stereotypy. Are these two phenomena related, and what do they tell us about the etiology of their stereotypies? One could investigate whether the subjects are generally unresponsive to environmental stimuli [this would not seem to be the case in isolation-reared mice, for example, as their ability to learn new responses is unimpaired (Morgan 1973)], or whether they are inclined to rely on central control (in which case they will be unresponsive even to small, intradimensional shifts in their environment), or whether they find it difficult to shift behavioral sets for some reason. As well as being interesting from a theoretical point of view, this might be useful clinically. Understanding the processes behind a stereotypy might reveal the sources of other problems in thought or behavior, for instance, under-
standing the mechanism or mechanisms that underlie the stereotypies of autism may help explain some of the other features characteristic of this condition. It might also narrow down where we look for explanations in the CNS (e.g., Hinde, 1970, p. 5), which could have therapeutic implications.

This sort of research may also lead to useful and valid classifications of stereotypy. Current classifications of this behavior depend on its age (is it “developing” or “established”), or on the circumstances in which it developed, for example, whether in a young, generally deprived individual, or in one that is in less impoverished conditions of caging. The ingrained nature of stereotypies shown by isolation-reared animals and animals who have had their stereotypies for a long time has been touched on at various points in this review. However, the validity of these classifications is weakened by the heterogeneity within the subgroups, and the fact that not all stereotypes dichotomize so easily (see Mason, 1991a). Studying mechanisms to give a more “fundamental” or “grassroots” picture of the differences between stereotypes might help with some of these classification problems. Furthermore, it might help with predicting the properties of various stereotypes, since mechanisms might reveal why a particular behavior pattern’s morphology, antecedent conditions, and emergent properties co-occur. In some cases, however, we are never likely to unravel the whole story. For example, some aspects of behavioral control in animals may always remain inaccessible to us. In humans the cognitive aspects of behavior can be used to distinguish a variety of apparently similar behavior patterns. A stereotypy may be regarded as a tic if completely involuntary, or as delusional if accompanied by a cognitive “justification” for its performance. These are regarded as quite separate from each other, and separate again from neurotic rituals (Jones, 1965; Frith and Done, 1990). In animals, however, all would be classed together by applied ethologists as stereotypies.

Future research should therefore try and identify the mechanisms underlying the development and control of stereotypes. We have suggested above some ways of doing this. They can be summarized as follows: (1) through careful observation of the behavior, which may reveal features diagnostic of one form of control and incompatible with others; (2) through experimental manipulation; and (3) through the identification of other behavioral correlates that could reveal the likely etiology of the stereotypy.

VI. ACKNOWLEDGMENTS

We thank the following for their advice and comments: Pat Bateson, Arnold Chamove, Barry Keverne, Fran Martel, Mike Mendl, and Trevor Robbins.

VII. REFERENCES


VII. REFERENCES


Mechanisms Involved in Stereotypies


Mechanisms Involved in Stereotypies


Mechanisms Involved in Stereotypes


Mechanisms Involved in Stereotypies

Robbins, T. W., Jones, G. H., and Sahakian, B. J. (1989). Central stimulants, transmitters and
Mechanisms Involved in Stereotypies


