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The Interaction of Cognitive and Stimulus–Response Processes in the Control of Behaviour

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TOATES, F. *The interaction of cognitive and stimulus–response processes in the control of behaviour*. NEUROSCI BIOBEHAV REV **22**(1) 59–83, 1998.—It is argued that both stimulus–response (S–R) and cognitive theories of learning and behaviour capture part of the truth, in that these terms involve two different types of process that are jointly responsible for the control of behaviour. The proposal that both processes coexist is investigated in the context of the production of behaviour. Evidence is presented to show that the weighting attached to S–R and cognitive processes can change as a function of (a) development; (b) experience; and (c) pathology. A model is proposed which is designed to sketch some ideas on how S–R and cognitive processes jointly determine behaviour, and it is related to the notion of behavioural hierarchy. It is argued that the model can help to develop a synthesis between psychology, ethology and neuroscience. © 1998 Elsevier Science Ltd. All rights reserved.

Motivation   Fixed-action pattern   Learning   Stimulus–response   Cognition   Hierarchy   Stereotypies   Displacement activities   Obsessive–compulsive disorder   Schizophrenia   Hippocampus

1. INTRODUCTION

DO ANIMALS learn cognitions (i.e., knowledge about the world not tied to particular behaviour) or stimulus–response (S–R) connections (i.e., links between particular stimuli and particular responses)? Historically, some of psychology's most famous battles were fought over this bit of territory (96,105,230). However, in a seminal paper on learning, Hirsh (96) proposed that both cognitive and S–R processes coexist in an intact animal and that hippocampal lesions convert a cognitively functioning rat into something like a (S–R) automaton. Subsequently, Mishkin et al. ((142) p. 66) noted the important implication of Hirsh's argument that:

"...both sides in the great debate between behaviourism and cognitivism must ultimately be declared the winners, since the evidence from the study of amnesia demonstrates that both types of processes must be constantly present in normal behaviour."

"If this radical resolution of that long and difficult debate proves correct, it will have enormous implications for both psychological and neurophysiological research."

Hirsh's paper was published 23 years ago and its importance has been widely acknowledged. Different memory systems, characterised by something like S–R and cognitive forms, are now recognised (43,196,126,201,243,244). Rather than competing theories, the terms S–R and cognitive now appear to describe processes that coexist in an animal. Although, within the study of learning and memory, multiple processes are acknowledged, the contention of the present paper is that the implications of these ideas for the control of behaviour have not been adequately explored. Hence the article reviews the literature with the aim of showing how a dual S–R and cognitive control can explain a variety of phenomena. The extensive literature on learning and memory will not be covered here, since a number of excellent reviews already exist (43,196,201). Learning and memory as such will be considered only in so far as they are directly relevant to the processes that underlie the control of behaviour. The paper suggests that the issues raised by Hirsh can provide a new link between psychology, ethology and neuroscience.

Contemporary behavioural scientists tend to favour cognitive theories whereas the S–R view is sometimes seen as being of historical interest only. I shall investigate which features of S–R theories are valid and, in terms of the control of behaviour, how they might be integrated within the dominant cognitive framework. For example, cognitive theories have difficulty with explaining such things as stereotypies and displacement activities. It will be argued that the apparently conflicting S–R and cognitive theories of behavioural control each describe a real and important aspect of the underlying processes.

Aside from historical differences amongst theorists, it must surely constitute an implicit assumption of almost all behavioural science that behaviour is under the joint control of: (a) external stimuli; and (b) internal cognitions and goals. However, we lack theoretical models that are able to suggest how the interaction occurs. What exactly is the role of stimuli in controlling behaviour? Are they simply a

source of information to cognitive processes or a direct trigger to behaviour? How do stimulus and cognitive factors interact? In producing behaviour, under what circumstances are stimuli (external factor) and cognitions (knowledge stored in the nervous system) in competition, and when do they reinforce each other's effects?

In much of psychology, study of the causation of behaviour in terms of physically present stimuli and behaviour has come to take a poor n^{th} place to cognition. As Spear and Isaacson ((200) p. 3) so aptly express it, an understanding of:

''....habitual, overlearned, elicited, short-latency behaviours that might even be characterised as species-specific— is of vast importance for our topic. This type of knowledge seems largely to have been ignored in theories of how humans process information, in favour of knowledge derived from language-mediated, 'higher-order' processing''.

Or, as Turvey ((233) p. 211) similarly notes:

''...it is curious that theories of perception are rarely, if ever, constructed with reference to action. And, while theories of perception abound, theories of action are conspicuous by their absence. But it must necessarily be the case that, like warp and woof, perception and action are interwoven, and we are likely to lose perspective if we attend to one and neglect the other...''.

Although the situation might have improved slightly in the last 20 years (e.g., (72,151)), there is still a real deficiency of integrative theory.

In some ways analogous to the difference of emphasis within psychology, classical ethologists (e.g., (124,216)) developed theoretical models in which sign *stimuli* played a central role in triggering fixed action patterns whereas contemporary ethology places explanatory weight upon cognitive processes. This change in emphasis raises a number of issues. For instance, in accepting cognitive processes, are we to reject the older ethological models? If both types of model capture real aspects of behavioural control, then how do these aspects act in combination in determining behaviour? It will be suggested that the model can form a bridge both within ethology and between ethology and other behavioural sciences.

Traditionally, theories of learning and response production (whether S–R or cognitively orientated) were developed in parallel with theories of motivation (e.g., (19,105,124,216,230)). Of late, the tendency has been towards compartmentalising these processes. The present paper is intended to break down these compartmental barriers. Therefore, the paper will address the issue of how the concept of motivation might be tied to a consideration of cognitive and S–R processes.

Many theorists in neuroscience, psychology and ethology have proposed hierarchical models of behavioural control, and indeed that of Gallistel (72) has powerfully influenced the present review. However, such models are usually discussed somewhat in isolation from other lines of theoretical development. This paper will argue that a consideration of S–R and cognitive controls inevitably has relevance to the topic of hierarchies. Cognitive and S–R processes imply controls at different levels in a behavioural hierarchy.

In proposing a joint cognitive and S–R control of behaviour, evidence will be reviewed which shows that the relative weighting of these processes as determinants of behaviour changes with: (a) development; (b) experience; and (c) pathology. In some cases, cognitive processes come to exert more control relative to S–R processes, as in the changes that accompany development. In other situations, S–R processes acquire more control relative to cognitive processes, as in habit formation and some cases of pathology where there is some loss of cognitive control.

Although there have been attempts to build bridges between ethology and psychology (e.g., (72,75,94,227)), a considerable gap still exists, even in the phenomena that form the topic of interest. The development of learning theory has always been largely within psychology, whereas sign-stimuli and displacement activities have fallen within the ethologists' domain, (216) and stereotypies and animal welfare are the responsibility of applied ethology (119,135). The favourite explanatory terms of classical ethology, e.g., sign stimulus and fixed-action pattern (216), have never had a secure place in psychology. Yet the observations that gave rise to these early concepts are no less valid today. It is hoped that the model will serve to integrate ethological and psychological approaches.

Models that consider how (a) external, stimulus, and (b) internal, cognitive factors jointly determine control, usually address only a part of the system and relate to a restricted set of tasks such as the Stroop (34). Workers in the rat (48) and human (164,165) areas make the occasional reference to phenomena that indicate modes of control generalizable across species. However, these areas of potential integration remain largely unexplored. The present article will propose a model with a potentially broad integrative power.

I hope to convince neuroscientists, psychologists (both of the human- and rat-orientated variety) and ethologists that it is worth looking over the traditional fences to see what is on the other side. Therefore, foolhardily, I stick my head above the parapet, and venture into such diverse fields as sign-stimuli in sticklebacks and schizophrenia in humans, using the S–R and cognitive distinction to look for common underlying processes of control. I cannot do justice to any given phenomenon, but I hope to broaden our perspective.

2. THE BASICS OF THE MODEL

Figure 1a represents the most basic assumption of an S–R theory, applicable to psychological and ethological schools. A stimulus (S) is assumed to have a certain strength of tendency to produce a response (R); that is, S has a response eliciting potential, which can vary from zero to some maximum value. The strength of this tendency will depend upon innate factors and learning. In some cases, the links between S and R are relatively strong (e.g., the sign stimuli of classical ethology).

The representation is only a first simplification to be adopted here. Complications and qualifications will later be discussed. A single direction of causation is not necessarily implied within every stage of the linkage. Depending upon the system under consideration, there might well be feedback within this chain of links. Neither does the term 'response' imply a single stereotyped motor output (cf. (197)). There might well be some flexibility. For example, a stimulus might have a strong tendency to elicit a response of turning left or of pressing a lever. At a fine-grained level
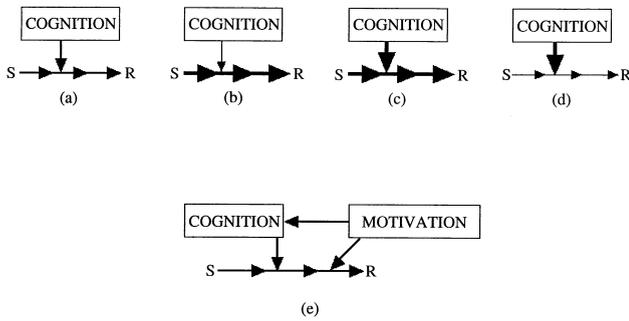
FIG. 1. Representation of relationship between S–R and cognitive processes. (a) Balanced weighting; (b) strong S–R and weak cognition; (c) strong S–R and strong cognition; (d) weak S–R and strong cognition; and (e) interaction with motivation.

these could be achieved by a variety of different muscular exertions. The term 'S–R' is used here to mean that given the stimulus, the animal has available to it a response to perform. This is based upon past experience or, in the case of some fixed action patterns, upon innate factors. In so far as information can be said to be encoded in the link between stimulus and response, it is of a procedural kind (45), and therefore can be described as more or less adaptive (in the ethological sense) to the existing circumstances.

Behaviour is also a function of cognitive processes. These are defined as processes that encode knowledge of the world in a form not tied directly to a particular behaviour (225,230). Information stored cognitively can be described as right or wrong with respect to the world (68). Cognitions do not prescribe behaviour but can be called upon in behavioural production. An animal might dither at a choice point in calling up cognitions and making an assessment of options (120). Cognition is shown in Fig. 1a as a top-down influence upon the links between S and R. It is difficult to see how cognitive factors might be translated into behaviour other than by exerting an influence over a motor pathway at least some of which must be shared in common with S–R processes.

The evidence to be reviewed will show that the relative weightings of S–R and cognitive links of Fig. 1a vary according to circumstances. There can be a strong S–R linkage present, and the cognitive factors might exert a relatively weak effect (Fig. 1b). This would represent a strong habit being performed in an automatic way. In Fig. 1c there is a strong S–R linkage and a strong cognitive factor. This could represent the situation where the animal is acting against the response-producing tendency of the stimulus, e.g., overcoming a strong habit. In Fig. 1d there is only a weak S–R link and consequently a strong cognitive link is needed in order to generate behaviour, e.g., negotiating a novel environment.

It is suggested that: (i) behaviour will always be a joint function of S–R and cognitive processes: and (ii) the change in relative weightings reflects adaptive considerations (43,225). It will be argued that where a behaviour is repeatedly performed under identical conditions it can most efficiently be mediated by a strong S–R link. S–R links cannot cope with sudden change, but are modified gradually over repeated experiences. Cognition engages limited capacity processes, which are costly and often relatively slow but have the advantage of flexibility and

the capacity to respond to rapidly changed circumstances (43,96,225).

It is suggested that the influence of motivational variables (e.g., sex hormones, hunger) on the control of behaviour can be mediated via either of the processes described, the S–R and the cognitive. Motivation can modulate the efficacy with which stimuli are able to elicit behaviour (e.g., oestrogen sensitising the efficacy of touch to elicit lordosis in rats (160) or by a link to cognition (e.g., hunger sensitises food-related goals (230)). The efficacy of sign stimuli depends upon such internal factors as testosterone level (216). A joint control can accommodate the dissociation that is sometimes seen in appetitive and consummatory measures of motivation. Figure 1e shows the way in which motivational factors exert control.

3. DEVELOPING THE MODEL

Figure 1 summarises the most basic assumptions that underlie the present paper. Figure 2 shows a development of the model. As one aspect of the control of behaviour, an array of external events (S_1, S_2,...) impinge upon the animal, shown as one set of inputs to Box C. As another aspect, there are: (a) cognitions, e.g., goals and expectations (Box A); and (b) physiological states, e.g., hunger (Box B). The cognitions activated depend to some extent upon the sensory events, but of course convey information that goes beyond that carried by these events.

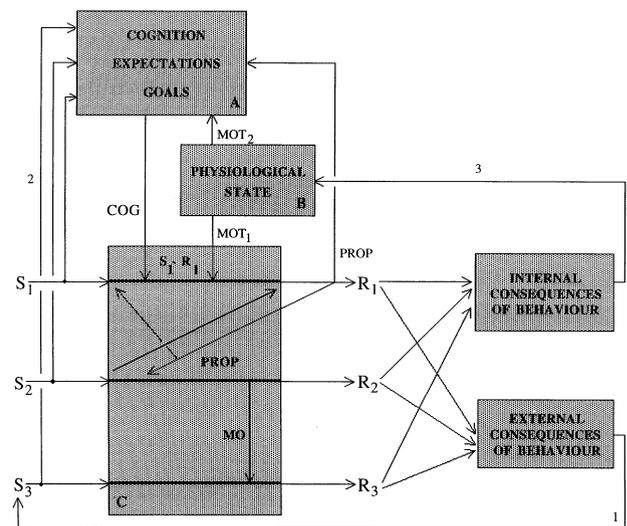A subset of stimuli, e.g., S_1 and S_2, tend relatively

FIG. 2. Model of the control of behaviour. A series of stimuli, S_1, S_2.. have a tendency to evoke responses R_1, R_2,.... The strength of association between a stimulus and a response is termed S–R (e.g., $S_1 - R_1$). The strength of S–R links is modulated by both cognitive (COG) and motivational (MOT_1) processes. A motivational factor (physiological state) influences goals, represented by link MOT_2. Box A represents the computation of cognitions, expectations and goals. Box B represents the contribution to motivation from such physiological states as testosterone and nutrient levels. There are proprioceptive consequences of responding (e.g., PROP) and other internal consequences such as nutrient assimilation or desensitisation with ejaculation (e.g., feedback loop 3). External consequences of behaviour change the stimuli impinging, e.g., loop 1. For example, a rival might flee as a result of an aggressive display or food become available as a result of gnawing. External information (via link 2) is compared with internal information. MO represents the link from one set of efferent stimulation to another.

directly to produce a particular component of behaviour R_1. In some cases, 'behaviour' might imply a link to a neural outflow to a gland or muscle but in general such rigid specificity is not suggested. Rather, I mean a range of possible behaviour within a certain functional class, e.g., turn left at a choice point using various muscle fibres (197). The type of link that lies between S and R is termed an S–R process. These processes can correspond to spinal links, but also to links involving the brain, even the cortex (discussed later).

Figure 2 shows that the strength of an S–R process is modulated by other processes: (1) motivational (physiological state); and (2) cognitive. Such control can have both the advantages of: (a) high speed of response to stimuli by means of relatively direct S–R processes; and (b) the facility for complex and often slow processing. The latter is based upon physiological states, goals, prevailing conditions and prior expectancies, as mediated by cognitive processes modulating the efficacy of stimuli to produce behaviour in accordance with goals. Link MOT_1 represents a direct modulation of S–R links by physiological states. Physiological state can also play a role in goal selection and hence the generation of flexible behaviour via link MOT_2 and then COG. That is to say, physiological states can bias goal selection towards appropriate targets and then link COG plays a role in producing behaviour.

The model points to some similarities between so-called reflex and non-reflex behaviour. First, both are modulated by cognitive and motivational processes, comparable to contextual supports in Tolman's ((230) p. 329) analysis. Thus a tactile stimulus can evoke a stronger response if accompanied by central electrical stimulation (193). Salivation depends upon motivational and cognitive processes such as state of nutrient deficit and attractiveness of food (18). A nutrient deficit potentiates both the capacity of food to elicit approach, involving instrumentally learned behaviour (links MOT_2 and COG), and ingestion (link MOT_1) (17). Sensitisation by oestrogen facilitates both instrumental activity towards a mate (links MOT_2 and COG) and the lordosis reflex (MOT_1) in female rats (160). Electrical stimulation of certain brain regions can enhance the capacity of tactile stimuli to elicit attack (MOT_1) (64). Following brain lesions, motivation might be high as indexed by a consummatory measure such as lordosis or ingestion of nutrients placed on the tongue, but absent as indexed by appetitive behaviour (149,189). Survival of intrinsically strong S–R links in the face of weakened cognitive links would predict this situation.

The model makes the site of feedback explicit and thereby extends Gallistel's (72) model. Feedback can be exerted through route 1 (i.e., changing the external world) and, in addition, through route 2 (the animal's perception of these changes). External consequences of behaviour feed back and modify the stimulus array ((195) p. 182; (197) p. 32). Thus, for example, the pupil light reflex alters the amount of light falling on the eye and the quantity of saliva produced depends in part upon the dryness of the oral cavity which then corrects dryness (56). Route 1 plus 2 represents part of the feedback that is involved in varying cognitive links as a result of a comparison between sensory information and goals, expectancies etc. (127). Through the changes in the world caused by behaviour, e.g., to S_3, external consequences of behaviour are fed back and compared with expectations in an iterative fashion (7,82,92) p. 260

(155). Feedback via route PROP represents proprioceptive information (2).

Within Box A there is a comparison of incoming stimuli and expectations on the basis of past experience. Depending upon the outcome of this comparison and via COG, specific S–R links are sensitised and others desensitised, so that appropriate responses are primed for production. These response 'possibilities' are given a bias but triggered only if and when the anticipated stimuli appear. Behaviour can either run its course, with a series of stimuli coming in sequence as expected, or the unexpected can occur. The unexpected will be detected by the comparison and the animal will then need to do a search from its possible actions for an appropriate response (cf. (82,83)). Behavioural inhibition can be exerted until a response is found. Internal consequences of behaviour (e.g., nutrient absorption) affect physiological state (e.g., nutrient gain, gastrointestinal illness), hence feedback loop 3.

As a cognitive process, goals, e.g., to reach a goal-box in a maze, modulate the capacity of particular stimuli (e.g., maze choice point) to evoke such behaviour (e.g., turn left) that in the past has been associated with meeting the goal (cf. (151)). For normal adaptive behaviour, the cognitive processes would depend upon goals being modulated by physiological states, e.g., hunger sensitises a goal representing food and thereby modulates the efficacy of stimuli in the maze to evoke behaviour directed to the food-related goal (18).

Stimuli can owe their capacity to generate behaviour either to innate organisation, e.g., sign stimuli, or to learning, e.g., S–R connections as a result of repeated reinforcement, or a combination of both. Thus the strength of links such as S_1–R_1 varies as a function of processes intrinsic to the link and by modulation from higher levels, e.g., via link COG. In the terms of Hirsh (96), an S–R process represents a 'performance line' link between stimuli and behaviour, whereas cognitive processes are 'off-line'. If, with repetition, the strength of particular S–R links increases, then a given stimulus will have a tendency to produce the same class of behaviour within a wider range of different cognitive sets, i.e., a certain autonomy from cognition will be attained.

Certain stimuli have privileged access to the control of behaviour (147) for a wide variety of both (a) other sensory events and (b) cognitions and physiological states also being present. An example is the orientation shown to calling out one's own name or the sign stimuli that elicit attack or fleeing in certain animals. For some stimuli, the strength of the behaviour-eliciting tendency can be so strong that behaviour is triggered in the absence of any facilitating modulation or even where the behaviour is at odds with the goals set.

Well-practised responses of animals running mazes are said to become 'ballistic' in the sense of developing some independence from conditioned incentive stimuli in the maze ((19) cf. (202)). As one way to account for this, proprioceptive feedback (2,31) is represented in the model (Fig. 2) by a link from response to input (PROP). In this way, there is the possibility of responses being organised in chains with S_1 evoking R_1, the feedback from which then serves as part of the cue for R_2, i.e., serial order in behaviour (2,118), p. 136. Such a sequence of events might well occur where there is not a rapid sequence of responses (31), but it

is not obvious that we can tease apart: (a) *feedback* arising from the response (PROP) triggering R_2; and (b) triggering at the level of response production, with the *output* triggering one response also tending to trigger the subsequent response, i.e., R_1–R_2. Feedback triggering might occur at the early stages of learning a task but Lashley (118) articulated why a time sequence of the kind: (1) proprioceptive feedback from R_1; and then (2) response R_2, i.e., PROP–R_2, cannot explain well-established and routinised fast skilled behaviour; a sequence of responses occurs too rapidly for there to be sufficient time. Contiguity alone can permit the firing of one neuron to influence another (79,91) p. 65; cf. (195) p. 176). This leads to a model in which a motor programme for prearranged sequences of responses is stored (a point argued by Alfred Kühn, as discussed by Lorenz (124), p. 317). In human performance studies, this is termed phasing (78).

To accommodate the motor input component, the strength of tendency to perform a response (e.g., R_3) is assumed to depend not only upon external stimuli (modulated by cognitive set) and proprioceptive stimuli that are linked to R_3, but also upon any habitually preceding response R_2 (79). This is represented by link MO. Although not shown, information within link MO would also be expected to travel upwards to the cognitive box, thereby representing the efference copy (72).

The application of the model will now be described, first in the area of neuroscience and psychology and then in the area of ethology. It is intended that common principles of control will be shown.

4. APPLICATION OF THE MODEL TO RESULTS IN NEUROSCIENCE AND PSYCHOLOGY

4.1. Modulation of reflexes

The literature contains frequent references to a distinction between reflexes and non-reflexes, the latter described in such apparently exclusive terms as 'motivational' (58), 'purposive' system or 'servomechanism' (73). However, Fig. 2, which is applicable to both classes of process suggests that reflexes and non-reflexes lie at different points on a continuum of weighting between S–R and cognitive processes. On the one hand, reflexes are modulated by higher levels and, on the other hand, goal-directed behaviour is effected by the exploitation of S–R links. Certain authors have attempted to delineate what is and is not a reflex, based upon such things as the absence or presence, respectively, of feedback (58). Consideration of the proposed model makes somewhat grey any such neat distinctions.

A closer look at so-called simple reflexes suggests joint control, and hence the model represents the assumptions of Dewey (46) and Sherrington (195) that the isolated reflex is something of a fiction. Both the intensity and direction of reflexes depend upon context (14). Lashley ((118) p. 163) wrote: ''I am coming to doubt the validity of the reflex-arc hypothesis, even as applied to spinal reflexes. There are many indications that the spinal reflexes are no more dependent upon isolated conduction paths than are cerebral functions''. Yet we must reconcile the speed of reflexes with the role of context, which the model can do.

Attention modifies the strength of the blink reflex, presumably by changing the strength of an S–R pathway (6). Anthony ((6) p. 168) writes:

''It is possible that the notion of reflex plasticity, although a familiar one to psychophysiologists, is a confusing one to some because of the involuntary and innate characteristics of such circuits. Such properties suggest a rigid and stereotyped action, controlled only by the properties of the eliciting stimulus. However, although a reflex response may be *obligatory*, the characteristics of the response (magnitude, latency, duration) may be markedly altered by concurrent influences from a number of levels of the nervous system''.

For ingestive reactions, Berridge (17) argues that a sharp dichotomy between 'mere' brainstem reflexes and affective processes of the forebrain as determinants of behaviour can be misleading in that the latter modulate the former.

That reflexes such as the sucking reflex show *accommodation* is a central feature of Piaget's (161) theory of child development. This involves flexibility, coordination, generalisation to new situations and modulation by feedback from consequences.

4.2. The orienting reaction

Certain stimuli evoke orientation (155). Stimuli are said to be compared against an internal model held in a working memory store and disparity evokes orientation. This implies a joint S–R and cognitive control. In terms of Fig. 2, a stimulus S_o has a certain strength of linkage to the orienting response R_o. This strength depends upon such things as the stimulus intensity and modality. However, the tendency will be modulated by cognitions including whether the current stimulus input matches internal representations. Some stimuli are voluntarily primed for attention, and then a match rather than a mismatch with expectation would increase the strength of the S_o–R_o link.

4.3. Cognitive set

Consider an animal given a history of reinforcement in the presence of certain discriminative stimuli. Following such training, stimuli S_5, S_6,... can tend to produce behaviour R_3, *only given a certain narrow cognitive set*, and R_4 for a different cognitive set (cf. (91), p. 107). For example, a green light given a few seconds before S_5, S_6 onset signals that one reaction R_3 would achieve an end-point whereas a red light signals that another (R_4) would do so. A more complex situation would be where the cognitive set varies rapidly as a result of changing circumstances and with it the modulation of S–R links.

In the literature on human performance, S–R links are said to be gated by controls at higher levels (114). Gating seems to correspond to a form of what is termed modulation here. The gate would increase the strength of certain S–R connections and decrease the strength of others. An experiment by Evarts and Tanji (60) illustrates this (114). A monkey was trained to either push or pull a lever when the lever was disturbed. A cue given prior to the disturbance indicated whether a pull or a push should be given. For both responses, the reaction became so rapid that it took the properties of a reflex (114). Thus two different S–R links were gated by two arbitrary prior cues.

The experiment of Wickens (245) might be interpreted in these terms, though the cues would not be arbitrary ones. Wickens trained subjects to lift a finger from an electrode in response to a warning cue, something for which a rather fixed motor response served well. However, most subjects transferred to the opposite motor response when the hand was turned over. Thus the response was one of end-point achieved, i.e., finger removed, rather than specific muscle employed. In terms of the present model, effective functioning could only happen as a result of a combination of fast reflexes gated by a cognitive assessment of the situations involving goals to be achieved.

A similar logic can be applied to well-trained animals performing a discriminative operant task in a Skinner box. The discriminative stimulus might, via cognitive links, modulate S–R connections between, say, the key and the response of pecking. The expression 'occasion-setting' (176) for stimuli that modulate other associations, such as an S–R link, seems to mean much the same as Skinner's 'discriminative stimulus' (197). That pigeons make an operant response, the form of which depends upon whether they are hungry and working for food or thirsty and working for water (143), might similarly be seen as modulating of particular species-typical responses via the MOT_1 link.

4.4. Stimulus equivalence and response equivalence

The model avoids the pitfall of defining S and R too narrowly, which would invite immediate falsification. If a learned S–R process exploits the consistent feature of the situation from trial to trial, then this cannot usually involve either the stimulus as defined in terms of, say, exact retinal stimulation nor the response as defined by particular motor neuron/muscular activity (197). For example, the actual leg movements involved in turning left in a maze will vary from trial to trial depending upon circumstances, i.e., motor equivalence (91,118). Tilting a maze slightly will alter the exact stimuli that impinge upon the rat and the necessary motor reactions, but the rat can still successfully negotiate the maze. Even flooding a maze will not disrupt a rat unduly. The way that even a well-trained rat achieves the end point of lever-pressing is different from response-to-response (49,197), and one can assume that the lever does not trigger identical sensory messages on each occasion (197). Rather, if we apply an S–R interpretation to a well-established habit, what is constant over a number of trials is: (a) the perception of a certain feature in the stimulus situation; and (b) a motor command above the level of the motor neurons, e.g., lower lever, project body through 90° to the left. Thus the model subsumes a range of individual S's and R's, having common features, under the generic term S or R (cf. (197)).

4.5. When there are no S–R links available to exploit

Suppose that amongst the sensory events there are no stimuli having privileged links to behaviour. The animal is in a relatively novel situation. A behavioural inhibition system might be switched in, to give time for scanning of cues or exploration (82,83). Alternatively, behaviour can involve 'dummy runs', vicarious simulations of the outcome of possible actions ((96,230) p. 206; (109)), which Tolman associates with consciousness. In a situation of

ambivalence, rats typically poke their noses into one arm of a maze and then the next before making a choice and Lewis (120) suggests that in so doing they are activating particular memories. In the absence of stimuli that have strong links to behaviour then weight will be given to high-level processing in order to establish cognitive maps, goals, expectations and extrapolations in terms of such sensory input as there is (146). The model predicts that, where there are only relatively weak S–R links, a strong potentiation from a cognitive link would be needed to effect behaviour.

4.6. Collaboration and competition

Behaviour suggested on the basis of stimuli (i.e., through relatively strong S–R links) might be at odds with the goals set. For example, suppose that a rat is trained in a + maze to run from the south end to the north (with a block applied to prevent it going straight ahead at the middle) and is reinforced for turning west at the choice-point (225,230) (See Fig. 3). It forms both a left turn S–R link and a cognition that food is to the west. In a case such as this where both the S–R link and the goal lead the animal in the same direction, then there is an additivity of their effects (177). However, suppose that after learning this the rat is then started from the north end. The goal representation would still be to the west, but the S–R links formed in the original position still suggest a left turn, which would now take it east and away from the food. There would be competition (177,231), the winner depending upon the relative strengths of the intrinsically strong but depotentiated S–R (left turn) link and the intrinsically weak but potentiated S–R (right turn) link.

4.7. Motor programmes and proprioceptive feedback

The evidence to be reviewed suggests that, with experience under constant conditions, the weight attributed to (a) external stimuli acting through S–R links, increases relative to (b) cognitions. Thus the same behaviour can be exhibited for a wider range of cognitive sets including even those involving goals at odds with the behaviour produced. However, in some cases the importance of motor programmes (e.g., link MO) and local proprioceptive feedback (PROP) increases relative to both (a) and (b). In other cases, although the weighting clearly changes, at present it is unclear as to which component is increasing in strength. For instance, the behaviour of rats studied by Carr and Watson (31), which bumped into the end wall of a maze whose arm was changed in length, might be explained by increased weighting being attributed to proprioceptive stimuli and/or motor programmes. However, it might have been based in part upon the rat responding on the basis of an
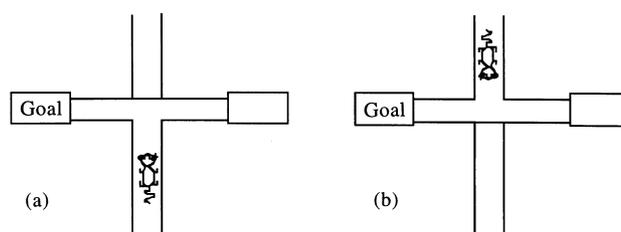

FIG. 3. Cross maze with rat negotiating: (a) from south; and (b) from north.

established cognitive map ((72,230) p. 78) and not taking the changed sensory matrix into account, or by a combination of all these factors.

5. APPLICATION TO ETHOLOGY

There are a number of phenomena in the ethological literature to which the model can be applied, and this section looks at a few of these. Although the phenomena have traditionally been studied by ethologists, it is clear that the explanatory model needed to explain them is one equally applicable to neuroscience and psychology.

5.1. Sign stimuli and cognitions

A building block of classical ethology was the sign stimulus, a stimulus that reliably triggers a particular species-typical behaviour (216). For example, a red belly or, according to anecdote, even a passing red Leiden post van, elicits attack in sticklebacks. In becoming cognitivised, contemporary ethology has largely turned its back on sign stimuli. This tends to create an unfortunate schism: the controls of behaviour can become dichotomised according to the tastes of the investigator. In emphasising the joint control of behaviour by stimuli and cognitions, the present model might start to bridge this divide. Although the stickleback responds to sign stimuli, it is also a creature of cognition in so far as, to quote Baerends (10), it is under the control of, for example, ''discrepancies between the feedback stimulation from the clutch and the optimal or expected values''. Thus, we need to explain how behaviour is caused and terminated by a combination of factors including the performance of species-typical behaviour and cognition in the form of changes in the environment (15). The proposed model suggests a framework.

Archer (7) proposed a cognitive theory in which aggression and fear are triggered by disparity between the actual state of the world and some inner model of how the world should be. However, he is left with the problem of explaining how certain stimuli are particularly effective in triggering these states even on first appearance, whereas other stimuli, presumably no less likely to create a disparity with expectation, leave the animal unaffected. A joint control could give the sign stimuli privileged access to the control of behaviour. Other external events would owe their efficacy in gaining control of behaviour to a comparison with expectation.

The phenomenon of supernormal stimuli (11), i.e., the capacity of exaggerated stimuli to evoke a particularly powerful response, remains a curiosity from classical ethology rather than a feature of behaviour that might be integrated into contemporary theory. In the present model this phenomenon would be represented by innately strong links between supernormal sign stimuli, S_{sn}, and particular species-typical responses, R_{st}.

5.2. Modal ('fixed') action patterns

'Fixed action pattern' (FAP) (124) refers to a rather fixed sequence of species-typical behaviour that is triggered by a sign stimulus and then tends to run a fixed course. Rather than being an ethological curiosity applicable only to birds and insects, FAPs exist also in higher primates (204).

Humans chew, swallow and yawn with the help of them. They are also evident in the stereotyped behaviour of human infants (see Section 5.4) and either become less evident with development or become adapted to normal rhythmic activities such as walking. An integrative model suggests that FAPs can be generated at least in part from processes that are also employed for non-FAP behaviour.

Early ethologists liked their behaviour to come in discrete packets, but on closer examination, FAPs are only relatively stereotyped and some (13,63) prefer the term modal action pattern (MAP), which is employed here. However, the sequence of components is usually fixed, R_1, R_2, R_3,..., and rarely starts with anything but R_1 (103). Occasionally a component, R_2, can be triggered by a different stimulus or form part of a different MAP. Once performed the tendency to show the MAP decreases, but the tendency increases as a function of time since last performance (13). MAPs might be interpreted in terms of an addition to Fig. 2 of a process involving timing and patterning, as shown in Fig. 4. In this way the MAP's interaction with other factors in the control of behaviour might be better understood (cf. (72,92) p.227).

A trigger stimulus S_1, termed a releaser (103), normally sets off response R_1. The addition to the model is that activation of link S_1–R_1 tends to both excite, and be excited by, activity in the MAP generator. Response R_2 could be triggered by a combination of MAP generator activity (MAP$_2$), motor links of the kind MO, proprioceptive feedback (PROP) and new stimuli S_2 that are present throughout or which arise as a result of the performance of R_1. In this case, the R_1–R_2 link (MO) would be innate rather than the result of experience.

Figure 4 added to Fig. 2 might account for some of the special properties of MAPs, as well as the properties that they share with other behaviour. Thus, behaviour can sometimes be a compound of MAPs and reflexes (103). Also, feedback is sometimes evident in MAPs, such that they can be adapted to the environment (13,32); the exact form of 'R' can involve some local feedback. Although for some MAPs, sensory and proprioceptive feedback modify the response, in other cases the output seems to be largely predetermined by central factors (13). This would seem to fit adaptive considerations: in some cases, e.g., swallowing, a fixed
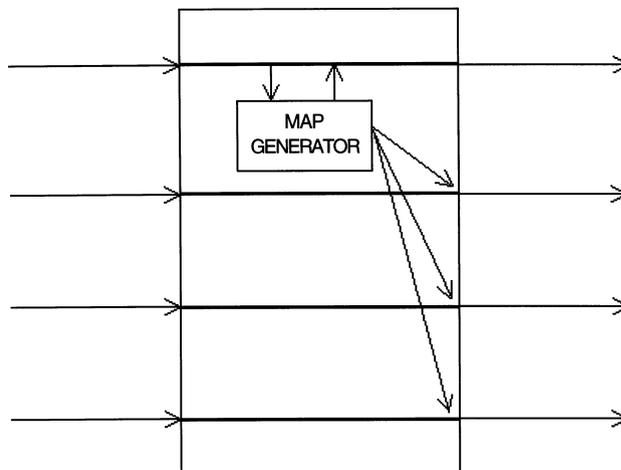

FIG. 4. Suggested addition to the model in order to account for modal action patterns (MAPs). The thicker line linking S_1 and R_1 indicates a strong connection here.

sequence can suffice. MAPs sometimes have some motor equivalence: the same endpoint of a given behaviour can be achieved by various motor patterns (103), implying negative feedback. Sometimes a MAP, once triggered, carries on to completion even in the face of altered environmental circumstances (i.e., whether S_2, S_3,..., are present or not), suggesting weak S_2–R_2 links (13). An unexpected stimulus can cause interruption of a MAP (13), possibly via top-down modulation. Motivational factors can facilitate or block rodent grooming patterns (62). A strong S_2 (e.g., an irritant on the back of a mouse) can result in a response R_2 (back scratching) that normally comes second in a sequence usurping control and displacing R_1 (face grooming) (13), which fits the assumption of joint control by an intrinsic MAP generator and external stimuli, as shown.

5.3. Displacement activities

A displacement activity is behaviour seen at a time of ambivalence, conflict or frustration and which seems irrelevant to the animal's principal activity (216). Their timing (e.g., breaking off a fight to preen) often appears bizarre. Suppose that there are stimuli present that would normally be sufficient to trigger the displaced activity, but that inhibition is exerted upon their tendency to do so. Removal of such inhibition is termed disinhibition. Adapting the idea that disinhibition is involved (127), the model suggests an explanatory approach. Displacement activities are sensitive to the strength of causal factor for the intruding activity (127). For example, the tendency to show displacement grooming is increased if there is a prior disturbance to the fur (63). Displacement activities correspond to behaviour that is simple, organised at a brainstem level, frequently seen in the animal's normal life, and which appear early in development, e.g., grooming, pecking (63). The cortex is attributed a role in the timing of such behaviour, not in its form (see later). Displacement activities commonly occur at times when goal-directed behaviour is disrupted (e.g., fatigue, thwarting, omission of goal object, ambivalence between two incompatible goals) (127), i.e., when top-down inhibition (via cognitive links) on behaviour might be relatively ineffective. A large disparity between expectation and actual state of the world represents a failure of current goal-directed behaviour and could disrupt cognitive control and allow an S–R process to seize control. There could be adaptive value in 'falling back onto' a more S–R mode of control when goal-directed strategies fail (cf. (127)).

5.4. Stereotypies

Stereotypies represent ritualised behaviour that appears to lack any obvious function or purpose (135), e.g., rocking and shaking by humans, tongue playing by calves and chewing by pigs. They are particularly evident in intensive agricultural systems, and are of welfare, ethical and economic importance. They appear to represent behaviour normally organised at a low level in a hierarchy (see later) gaining some autonomy from its original eliciting conditions (38,112,223). In terms of the present model, they represent a shift in weighting away from cognitive control. In Fig. 2, repetition might be due to the motor output for one bit of behaviour R_1 triggering another R_2 which then reciprocally triggers R_1 and so on indefinitely. Additionally,

proprioceptive stimuli from the performance of one part of the stereotypy might promote a second part.

The bases of stereotypies vary with experience (112,136), there being three developmental stages of acquisition (154):

1. Behaviour is goal directed, e.g., an animal will attempt to escape from a frustrating situation.
2. Behaviour becomes 'fixated' or 'automatic', but is only evident in the original situation.
3. Behaviour shows some emancipation from the original stimulus; it is performed even if the situation is changed. (Only in stage 1 can it be inhibited by anxiolytics.) For example, caged hens sometimes continue to pace against a door even after the door has been opened (136).

Parts of a similar sequence of stages are apparent in amphetamine-induced stereotypies. Initially stereotypies tend to develop out of the behaviour that the animal is exhibiting at the time that the injection is made, involving interaction with a particular object, e.g., sniffing or exploring (57). However, with time the behaviour becomes divorced from such objects and similar to ''the objectless fingering and mouthing stereotypies in schizophrenics'' (p. 12) (see Section 15.3). Ellinwood and Kilbey (57) report that stereotypies develop out of prepotent responses. Relatively strong S–R processes might normally form the basis of the behaviour, and these would get still stronger as a result of amphetamine, i.e., a reinforcement process (79,239). This represents a transition in which the weight attached to external stimuli increases and finally the weight attached to proprioceptive and motor factors increases relative to that of external stimuli. The opioid antagonist naloxone has a greater effect on reducing stereotypies earlier rather than later in their history of acquisition (37,112,187); naloxone insensitivity might well correspond to the switch to automaticity.

Something similar to the stereotypies of domestic animals is observed in human infants (212). Normal infants go through a developmental sequence of acquisition and loss of a variety of stereotypies in their first year. Children raised in social isolation show an exaggerated and more protracted display of such behaviour. Thelen (212) suggests that such patterns are organised at lower brain centres and normal maturation brings them under a restraining control.

This section and the last have shown that a number of results, in neuroscience, psychology and ethology might be better understood with the help of a single model with which greater theoretical integration becomes possible. The next section continues this theme, specifically in the context of motivation.

6. MOTIVATION

Motivation has been a topic of great concern to behavioural scientists taking various approaches, but fragmentation has often characterized the literature that has emerged. Implicit within the model proposed here, there is both flexibility of behaviour in enabling goals to be reached by various routes and more fixed, species-typical aspects of behaviour (19,219). Motivation plays a role in both aspects of control, the model indicating outputs from motivation going both to S–R links and to the goal-setting part of the system. This section focuses upon the relationship between

motivation and the S–R links. The goal-setting part will be discussed later.

6.1. Traditional psychological approaches

Feeding and drinking are controlled by external (e.g., taste, sight of food) and internal (e.g., nutrient state) factors. Internal state modulates the efficacy with which external stimuli trigger ingestion (17,183,218,219,247). That is to say, feeding and drinking are organised by neural circuits triggered by external stimuli (234,248) and modulated from higher-level controls concerned with tissue needs and predicted consequences of ingestion. An analogous joint control can be proposed for sexual behaviour (219). At times, both rats and humans ingest highly palatable substances to excess (106,217,247), it would seem *in spite of* a nutrient surfeit rather than because of potentiation from a nutrient homeostatic deficit signal. The links between taste and ingestion, though modulated by nutrient state, are not the slaves of it. The rat has a lexicon of stereotyped acceptance and rejection reactions to nutrients placed on the tongue (17). However, the reaction is not triggered by the physical property of the substance on its own. Rather the taste is processed in terms of past associations and current nutrient needs etc., which modulate a subset of available reactions.

The means by which nutrients are gained is important. When animals are presented with an operant task for intravenous or intragastric nutrients or water, if they succeed they do so by chewing and licking the lever at the time of pressing (148). This suggests that they are recruiting some fairly hard-wired lower-level controls underlying consummatory behaviour, exploiting prepotent S–R links (cf. (79)). Similarly, rats performing an operant task for the reward of drug infusion, gnaw and chew the cue light that predicts reward (232). Such observations offer some common ground with the classical ethological model of motivation, which emphasises the motivational significance of performing species-typical behaviour. Similarly, the fact that it is difficult to switch off ingestive behaviour by infusions that bypass the oral route (148,218) points in the same direction, to the importance of performing at intervals such MAP-like behaviour which can be *modulated by*, but not simply *driven by*, motivational factors.

Modulation by nutrient state might be relevant to the phenomenon of resistance to satiation (144,145). If behaviour such as lever-pressing for food is determined only by a goal such as nutrient repletion, behaviour would be expected to reflect faithfully the state of satiety. However, in many cases, animals that appear to be satiated by the criterion of not ingesting food, nonetheless continue to show operant behaviour that leads to food gain. If behaviour reflects the modulation of well-established patterns by motivation, it might develop some autonomy from these states.

6.2. The energy model—a classical ethological approach

The classical model of ethology involved particular stimuli playing a role in producing particular responses. This model has largely gone out of favour, though the data that gave rise to it are still valid. The present model suggests where the classical ethological model might be fitted into a broader framework.

Unlike models in psychology, that of classical ethology involved a build-up of 'action-specific energy' with the passage of time, energy being dissipated in the performance of species-typical behaviour (124,216). With some notable exceptions (e.g., (103)), subsequent ethologists tended to ignore this model, to reject it (8,39) or to consign it to the category of 'historical interest only' (51) preferring the psychologists' models. One problem with the energy model is the ease with which the notion of energy can be dismissed as a viable component of the nervous system, in spite of appeals to its *as if* explanatory status. However, identical predictions arise if one is allowed to speculate that in some cases neurons within the link S_1–R_1 in Figs. 1 and 2 can show both some spontaneous activity and increasing sensitivity over time since the stimulus was last applied. There is evidence for the existence of neurons (28,181) and circuits of neurons (26) with such properties though whether they are located as in pathway S_1–R_1 remains to be determined. Alternatively, changes in the activity of the MAP generator as a function of time (Fig. 4) might increase the strength of S_1–R_1.

Some behaviour still stubbornly fits the predictions of the Lorenz model (102,228), including play in human infants (45), though of course some does not (51). A viable model should assimilate those features of both classical ethology and contemporary theory that fit the data, whilst rejecting those that do not. The proposed model can do this, with its assumption that a determinant of behaviour arises from the strength of certain stimuli. Thus, such things as cognitions and nutrient depletion increase the *general* tendency to seek food and to feed, involving broad classes of behaviour. In addition, the tendency to engage a *particular* species-typical food-seeking behaviour increases as a function of the time since it was last performed. Even very weak stimuli might then be able to trigger behaviour (124).

The idea of species-typical behaviour with its own motivational potential might dovetail with the argument of some psychologists and ethologists that the performance of certain behaviours *per se* has some intrinsic reinforcement (57,79,93,98,104,144,219,228,239), self-stimulation (81), self maintenance (e.g., 'sucks for the sake of sucking') ((161) p. 48) and/or satiety ((54) p. 53) value.

Behaviour is activated and switched off by events at various levels (cf. (63)). Such things as restoration of nutrient state affect the overall direction of behaviour, to make any sort of food-directed behaviour less likely (as in psychological models), but performance of species-typical feeding patterns could act at a lower level to reduce their own tendency to occur.

7. COMPARING SPECIES

Whereas a number of mammalian species seem similar in their ability to use S–R processes, differences are evident in their ability to perform tasks that require cognitive processes (142). Passingham (159) compared rats and rhesus monkeys (*Macaca mulatta*) on a task in which an S_1–R_1, S_2–R_2 distinction was required, e.g., push a white door but pull a black door, and found that they did not differ on number of trials to attain criterion. However, the monkey is incomparably superior to the rat in solving problems where the cue for the correct response is remote in space or time from

the stimulus, involving a memory rather than a physically present stimulus (see Section 14.2).

In monkeys, what Mishkin et al. ((142) p. 73) term the memory system (comparable to the information within 'cognitive control', as the term is employed here) develops later than the habit system (comparable to the present S–R). By implication, these authors believe that there is a similarity between ontogeny and phylogeny in this regard:

''There is one area, however, in which the behaviourist position will always remain unchallenged, and this is in its applicability across the entire phyletic scale. Even animals with the simplest nervous systems are capable of response adaptation; the acquisition of information or knowledge, by contrast, may require the evolution of a system analogous to the cortico-limbo-thalamic pathway of mammals''.

There are some notable cases of invertebrates exhibiting a control of behaviour by cognitive processes (216). However, that is not to deny the evidence from the learning literature that there are important qualitative species differences (20) in the weightings given to S–R and cognitive processes. With cognitive development, both ontogenetically (discussed later) and phylogenetically, there is an increase in the possibilities for various forms of cognition to play a role in behaviour and an increase in the extent to which cognition can oppose S–R tendencies.

8. HUMAN STUDIES

So far, the review has mainly concerned the application of the model to non-humans. Though there is little contact between the two groups of researchers (75), in the present context similar considerations apply to human and non-human behaviour. In both cases, a joint cognitive and S–R model can be applied. This section will look at the possibility of synthesis through application of the model to humans, in particular to studies generally placed under the heading of 'human performance'.

8.1. Stimulus–response compatibility

In *stimulus–response compatibility*, the dominant role of S–R processes is evident where there is a compatible matching between the S and R required, e.g., point left in response to a left-pointing arrow (199). The reaction time is fast. It could be argued that privileged links exist to underlie such a task. Where incompatibility is involved, e.g., point right in response to a left pointing arrow, reaction time is slower. Presumably the time taken for processing within cognitive processes would be involved, with a slowing up of reaction time.

8.2. Automatic and controlled processing

An important concept in human performance studies is a distinction between automatic processing (unconscious, fast, inflexible, parallel, effortless) and controlled processing (conscious, slow, flexible, serial, effortful) (12,192). Broadly speaking, the distinction between automatic and controlled processing appears to map onto S–R and cognitive processes respectively. However, it is suggested here that there is no absolute dichotomy between controlled and automatic processes, rather a difference in weighting between the two.

The notion of the automatisation of behaviour with practice has a long and distinguished history in human psychology (William James, cited by Norman (150), and also (123,163,167,172,173). With extensive repetition the weight of control shifts from controlled to automatic processing thereby circumventing time delays that might otherwise be involved in cognitive processing (5). Automaticity arises where, with practice, there is a consistent and repeated mapping between stimuli and responses (123). (Interestingly, a similar idea, now largely forgotten, was proposed by Guthrie (89) to underlie habit formation in rats running mazes).

Although, when a task is well practised, information between S and R does not need to travel through the higher-level cognitive processes, the model suggests that they are still involved in behaviour. The cognitive set still sets the stage for the responses that can be produced within a framework of goal-achievement, e.g., a prior instruction to whisper or shout the 'now automatic' response, as requested by the experimenter. As Logan ((123) p. 512) notes: ''phenomenal experience suggests that automatic processing is closely controlled''. Behaviour exhibited when on 'automatic pilot' is generally both coherent and goal-directed. In well-practised reaction time tasks, the subject is aware of the goal and expected response, but when the target is presented, the response is performed very rapidly without awareness (151). An error will come into awareness, presumably via feedback routes 1 and 2. This suggests a potentiation of certain S–R pathways by prior attentional and goal-directed factors.

8.3. Competition between processes

A compatible S–R mapping that is at odds with the task required can strongly interfere with goal-achievement. In this case, conscious control has difficulty overcoming control exerted by the lower-level process. The best-known example of this is the Stroop task (34). A subject is asked to name the colour (e.g., red) of ink in which a word (e.g., GREEN) is written. Naming 'red' is interfered with by a tendency to respond 'green'. Rather like top-down potentiation, Cohen et al. (34) argue for sensitisation:

''Attention can be thought of as an additional source of input that provides contextual support for the processing of signals within a selected pathway''.

They suggest that few, if any, processes are immune to some controlling influence of attention.

The distinction between controlled and automatic processing is relative rather than absolute (34). Task A that is performed in controlled mode when in conflict with a more familiar task B can be performed in automatic mode when in conflict with a less practised task C. This fits the present model where the mode of control depends upon the relative strengths of S to R mappings.

8.4. Drug taking

There is evidence that a history of taking such drugs as opiates leads to an increased weighting of automatic processing (214,232,239), with some bypassing of goal-direction

that was evident in the early stages of acquisition (180). Robinson and Berridge (180) see a similarity with obsessive–compulsive disorder (see later). Whereas urges to take drugs can remain cognitively mediated (214), when in the presence of the instruments used for taking the drug, weighting can switch to a more automatic process (214,232). Thus even in the absence of an urge, the habitual user can be triggered by cues with strong associations with drug taking. Tiffany (214) suggests that if cognitive capacity is occupied, as in a stressful situation, it could prove unavailable to oppose drug-taking as driven by more automatic processes. Cigarette smoking shows many of the characteristics of an automatic activity (214,243).

9. ADAPTIVE CONSIDERATIONS IN SHIFTING THE WEIGHTING OF CONTROL

From adaptive considerations, why should there be a switch from cognitive (controlled) to S–R (automatic) processing? Controlled processes are of limited capacity and generally relatively slow compared to automatic ones (77). The capacity of automatic parallel processes would seem to be unlimited. The advantage of freeing a limited capacity system for more demanding tasks such as vigilance and association formation is not difficult to appreciate. There is also the bonus of speed.

If the controlled processes are of limited capacity, there is presumably a cost attached to employing them (cf. (92) p. 319), a mental currency that can notionally be measured in 'action units' (107). Spending units on the organisation of motor responses means that they are unavailable for other tasks. Hence there is adaptive value in switching to automatic control, which involves freeing some processing capacity, and mental processes can be occupied by other tasks. This occasionally proves maladaptive as, for example, in everyday errors such as when we follow our familiar route and end up somewhere we don't want to be or even in serious accidents (150,172,173), but presumably in general it is of adaptive value.

10. LEARNING AND THE CONTROL OF BEHAVIOUR

The role of learning has been implicit in much of the discussion so far. This section relates the model more explicitly to the body of knowledge entitled 'learning theory'. It investigates the extent to which learning can be understood in terms of changes in cognitions, changes in S–R connections or both. The question of 'what is learned?' has already been extensively investigated by learning theorists, and this section relates this discussion to the model. Theorists have also asked the related question—how do cognitions link to muscles? However, much less attention has been paid to the related questions of: (a) the relevance of this discussion to the control of behaviour; and (b) the possibility of a change in weighting of 'what is learned' as a function of experience and other factors. The section will emphasize these considerations.

Some distinct positions on the question of what is learned have been taken, as follows.

1. Changes in S–R links are a viable way of explaining learning (105)
2. S–R theory is wrong and is now at best of historical interest only (cf. (19,73,229)) or of very limited application to a few innate reflexes (103).
3. S–R theory and cognitive theory say much the same thing but in different words or with reference to different explanatory systems (110,185).
4. There are distinct S–R and cognitive processes that can complement or compete with each other in the control of behaviour (68,133,142,222). That is to say, learning occurs at different levels (4,141,171,215,242).

Position 4 is adopted here, i.e., changes in either S–R links or cognitions or both can be reflected in changed behaviour. Kimble (113) presents evidence for the parallel formation of cognitive expectancies and S–R associations, with the cognitions able to exert inhibition on the S–R links. Possibly relevant to this is the observation that salivation can be stronger in decorticated animals. Miller ((138) p. 261) notes that some theorists:

''...assume different levels of learning—a lower S–R one to explain stupid behaviour and a higher cognitive one to explain intelligent behaviour''.

In a similar vein, Oakley (153) writes:

''The straight alleyway, Skinner box and Pavlovian chamber are not ideal places for thinking animals to display their cognitive skills, and this may be the reason why the neodecorticate has so often outshone his normal counterpart in these situations''.

Mishkin et al. ((142) p. 72) refer to the learning of an ''approach response, as an automatic consequence of reinforcement by food'', this being ''not cognitive information but a non-cognitive stimulus–response bond''. This learning is said to reflect ''the changing probability that a given stimulus will evoke a specific response''. Implied by the description of the response as 'approach' is the assumption that even for such a habit the animal has not learned a fixed set of motor reactions, in keeping with the assumptions made here. Mishkin et al. obtained evidence that ontogenetically the cognitive system is slower to develop in monkeys than is the S–R system. They suggested that the corticostriatal system plays a crucial role in habit formation.

Some current theories involve a mapping between stimuli and responses that bears some familiar echoes of psychology's S–R past, though cognition is now introduced in the intervening variables (34). Also the contemporary distinction of declarative vs procedural (45) seems similar to the old cognitive vs S–R dichotomy.

Animals can learn some responses irrespective of context. Suppose rats are placed in a maze containing three arms at 120° to each other. The correct response always consists of a right turn, irrespective of the arm in which the rat is placed. Rats can learn this response, which presumably involves an S–R link (131). In response to food reinforcement, animals can learn an arbitrary discrete response, such as a head turn or the raising of a leg (131). Hippocampally-lesioned rats (discussed later) lose cognitive capacities and act like the predictions of pure S–R theory (96). Rats can learn tasks that involve either: (a) a consistent response irrespective of goal place achieved (e.g., in a + maze (Fig. 4), always turn left); or (b) arriving at a consistent place irrespective of the response needed to get there (e.g., in a + maze, always take the west turn) (231). This suggests that, in situation a, where

stimulus and response are constant, with repetition behaviour is dependent simply upon S–R links. However, we should not underestimate the rat's capacity for utilising a richness of cues (74). It might be exploiting information about place and conditionally increasing the attraction of the two alternative goal-locations according to orientation or location in space. Situation b was learned faster: rats found it easier to learn a place regardless of the response needed to get there.

10.1. Some qualifications to an S–R model

One problem with S–R theory was that 'response' was defined rather liberally, e.g., as anything from the activation of a single muscle fibre to the building of a skyscraper (John Watson, discussed by Skinner ((197) p. 42) and Tolman ((230) p. 6)). With such scope, it is difficult to imagine any behaviour that could not be accommodated under the S–R heading. Thus, if one goes too far in the macro direction, the term S–R seems meaningless. I do not use 'response' to cover all classes of behaviour, but to refer to a circumscribed bit of, to some extent predictable, behaviour that follows closely the exposure of the animal to particular stimuli (cf. (197)). (Fuster (69) considers a similar level of organisation). The notion is tied to a history, either of the individual or the species. However, as noted earlier, if one goes to the micro level then it is difficult to see how the flexibility of behaviour can be accounted for on the basis of learning links with motor neurons. Even stereotyped animals consistently turning, say, left in a maze and animals showing modal-action patterns do so with some degree of flexibility in their motor output. Thus the R of S–R needs to be something between the extremes, e.g., turn left at a particular choice point.

10.2. Some qualifications to a cognitive theory

Whereas the terms of S–R theory need to be moved slightly away from motor neurons to deliver a viable rat that is not thwarted by, say, a slight tilt in the maze, so the terms of a cognitive theory need to be related in some way to motor neurons for the rat not to be left buried in thought. Cognitions must make contact with the outside world through muscles (45,72). The present paper emphasises that cognitions will exploit links between stimuli and responses in their expression as behaviour by means of modulation of these links. When the considerations discussed in this and the last section are taken into account, a meeting ground between cognition and S–R is evident.

10.3. A working model

Although the distinction between storing information as cognitions or as S–R links is clear, control cannot be an either/or phenomenon, dependent exclusively upon one or the other process. Various weightings of control could be exerted by either process depending upon the strengths of the links. Cognitive and S–R controls could reinforce their effects or compete, which is indeed seen in practice (177), discussed earlier. The weightings might be expected to shift over time, as discussed in the next section. For example, as noted, with repetition there is evidence that S–R control is strengthened.

Changes in the relative strengths of factors

With experience, greater weight becomes attached to stimuli in the control of behaviour, relative to cognitions. Simply repeating behaviour in a given situation might well be sufficient to strengthen links between the stimuli present and behaviour (79,239). As was noted earlier, with further experience it appears that the weight attached to motor programming changes such that behaviour can become more ballistic and less under either cognitive or external stimulus control.

Animals learning a maze ((111,129) p.426 (130,230) p153) or Skinner box (48) tend to start out in cognitive mode and then with extensive practice switch into something like an 'auto pilot', S–R mode in which the role of the goal and associated cognition becomes less evident. This can be revealed by looking at the rat's reaction to a food substance (reinforcer) after the substance has been paired with gastrointestinal illness, which is described as devaluing the reinforcer. After initial training, a rat's instrumental activity is sensitive to reinforcer devaluation (i.e., cognitively mediated) but after extensive training it loses this dependence, suggesting a strengthening of S–R links such as to gain independence from cognitive processes encoding reinforcer information (1). Rescorla (176) found that even if the reinforcer was devalued such that none was ingested, rats still performed operant behaviour that had been rewarded with this food, which he suggested might be explained by a residual S–R process. Sensitivity to reinforcer devaluation means that the goal state as represented in Box A in Fig. 2 is still influential in exerting modulation. Rats trained in a T-maze with food to one side and water to the other and run for a series of trials hungry tend to continue the same response even when food-satiated and thirsty (110). Again, this suggests that habit can override a goal representation.

Avoidance behaviour that takes the form of jumping over a chain or negotiating around obstacles can continue after the chain or obstacle has been removed (61,74,152), suggesting development of some autonomy from stimulus control.

Rescorla (175) looked at second order conditioning. A rat was taught an $E_1 \rightarrow E_2$ association, E_1 being a light and E_2 a shock. It was then exposed to an $E_1' \rightarrow E_1$ contingency, E_1' being a tone. E_1' was never associated with shock. E_1' acquires a fear-evoking capacity. However, extinction of the fear reaction to E_1 did not extinguish fear to E_1'. It is suggested that the system short-circuits the cognitive sequence $E_1' \rightarrow E_1 \rightarrow E_2 \rightarrow$ (behaviour) and forms an $E_1' \rightarrow$ (behaviour) link. Speed could well be advantageous in such a situation. In experiments on amphioxi, Razran ((171) p. 65) noted a tendency for conditional responses (CRs) to continue even after unconditional responses (URs) had been habituated. In humans frequently triggered memories also appear to short-circuit certain cognitive processes and go more directly to response production (33).

10.4. Strengthening behaviour

It is suggested that, corresponding to the two processes underlying the control of behaviour, there are two processes for strengthening behaviour. First, at a cognitive level, feedback on the consequences of behaviour occurs and a comparison is made at a high-level between expectations and

consequences. Early in a learning task, cognitions of the kind 'food is by the window' would be strengthened as a result of experience. Secondly, it is suggested that there is a process of strengthening S–R connections merely by repetition (cf. (79,89,128,239)). This could play a part in the generation of stereotyped behaviour. After control has moved to a more automatic mode, there is reason to suppose that the cognitive comparison process still occurs. Errors such as that of the Freudian slip are quickly noted by the speaker. Even well-trained animals, presumably operating in an automatic mode, will extinguish in time when reward is removed. The model suggests that this would involve cognitive control exerting inhibition upon S–R controls.

10.5. Operant and respondent behaviour

Some behaviours are more strongly elicited by stimuli, whereas others are the outcome of internal decisions, albeit ones that are informed by external circumstances (197). In the latter category, one might want to place operant behaviour exhibited in those conditions where no cue to reinforcement availability is given. Vanderwolf and Robinson (235) note that what they term voluntary behaviour can readily be shaped by operant procedures whereas a number of what they term involuntary behaviours are resistant to shaping. Razran's ((171) p. 82) suggests that ''spontaneous operant behaviour is a developmental emergent of corresponding respondent manifestations''.

10.6. Frustration and fixations

Maier (132) trained rats with a Lashley jumping stand in which either a consistent position (e.g., jump to the position to the right) or a consistent target (e.g., the black circle) was reinforced. Rats learned this task. If the problem was made insoluble by inconsistent reinforcement, e.g., sometimes the left choice and sometimes the black circle was positive, rats adopted a stereotyped response, e.g., always jump to the right or always approach the white circle. When the problem later became soluble by the introduction of consistent reinforcement (e.g., black circle is now always positive), stereotyped behaviour was more resistant to change than was comparable behaviour established by consistent reinforcement (e.g., white circle had always been positive) and now put on extinction. It would seem that when a cognitive solution is impossible, weighting is switched to an S–R process. The strength of the switch is stronger than that which occurs simply as a result of repetition of a rewarded response. Maier (p. 31) argued that frustration caused not simply a disruption of behaviour but made a positive contribution in that it ''introduces a type of behaviour'', a type that is not goal-directed. The response that became fixated tended to be the one that was in Maier's terms most 'available' in the sense of being the response the rat showed on initial exposure to the test.

10.7. Taste-aversion learning

Throughout this paper examples are given of information first stored cognitively being transferred to a more automatic form. By contrast, taste-aversion learning is an example of where information is held initially in an S–R form and then later extended also to a more cognitive form. A rat, or even the occasional psychologist (49), experiencing a noxious after-effect of a particular flavour exhibits a rejection reaction to the flavour but typically still shows goal-directed behaviour towards the food. Only on subsequently encountering the food is goal-directed behaviour towards it attenuated in parallel with the reaction to the taste. In terms of Fig. 2, information is held in Box B and via link MOT_1 immediately affects an S–R taste–reaction link. However, only when the taste (S) is encountered again are cues associated with the taste devalued such that an influence is exerted through link COG.

10.8. Awareness and levels of learning in humans

Razran (171) argued for the existence of different levels of learning, higher levels building upon the lower. The relationship between the higher level and the lower (p. 24) ''will be either synergic or antagonistic''. In salivary conditioning, Razran ((171) p. 139) notes that the psychological attitude a subject adopts can have either a positive, a negative or no effect upon the response. Awareness can be important in autonomic conditioning. Awareness of the contingency seems to come first and autonomic conditioning second (42). According to the 'necessary-gate' hypothesis (41), awareness of the conditional stimulus–unconditional stimulus (CS–UCS) relationship is a necessary but not sufficient condition, and is a gate but not analogue condition, for autonomic differential classical conditioning. However, although awareness is necessary for the establishment of conditioning, when extinction conditions are applied the subject can articulate the belief that the UCS will not follow the CS but still show an autonomic reaction to the CS (42). This suggests a move to a more automatic mode of responding.

In humans, there is evidence that learning occurs at different levels in parallel. Normal subjects transfer their conditioning (i.e., generalise from one CS to another) more easily to semantically related words (e.g., from 'surf' to 'wave' rather than 'serf'), whereas young children and schizophrenics (see later) transfer more easily along phonetic dimensions ((171) p. 277). Under fatigue or intoxication, normal adults revert to the phonetic generalisation mode. Razran ((171) p. 325) speculates that mental abnormality represents disparity between the different levels, e.g., unconscious vs conscious learning. At least two factors play a role in the placebo aspect of pain relief: (1) learning through direct experience of pain relief; and (2) expectancy through knowledge, e.g., being told about an analgesic effect (236).

10.9. Summary

The evidence reviewed here supports a model in which learning can occur at more than one level, and thereby this learning becomes manifest in exerting an influence on behavioural control at more than one level. Corresponding to a shift in the level of 'what is learned' as a function of experience, the weighting of control can shift.

11. HIERARCHIES OF CONTROL

The notion of a weighting between internal and external factors in the control of behaviour, control being exerted at different levels and a shift of weighting with experience

((116) p. 191) leads logically to the notion of a hierarchy of behavioural control. This section will explore the relevance of the notion of hierarchy to the proposed model. That the controls of behaviour are organised in a hierarchy has had a distinguished history in behavioural science, though the literature on this topic has relatively little overlap with the theoretical considerations discussed here. It is useful to distinguish hierarchies of connection and hierarchies of classification (99). The present account assumes that there are hierarchies of connection as well as classification.

Hierarchies have been proposed by researchers into the psychology (24,72,97,101,182,215,221–225) and ethology of animal behaviour (10,13,38,40,63,116,124,216,242), the control of human performance (27,53,87,128,151,167, 199,233), human development (45,184), physiological psychology (36,69,140,178,189,248), abnormal behaviour (67), control theory (166), artificial intelligence modelling (205,246) and the neurophysiology of movement control (Hughlings Jackson, see (208)).

Given that so many are agreed that the controls of behaviour are organised hierarchically, it is surprising that there is little cross-border cooperation or even contact between theorists. That hierarchy either has no place or a very insecure place in textbooks of ethology (51), and psychology indicates the lack of theoretical organising structure in behavioural science. Hierarchy fails to make even an index entry in many of the better known texts. This lack of integration is surprising since the various models have something in common: a hierarchy extends from broad and abstract layers at the top (goals, intentions, cognitive maps) to the more specific and restricted (e.g., motor neurons, specific bits of behaviour) at the bottom. In Fig. 2, upper layers of a hierarchy correspond to cognition, motivation and general goals to be pursued whereas the lowest level corresponds to motor neurons. Learning of cognitions affects the hierarchy at a high level. S–R learning is represented at a lower level, strengthening the relation between stimuli and a level somewhere above motor neurons, corresponding to coordination of activity in a particular direction. Hierarchies have the facility for information stored at one level to be transferred to a different level (97), automatisation corresponding to increased weighting being given to a lower level.

For a hierarchy to function, higher levels need to receive feedback from lower levels on the progress of command implementation (205). In addition, the hierarchy is not static (10,213), p. 49; (233): lower levels can influence the decision-making at higher levels, something more like a heterarchy. Kortlandt ((116) p. 245) presents evidence that:

''...in the long run a subordinate instinct, especially when regularly and strongly activated by environmental stimuli, is able to *prime the tendency* next above it''.

Thus although by analogy (72,87) the President is at the top, the generals in the middle and the foot soldiers at the bottom, the generals occasionally have a line to the White House. In the model proposed, not only do the generals have a line but they are capable of usurping power occasionally and dictating national policy. In William James' famous case (cited by Norman (150), the link between (1) the bedroom and taking one's clothes off and (2) getting into bed was so strong that the whole body was persuaded in this direction in spite of the existence at some level of the goal of merely changing for dinner.

If a 'hierarchy' is not static, can it be a hierarchy in any meaningful sense? My answer is yes, on the grounds that in each hierarchy there is a divergence going from top to bottom, e.g., a single item within conscious awareness at the top, going through successive branches to millions of motor neurons at the bottom. The top level is assumed to be the executive, and even if lower levels can usurp power they might do so through engaging the top level.

12. CONSCIOUSNESS

In the terms developed here, it is suggested that consciousness is a specialised aspect of cognitive control (9) and corresponds to a high-level in a hierarchy (9,150,173,194). Much behaviour can be organised perfectly well at an unconscious level. Consciousness can be occupied with other things, and need only be alerted when things don't go according to plan ((92) p. 281), when novelty is involved or when we must overcome a strong habitual response or temptation (151).

The model fits some of the ideas of Wilhelm Wundt (see (147)). Wundt suggested, as a criterion of automaticity, a mapping between a sensory event and a motor action that does not depend upon conscious *guidance*. However, the efficacy of the link does depend upon an appropriate goal being in consciousness, involving the kind of joint control expressed in the present model. In the present analysis, there is the facility for such mediation but, on occasion, links can be so strong that actions can run counter to the goal.

Given that much behaviour is organised at an unconscious level, what is the adaptive value of consciousness (84)? How can consciousness effect adaptive control, since much behaviour is organised at a speed too fast for a sequence (1. stimulus) → (2. conscious awareness) → (3. conscious decision) → (4. action) (122). Therefore, how did it evolve?

A possible approach is as follows (224). (a) Some actions that can be organised at a low level even in the absence of conscious awareness can also be organised and effected by conscious processes, albeit more slowly. (b) Even when speed is such as to bypass moment-by-moment involvement, higher-level processes can still modulate the strength of connections underlying behaviour organised at a lower level. For instance, a state of fear arising from fully conscious processing might sensitise our startle reflexes to a sudden noise without processes involving conscious awareness being part of the pathway mediating the S–R link.

Having the conscious aim of committing aggression, someone might well fire a gun at the sight of a trigger stimulus (224). This does not mean that a conscious representation was involved in the causal sequence but neither does it mean that conscious intention was irrelevant. Although conscious decision-making does not need to enter the temporal sequence leading to trigger pulling, it might play a biasing role. However, even without the conscious intention to be aggressive, if there is a strong S–R linkage present, a powerful trigger stimulus might evoke an aggressive reaction, such that conscious intentions would be at odds with the result that prevails. Such issues are of central concern to theories of ethics, responsibility and law.

Weiskrantz (241) notes that patients with the amnesic syndrome or blindsight are able to show sensory-motor actions without conscious awareness. He suggests that they:

''...can process information if it leads to a straightforward and unambiguous route from stimulus to response, in the absence of 'thought'.''

13. DEVELOPMENTAL EFFECTS

Either explicit or implicit within the literature on development is the idea of a changing of the locus of control of behaviour. Development is associated with gaining autonomy from sensory control (23) and acquisition of top-down control over behaviour that is organised at a lower level. Reflexes become integrated into cortical control (161). Such control will perhaps most usually be inhibition, but excitation might also occur. The infant moves from dependence upon sensory stimuli (S–R processes) to the use of representational capacities involving matching sensory information with internal representations (cf. cognitive mediation) (45).

In rabbits, reflexes such as washing and scratching, which can be elicited in early postnatal life by specific stimuli at specific body regions, later become: (a) spontaneous; and (b) unresponsive to the original stimuli ((171) p. 81). The stimuli again become effective following decortication or anoxia. The feeding behaviour of many neonatal animals is independent of food deprivation, and only with experience does motivation acquire control over feeding behaviour (100). (see also Section 6). This suggests that there are innate species-typical feeding processes at a low level in a hierarchy and with experience they become modulated by motivational factors. The sucking reflex in infant rats is triggered at first by the presence of a nipple irrespective of the state of nutrient balance. As development proceeds so sucking comes to reflect nutrient need (90). In some cases, patterns shown in infant animals, human and non-human, reappear as regressions in the adult animal ((54) p. 239 (45)). In older people suffering from degenerative diseases of the nervous system, a reappearance of infantile searching, oral orientation and sucking movements can occur. The loss of stereotyped behaviour by human infants is a part of normal development ((212); see Section 5.4). In human infants, by 3 months, the sucking reflex can be utilised to obtain an arbitrary goal such as changing illumination levels (23).

In human infants of 5–6 months of age, visually-guided reaching has an almost compulsive look to it (165). They reach along the line of sight even though a Plexiglass barrier thwarts behaviour, whereas a detour from the line of sight would solve the problem. Development of the frontal lobes corresponds to development of the capacity to inhibit reaching along the line of sight (165). In a similar way, monkeys with frontal lesions have difficulty in thwarting a reaching movement (see also earlier).

Children of 14–18 months can follow a verbal instruction, e.g., 'give me the teddy bear', but when a rival attraction is nearby such as a toy dog, the first reaction might be thwarted by handing the dog to the experimenter (125). A child being asked to put rings on a stick has difficulty reversing the behaviour in response to the counter-instruction to take them off. Rather the child will continue with the first task to completion. Luria and Homskaya argue ((125) p. 357) that ''The behaviour of a small child can be initiated by a verbal instruction, but it cannot be *arrested* or *reprogrammed* by the instruction''. They suggest that the development of the capacity to follow chains of actions corresponds to the maturation of the frontal lobes (see earlier).

Rothbart and Derryberry (44,184) see development as being a process of *reactive* performance giving way to *active* performance. The nervous system is assumed to develop more rapidly at the lower hierarchical levels, which reach maturity before the cortex. Maturation of higher levels corresponds to increasingly fine inhibitory control exerted top-down. Certain reflexes that are organised at the level of the brain stem (e.g., Babinski) and present during the first months of life are progressively inhibited with age. However, acquisition of high-level control is not merely a process of more inhibition being exerted since new forms of reacting to the environment also emerge and it is assumed that these are mediated at the higher level.

An object can be located at one of two places, A or B, shown to the subject, a distracter imposed and then the subject's choice allowed ((35); see Section 14.2). Humans younger than 6 months and monkeys with lesions to the frontal lobes can only solve the task provided there is no delay between cue and testing. For even a 2 sec delay they tend to repeat a response reinforced previously. Human children of 5 years or more can successfully retrieve with a delay of 2 min or more.

14. BRAIN REGIONS AND THE MODEL

It is desirable that ideas expressed in rather abstract terms can be related to actual neural structures (cf. (36)). This section looks at some neural structures whose function might be related to the S–R versus cognitive distinction. Ideally, we would like to be able to associate shifts in the mode of control with changes in different brain regions. Also, some behavioural abnormalities might be understood *in part* as a shift of weight between regions. However, a caution is in order: it will be argued merely that aspects of abnormality might be understood in these terms. Thus there are similarities between frontal lobe and hippocampal damage. In turn, these have similarities with some aspects of schizophrenia (discussed later). Throughout, there is some loss of cognitive (top-down) control. The fact that the paper highlights similarities should not be interpreted as playing down the important differences and the intention is not to view all of these conditions as being represented simply by removal of the top layer in a hierarchy.

14.1. The motor cortex

Rats and cats that have been decorticated show ((235) p. 473):

''...preservation of the many distinctive motor patterns normally observed in these species''.

Subcortical mechanisms are largely able to generate the 'motor score' (cf. (79,149)). The cortex plays a part in determining when behaviour occurs (cf. (92) p. 27). This

suggests a cortical involvement in cognitive control over S–R links formed subcortically. The capacity to perform behaviour survives decortication, but typically timing and coordination between the component activities in relation to environmental events and other components of behaviour is lost (234). Vanderwolf (234) suggests that, in intact animals, the cortex acts upon brainstem-cerebellar output circuits to activate and inhibit, to coordinate with environmental events. In fish, amphibia or reptiles, destruction of the forebrain usually neither abolishes any given behaviour nor does it seriously affect its topography but changes the frequency with which it is exhibited. He quotes (p. 87) Sherrington that one of the prime functions of the motor cortex is ''breaking up compounds already constructed by lower centres''. With extensive experience, there is evidence that some motor functions organised in the motor cortex can be ''relegated to subcortical structures'' ((71) p. 161). However, other functions, though switching into a more automatic mode still remain organised cortically (117,92) p. 166 (174). Some layers of the hierarchy can be bypassed in some cases by the pyramidal neurons from the motor cortex (73,99).

14.2. Frontal lobes

The frontal lobes have a role in mediating cognitive control, i.e., tasks that involve representations and hypotheses and which cannot be solved on the basis of current sensory input alone (80). As Luria and Homskaya (125) express it (p. 353), the role is:

''...to anticipate future events, to provide 'prognoses' of the probability of their occurrence, and to be ready for them by constructing appropriate series of actions''.

Actions performed are compared with intentions and disparity noted.

Correlations exist between ontogenetic and phylogenetic development and the proficiency with which animals perform such tasks as delayed response and alternation. The prefrontal cortex, which is functionally immature in young primates, is essential for these tasks (69,159). Fuster ((69) p. 126) defines the function of the frontal lobes as ''the formation of temporal structures of behaviour with a unifying purpose or goal'', at the highest level in a hierarchy (71).

Frontal lobe damage suggests a loss of top-down control and gain of control by lower-level processes. The Stroop test and Wisconsin Card Sort Task are especially difficult for these patients (35). Luria and Homskaya (125) speak of the frontally-lesioned animal being unable to evaluate the consequences of its behaviour. This suggests a failure to compare the actual state of the world with an expectation updated on the basis of contingencies across time and involving behaviour itself (71,82,83). Frontal patients are unable to benefit from their own errors (70). Fuster ((69) p. 115) notes ''one action succeeding another in more or less stereotyped succession with little or no regard for either the origins of the succession or its goal''. The frontal animal is able to learn easily new and simple habits provided that they can be performed on the basis of 'clear and unambiguous cues' (69).

For flexible and adaptive goal-directed behaviour, goal-representations need to be able to inhibit some S–R connections that are potentially able to be expressed in a particular

environment (52). Impairment in this capacity is a hallmark of the frontal syndrome. Goal pursuit often involves accentuation of intrinsically 'weak' behaviours (in our terms weak S–R links) in the face of what might normally be triggers to much stronger and more frequently expressed behaviours (35). The frontal lobes are thought to exert an inhibitory role on drives (23,25), lesioning is followed by stereotypies ((168); cf. (118) p. 85 (138)), a voracious appetite and aggressiveness (69), increased appearance of unconditional reflexes and positive conditional reflexes, disinhibition of inhibitory conditional reflexes (cf. (144)) and errors of commission in a go/no-go situation (69). According to Fuster ((69) p. 63), disinhibition is shown ''...in the inordinate ease with which a host of sensory stimuli and perhaps internal impulses and tendencies can release maladaptive motor responses''. The distractibility of frontal animals suggests that physically present stimuli can evoke behaviour where otherwise the capacity of the stimulus would be inhibited. When a monkey was offered a grape while already eating one, it would drop one grape and reach for the newly offered one, with the result that the floor was covered in uneaten grapes (26). This is similar to the so-called 'capture error' of humans (150). Frontal patients performing a stylus maze task are unable to inhibit a tendency to enter a blind alley (139). This was seen as an inability to inhibit ongoing response tendencies and was compared with lesioned animals where there is a decrease in the responsiveness to the immediate consequences of action. Frontal patients have difficulty in withholding the reaction of reaching out and grasping familiar objects brought to them (121). However, it might be wrong to see the frontal lobes simply as a source of inhibition, since the bridging of gaps in time might as much require excitation of behaviour by appropriate memory traces as the inhibition of tendencies that would otherwise occur.

Frontally-lesioned animals have difficulty withholding reactions because their *ability to utilise* a memory trace (e.g., a memory of seeing the way the targets have been baited) is weaker relative to the power of stimuli physically present at the time (115). In frontal humans, the effect of verbal instructions is similarly relatively weak when to follow them would place the subject in a competition situation with stimuli physically present. Such patients can later verbalise what they are expected to do but have difficulty doing it (211). This fits with the interpretation that there is joint control of behaviour by S–R processes and cognition and there can be competition between them. The memory trace itself is not weaker, but the power to utilise it is.

Once frontal animals have learned a discrimination (they are able to solve a simultaneous—but not a successive—discrimination), they retain it doggedly (69). A deficit in learning reversal seems again to be due to the disproportionate power of physically present stimuli. Presumably in intact subjects reversal would be associated with a new hypothesis being formed (i.e., previously positive stimulus is now negative) and being able to exert control. Similarly, frontal animals show excessive orienting towards stimuli, which suggests that they are 'stimulus bound' (115).

Brutkowski ((26) p. 730) notes that ''...once a motor behaviour pattern has been initiated, it gets stuck and persists indefinitely, being continuously executed or perseverated in spite of the absence of the stimulus originally

responsible''. This is similar to the performance of stereotypies and modal action patterns (see above). Such hyper-activity stops on placing the animal in darkness which suggests a hyper-responsiveness to certain stimuli.

14.3. The hippocampus

The hippocampus has long held a special place in the hearts and minds of psychologists. It enjoys its own journal, and five major reviews have appeared since 1979 in *Behavioural and Brain Sciences* (55,83,156,157,170), each suggesting a somewhat different function. The theory of Hirsh (96) was noted in the introduction. This theory and that of Wickelgren (244) arguing that S–R processes are spared following hippocampal lesions form a foundation for the present section. The section is designed to show where considering the evidence in the terms of a dual control of action might sometimes be insightful. Not surprisingly, it can make no claim to a comprehensive theory of hippocampal function.

The hippocampus seems to mediate (in collaboration with the prefrontal lobes (80)) cognitive control either in the absence of stimuli that can engage S–R processes or in opposition to them (223–226,244). Lesioned rats are much like normals on a one-way avoidance task, which can presumably be solved on the basis of either an S–R link alone, a cognition or both (156). Both processes would produce behaviour acting in the same direction. However, lesioned animals are superior to normals at two-way avoidance. Two-way avoidance might best be solved by an S–R connection. Cognition could interfere with this task by creating conflict involved in approaching a location associated with shock (156).

If comparison of incoming information with expectations is such that S–R processes are able to effect behaviour compatible with overall goals, then the hippocampus is able to delegate control to these lower structures. If not, the hippocampus puts behaviour control in a different mode (cf. (82,83)), with a greater weighting upon cognitive processes at a high level in the hierarchy. It retrieves possible solutions from store, and helps organise such things as vicarious trial-and-error behaviour. Without the hippocampus the rat is dependent upon S–R processes (96,97,186). As Hirsh ((96) p. 439) puts it: the hippocampally lesioned rat ''is everything for which early S–R theorists could have wished''.

Controversy has raged as to whether the hippocampus is a behavioural inhibition system (82,83). As a function of its maturation, the hippocampus comes to play a role in inhibition of certain responses and coordination of goal-directed behaviour (22). According to the present interpretation, the hippocampus has a role in the inhibition of some behaviour (where a potent stimulus suggests behaviour at odds with the current goal). It also has a role in the potentiation of other aspects (where there is no obvious physically present stimulus with a history of behaviour production present that can guide behaviour).

In an Olton maze, the lesioned rat is unable to solve a win-shift task (158). To solve this, it would have to abandon an arm in which reinforcement was recently received and presumably for which an S–R link was strengthened. It would involve the cognitive revision 'arm is baited' to 'arm is now depleted', and its use in opposing the S–R tendency.

Lesioned rats are deficient in a situation where they are reinforced for cue A or B, but not for the combination A and B (A + , B + , AB −). This task might involve the hippocampus in sensitising the cortical representation of the combination AB as opposed to that of either A or B (186). Inhibition needs to be exerted upon the response evoking capacity of either A or B.

The lesioned rat is bad at withholding responding on a task that rewards low rates of responding (82). Presumably, the link between the physically present stimulus of the lever and the tendency to respond is strong and the control of behaviour has no cognition that is able to oppose the S–R link of the kind available to intact rats: 'reward will be delayed by pressing'.

Spontaneous alternation by animals in a T-maze requires an intact hippocampus (50). Alternation depends upon an inhibition not of a response *per se* but of the tendency to select the arm chosen on the last occasion. The situation might be described as the animal behaving on the basis of a cognition (memory of last arm visited) and this exerting inhibition on the tendency (S–R link mediated) of the same arm to produce a turning/approach response. In other words, alternation requires the utilisation of information not present in current sensory events. The fact that hippocampally-lesioned animals lose their tendency to alternation suggests that they are simply reacting on the basis of current sensory input.

Early in life, most animals tested have been found to show a random choice or perseveration of a choice, the tendency to show alternation appearing rather suddenly. This happens at an age of 25–30 days in the rat, 11 days or earlier in the guinea pig and at 4 years in humans. Douglas (50) suggested that these ages represent hippocampal maturity.

15. NEUROPATHOLOGY AND PSYCHOPATHOLOGY

Evidence points to certain pathology corresponding to a disruption of the normal pattern of joint S–R and cognitive control of behaviour, with S–R processes either: (a) adaptively taking over some of the function of lost cognitive controls; or (b) competitively and maladaptively assuming undue influence over the control of behaviour in the face of higher-level goals.

15.1. Motor cortex damage

Patients with damage to the motor cortex are sometimes still able to make the right movements, provided that a powerful stimulus is presented ((167) p. 241). For example, a war veteran suffering from paralysis of the hand would find himself able to rotate a door knob with the hand in the event of a fire.

15.2. Parkinson's disease

In Parkinson's disease, there is a disconnection between the will and the ability to execute its commands (67). However, if there is a powerful stimulus to action and an obvious associated response then behaviour can appear to be nearer to normal. For example, an otherwise immobile patient can leap into action in response to a fire. Walking

can be improved by providing support stimuli, such as martial music and white lines painted on a path.

There are possible animal models that show a dissociation between an ability to respond to physically present cues and an inability to perform the same behaviour in their absence (210,234). A monkey with deafferented limbs is unable to use them in voluntary behaviour, but can use them in an avoidance task ((23) p. 30). The predominance of control by physically present stimuli over cognitions points to one similarity between Parkinson's disease and schizophrenia (35).

15.3. Schizophrenia

Schizophrenics fare particularly badly in the Stroop test. There is a suggestion of frontal cortex abnormality in schizophrenia (240), and thereby a relative weakness of cognitive control. Schizophrenics perform badly in tasks that involve contextual cues (33), e.g., a cue presented earlier but which is *no longer physically present* ('degradation' of the contextual cue). In a sentence like 'The farmer needed a new *pen* for his cattle', schizophrenics tend to interpret pen as a writing instrument rather than an enclosure, reflecting a greater weighting to a stronger but contextually inappropriate association (33).

Schizophrenics tend to exhibit a response ''that is appropriate to an immediate stimulus, but is not appropriate to his current goals and plans'' (67), termed 'immediacy theory' (188). Schmolling (191) suggests that the failure ''allows individuated, segmented subsystems to function autonomously''. Schizophrenia is characterised by a disruption of voluntary behaviour, whereas the involuntary can be normal or even super-normal (29,235). Frith (66) suggests that a bank of stimulus–response associations are represented in preconscious processing, and there is a failure of a filter mechanism that normally filters predictable stimuli from conscious awareness.

Callaway and Naghdi (30) suggest that schizophrenics exhibit a deficiency in limited capacity, serial, controlled processing rather than automatic, parallel processing. That the schizophrenic might be deficient in an ability of cognitive processes to oppose an S–R like process is suggested by the observation that redundant stimuli tend not to be ignored (85). A similarity between schizophrenia and hippocampal lesions, which is apparent from the present discussion, has also been noted (190).

Discontinuity between a more automatic level and conscious awareness is illustrated by the report of a schizophrenic (67):

''When I reach my hand for the comb it is my hand and arm which move, and my fingers pick up the pen, but I don't control them.... I sit there watching them move, and they are quite independent. What they do is nothing to do with me.... I am just a puppet that is manipulated by cosmic strings. When the strings are pulled my body moves and I cannot prevent it''.

Schizophrenics show an increased frequency of stereotypies and tics (134), suggestive of a failure of higher controls to inhibit low-level behaviours. Manschreck (134) echoes Hughlings Jackson's (see (208)) interpretation in terms of a hierarchy of control and loss of control from higher levels.

15.4. Gilles de la Tourette syndrome and Huntington's disease

Gilles de la Tourette syndrome (GTS) and Huntington's disease (HD) are disorders of the basal ganglia, associated with hyperkinetic movements and attention deficits (76). Georgiou et al. (76) suggest that these disorders disrupt connections between the basal ganglia and the frontal lobes, and indeed there are similarities with frontal symptoms. Georgiou et al. investigated the extent to which GTS and HD patients were affected by the parameter of S–R compatibility and incompatibility (see earlier). Relative to controls, they had particularly slow reaction times in situations where cognitive set was needed to determine the S–R mapping or where cognitive set needed to be reversed.

GTS (179) might be characterised as a conflict between: (1) a tendency to perform behaviour (e.g., jerk a leg, express an obscenity) organised relatively automatically at an intermediate level in the hierarchy; and (2) a top-down inhibition on this behaviour organised at a conscious level. Thus, rather like stereotypies in domestic animals, the tendency to show tics and vocalisations is increased by anxiety, fatigue and stress. Although GTS is classified as an involuntary disorder, the patient is able to suppress responding at certain times, e.g., during an interview. A sufferer from GTS reports that ((21) p. 1344):

''Each movement is the result of a voluntary capitulation to a demanding and relentless urge....''

and

''The movement only *seems* involuntary because of the instant capitulation to the unrecognised sensory stimulus. It can be detected and interrupted when in progress and at any stage''.

Determinants of behaviour that seem to be organised at a low level can gain access to high-level decision making. Thus the patient is aware of the urges and can inhibit or 'go with' them.

15.5. Obsessive–compulsive disorder

It is tempting to view obsessional–compulsive disorder (OCD), characterised by interminable and often seemingly-pointless rituals, as an example of some lower-level S–R type organisation seizing control in the face of the relative impotence of rational cognitive controls. Indeed, one authority compares it to the persistence of the hippocampally-lesioned rat (162). However, such a perspective needs to be countered or at least qualified by a number of observations:

1. obsessionals have insight into their condition ((174));
2. they can articulate a goal to be achieved by their excessive behaviour (220) and can experience conflict between two high-level goals (cf. (163)), e.g., to stop or to follow the commands of the abnormal cognition;
3. they have, if anything, hyperfunction of the frontal cortex (207) and abnormally high arousal levels (169).

Some (82,163,174,220) characterise OCD as failure by a negative feedback system to achieve a high-level goal.

In OCD, weighting of control can shift from a cognitive to an S–R level with extensive repetition, i.e., a 'fixation' of neurotic habits ((230) p. 299). Rachman and Hodgson

((169) p. 18) observed:

''Some compulsive activities are extraordinarily stereotyped. It would appear that with increasing practice the ritualistic behaviour becomes increasingly mechanical, precise and unchanging''.

After extensive 'practice', it seems that a programme can be switched in, which then runs its course with some autonomy from instigating cognitions. The longer the ritual has been performed, the more likely is the patient to describe it as senseless. After extensive experience, the compulsive behaviour can even be performed in the absence of the original disturbing cognition ((169) p. 125) or the central emotional state (237). Extinction of the emotional disturbance can leave the behavioural disorder still in place. It appears that the weighting given to cues that accompany the behaviour increases with time (237).

A possible animal model is the fear shown by rats on an avoidance task, which decreases with practice (108), suggesting a move to S–R control (203). Many obsessionals perform their rituals at a particular location (e.g., the bathroom of their home) and thereby give every opportunity for the process to switch into S–R control.

A shift into automatic mode might play a part in the difficulty that some obsessionals have in utilising their most recent memory to change behaviour away from that which is compulsively pursued (e.g., 'did I really check the door this morning or was it yesterday?'). The obsessional sometimes has a correct memory for a completed action but is unable to utilise it in the control of behaviour ((220) p. 44). A possible help is to try to characterise uniquely each day's check at first performance, so that it subsequently stands out when reviewed later in the day ((220) p. 124), and there is some indication that this works (238,206). It might 'pull the memory out' of the automatic mode and give access to a more cognitive mode.

16. COMPARISON WITH OTHER MODELS

In proposing a distinction between cognitive and S–R controls of behaviour, the present model can be compared with earlier theories. Various authors have proposed dichotomies in the control of behaviour, e.g., sensory and non-sensory (91), declarative and procedural (47,246), controlled and automatic (192), top-down (concept-driven) and bottom-up (data-driven) (86), conscious and unconscious (9), and rational and experiential (59). The controlled and automatic dichotomy and the declarative vs procedural dichotomy have been explored already. The top-down versus bottom-up distinction is implicit in the present model as is the distinction (91) that some behaviours appear to be determined by sensory stimulation and others do not. The remaining dichotomies will now be briefly addressed.

16.1. Unconscious and conscious processing

Seen as a subset of the cognitive and S–R distinction, the present model suggests advantages of conscious processing (flexibility, creativity) and disadvantages (slowness, limited capacity) that are the reciprocal of the pluses and minuses of unconscious processes (cf. (9)). If behaviour is the outcome of evolutionary selection for adaptive traits, whatever dichotomous processes exist in humans might be evident, even in only a rudimentary form, as adaptive processes in non-humans. Psychologists have been willing to give due credit to such a premise (e.g., (65)) and it was employed by Epstein ((59); Section 16.2) in favour of his own model over that of Freud. However, at best, the authors of some revised dichotomies (e.g., (59,65)) merely indicate how their models have been sanitised of the maladaptive features of Freud's model, rather than being able to describe how they incorporate a process having both positive adaptive value and some evolutionary continuity. The present model allows such suggestions.

16.2. Epstein

Epstein (59) argues that ''once a certain way of behaving has become sufficiently practised, it becomes automated and is thereafter carried out routinely with minimal emotional arousal''. Comparing modes of operation, Epstein describes the experiential system (ES) as ''more rapid, less effortful, and therefore more efficient in many circumstances''. The ES is ''experienced passively and preconsciously''. By contrast, the rational system is said to be ''better suited for abstraction and delay of action''.

16.3. Sloman

Sloman (198) studied thinking processes. Two parallel systems of reasoning, associative (cf. S–R process) and rule-based, goal-oriented (cf. cognitive) systems, having different properties were proposed. The two specialise in different styles of processing, but might jointly contribute to a given bit of processing. The subject is aware only of *the result* of associative processing, not the processing itself. Associative responses can intrude into the outcome of rule-based processing and remain compelling even if in clear contradiction to results obtained by using the rule-based system. Again, similar to the processing described here, frequent repetition of a bit of thinking based upon the rule-based system can result in its transfer to the associative system. The rational becomes intuitive.

16.4. Groves and Thompson

Specifically to deal with the habituation of reflexes, Groves and Thompson (88) proposed a model involving on-line and off-line changes in parameters similar to that advanced here. However, the present model was intended to cover the range of phenomena from so-called reflexes to voluntary behaviour. Subsequent research might be able to assimilate their model into the broader approach adopted here, seeing it as a special case applicable to a subset of phenomena. In their model, two pathways mediate between S and R, a *direct S–R pathway* and an indirect *state pathway*. The state pathway (cf. cognition) determines the general level of responsivity of the pathways. As here, the final response is dependent upon both pathways in interaction. The examples of S–R pathways that they discussed were innate links that are prone to habituation in the S–R pathway. Some of the pathways discussed by Groves and Thompson can be subject to either habituation or amplification as a function of stimulus presentation (95) and so a

model of the kind proposed here might prove to have more generality.

17. GENERAL DISCUSSION

The paper has demonstrated the wide application of a model of behavioural control involving S–R and cognitive features. The level of control exerted by these processes has been associated with the notion of behavioural hierarchy. According to the interpretation given here, a feature of behaviour is that the relative weighting of the S–R and cognitive processes changes as a function of: (a) development; (b) learning; and (c) malfunction. The fact that the same basic model has relevance in such a diverse range of situations, covering psychology, ethology and neuroscience might be a step towards a greater theoretical synthesis across traditional boundaries. A wider recognition of the changes that can occur in the mode of control might prove to be of practical application. Thus, drugs, environmental manipulations or therapeutic procedures that might be relevant at one stage (e.g., domination by either S–R or cognitive processes) might prove ineffective at another as a result of the change in the basis of control.

The model might go some way towards reconciling what are apparently conflicting positions. For example, Lorenz (124) described the strong opposition that his ideas on the spontaneity of behaviour received from S–R theorists, but the message of the present paper is unambiguously that both processes might happily co-exist. It is unfortunate that Lorenz achieved most fame in the context of aggression, where perhaps there is the least evidence for spontaneity and most reason to argue that it would be maladaptive (8).

The generality of a shift towards automaticity has been discussed in the context of looking for common ground between the human and rat literatures. As both ethologists ((124) p. 318) and psychologists (137) argue, skilled actions become more like fixed action patterns. Such a shift in the basis of control has been recognised by various authors as functional autonomy (3) or a 'progression toward economic output' (13). Teitelbaum (209) refers to the 'deencephalization' of behaviour that occurs with repetition.

In normal behaviour, the importance of cognitions in the face of prepotent stimuli is emphasised in the behavioural disorders shown in frontal lobe and hippocampal damage as well as in schizophrenia and Tourettes syndrome. Such disorders are to be understood at least in part as a domination of the S–R process over the cognitive. Both the frontal lobe syndrome and schizophrenia are to be understood partly in terms of the dominance of prepotent connections over the contextual mediation of intrinsically less strong associations (33).

This review has relevance to the philosophical issue of free will and determinism and emphasises the validity of a qualified distinction between voluntary and involuntary behaviours. Thus the Parkinson's patient can respond to physically present stimuli but have difficulty with voluntarily organising a similar behaviour. However, it suggests classifying behaviour not in terms of an absolute dichotomy such as voluntary vs involuntary, but to see more or less high-level cognitive involvement in the determination of a given behaviour (cf. (36)). This would place a given behaviour somewhere on a continuum rather than as one or other category (36). The notion of conscious biasing of lower levels (Section Section 12) might be useful here.

The model might prove relevant to genetic differences between animals in terms of behavioural strategies (16) in which different weightings are placed upon external stimuli.

The review has employed a distinction between cognitive and S–R processes that derived from the grand days of behaviourism (105,230) and shown it to still have considerable theoretical utility. However, perhaps it is safest to see this as only a provisional distinction and we now need to explore how a more up-to-date one could be used. Also the paper has seen the distinction in terms of, on the one hand, relatively fast automatic *behaviour production* processes that are triggered by external stimuli and, on the other hand, cognitions. Development and refinement of the model could allow a broadening of the terms to include cognitive processes which themselves show something of a move to automaticity, with associated speed gains. For example, obsessional thoughts seem to show the characteristics of repetition, lack of goal-direction and resistance to rational controls (220). Such a development might then dovetail with the work of Epstein (59), Sloman (198) and others on multiple processes underlying cognition.

The author's hope is that neuroscientists will be able to put some real neural structure onto the processes described in the paper.

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