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# An associative model of rat serial pattern learning in three-element sequences

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Hypotheses ranging from subsymbolic to symbolic have been proposed to account for rat sequential behaviour, and in the subsymbolic domain alone there are multiple proposed subsymbolic processes or factors thought to affect serial behaviour. A behavioural study and computer simulations were conducted to evaluate these hypotheses, and a new computational associative model based on pairwise associations and generalization was evaluated. Seven 3-element sequences were selected for study that systematically (1) varied sequence discriminability, (2) varied reward magnitude, and (3) manipulated the order of food quantities. Neither element discriminability nor response enhancement subsymbolic processes in isolation were able to account for the behavioural data; however, simulations from the computational model known as the sequential pairwise associative memory (SPAM) model with a log-linear mapping of stimulus dimension items to food quantities correlated well with the behavioural data. SPAM accounts for differential element anticipation in different sequences by appealing to pairwise association of sequence events and generalization between cues as the principal factors mediating pattern tracking in three-element sequences.

Extensive research has been conducted on the processes that mediate serial behaviour. Several theoretical explanations have emerged from the work on serial pattern learning in rats that range from purely stimulus bound or subsymbolic in nature to highly cognitive or symbolic in nature. These include the subsymbolic stimulus memory view of Capaldi (Capaldi & Molina, 1979), the serial position view of Roitblat (Roitblat, Pologe, & Scopatz, 1983), and, at the other symbolic extreme, the rule-learning view of Hulse (Hulse, 1978), to name but three. Theories of behaviour are termed "symbolic" if they rely on the manipulation of representations by a symbolic process to explain behaviour. For example, rule-learning theory of rat serial pattern learning assumes that during acquisition of a sequence, an animal encodes the rules that relate successive sequence items. As the number of rules required for encoding a sequence increases,

the difficulty of learning the sequence also increases (Simon & Kotovsky, 1963). After the rules have been encoded, subsequent performance reflects processing the sequence stimuli according to the set of rules encoded. In contrast, "subsymbolic" theories explain behaviour as the result of interactions between representations. Consider discrimination training with a stimulus that signals reinforcement (S+) and a stimulus that signals no reinforcement (S–). When the S+ and S– are similar, learning the discrimination is difficult; however, when the stimuli are more different, the discrimination is easy. The difficulty of learning the discrimination reflects a summation of excitatory and inhibitory strength that has accrued to both stimuli (Spence, 1937). Sequential behaviour is explained in terms of the formation of multiple associations between adjacent items. If the sequence items are highly discriminable (i.e., low amounts of generalization), then sequence learning will be easy. If the sequence items are highly similar (i.e., high amounts of generalization), then sequence learning will be difficult. While both symbolic and subsymbolic theories posit that serial information is represented, the critical difference between these theories is the presence or absence of computation on representations, respectively. This paper reports evidence from behavioural tests of a computational model that supports the notion that the subsymbolic processes central to discrimination learning—namely, pairwise association and generalization—are sufficient to account for rat serial pattern learning in three-element sequences of food quantities.

A classic view of serial learning is that it depends on subsymbolic processes such as discrimination learning, chaining, remote associations, and similar processes (Capaldi, 1967, 1985; Hull, 1931; Hunter, 1920; Skinner, 1934). In recent years, Capaldi and colleagues proposed that when rats learn to anticipate food quantities presented in a consistent series (e.g., 1 food pellet followed by 29 pellets followed by 0 pellets: 1–29–0), memories for past stimuli serve as cues for future food quantities in the series, and generalization between these memories can increase the difficulty of learning the series (Capaldi, Blitzer, & Molina, 1979; Capaldi & Molina, 1979). To test this view, Capaldi and Molina examined sequence tracking in patterns in which the discriminability of pattern elements was varied. The highly discriminable sequence 1–29–0 produced better tracking of the final 0-pellet element than did the less discriminable 20–10–0 sequence. Work in this vein has also shown that element discriminability is an important determinant of serial pattern "extrapolation" in which rats are tested on their ability to anticipate an item added to the end of an already-trained sequence (Haggbloom & Brooks, 1985).

The foregoing work tended to support a subsymbolic discrimination learning view of rat sequential behaviour based on simple associations and well-understood principles of discrimination and generalization. Capaldi has also described additional processes thought to be necessary to explain rat serial learning in short sequences of two and three elements. First, Capaldi, Verry, and Nawrocki (1982) suggested that multiple hedonic memories are formed from a sequence of food quantities—for example, the first component of a three-element sequence is able to retrieve a representation of Element 3 as well as a representation of Element 2. Rats can use these memories as simple cues, configural cues, or remote associations, even when learning is impaired as a result of doing so. Second, Capaldi has also proposed that response-enhancing properties of larger rewards account for differences in rates of discriminative responding observed early in acquisition (Capaldi, 1998). Response enhancement refers to the observed effect that large food quantities enhance responding (increase running speed in runways) on trials that follow the large reward.

In summary, it is clear that theories ranging from subsymbolic to symbolic have been proposed to account for rat sequential behaviour, and that in the subsymbolic domain alone there are multiple proposed subsymbolic processes or factors thought to affect serial behaviour. Among these are pairwise association of stimuli or responses, discrimination/generalization, response enhancement, and multiple-hedonic memory. Whether these factors represent independent processes is not known, and what relations might hold between them is equally unclear. To begin to answer these questions, seven 3-element sequences were selected for study that (1) systematically varied sequence discriminability, (2) systematically varied reward magnitude, and (3) systematically manipulated the order of food quantities. The chosen series directly pitted earlier hypotheses against each other in a way not attempted before in a single study. First, the sequences 1–1–0, 1–4–0, and 1–16–0 were included because they contain successively more discriminability between the Trial 1 and Trial 2 sequence elements. Capaldi's idea that greater discriminability should facilitate learning would predict successively better anticipation of the 0-pellet quantity in Trial 3 for these sequences. In the foregoing sequences, discriminability is confounded with increases in Trial 2 food quantity. To evaluate the effects of food quantity under conditions where discriminability of Trial 1 and Trial 2 quantities is held constant, the sequences 1–1–0 (aforementioned), 2–2–0, and 4–4–0 were included. The sequences 4–1–0 and 16–1–0 were included to examine, in comparison to sequences 1–4–0 and 1–16–0, respectively, how the sequential order of elements affects sequence tracking when element discriminability is conserved. Comparisons of anticipation for the 0 pellet between the 4–1–0 and 1–4–0 sequences or between the 16–1–0 and 1–16–0 sequences can also be used to assess the importance of response enhancement in sequential learning.

We also evaluate whether an associative computational model known as the sequential pairwise associative memory (SPAM) model (Wallace & Fountain, 2002) is sufficient to account for rat sequential learning for these representative three-element sequences. The SPAM model is based on two dominant notions in learning theory—namely, pairwise associations and generalization. The model has already accounted for a number of phenomena that were at the heart of the subsymbolic (discrimination learning) versus symbolic (rule-learning) debate in the area of rat serial pattern learning (Wallace & Fountain, 2002). Specifically, the model has accounted for food quantity serial pattern tracking for some monotonic and nonmonotonic patterns of three to five items (Capaldi & Molina, 1979; Hulse & Dorsky, 1977), serial pattern "extrapolation" (Fountain & Hulse, 1981; Haggbloom & Brooks, 1985), and "rule generalization" (Haggbloom, 1985; Hulse & Dorsky, 1979). In addition, the model has successfully accounted for phrasing effects observed in acquisition of response sequences in a circular array of levers (Wallace, Benson, & Fountain, 1999). While the success of the model in accounting for existing data supports an associative account of rat serial behaviour, it remains to be determined whether novel predictions of the model will parallel behavioural data observed in rat sequential learning.

In order to determine whether novel predictions of the SPAM model would parallel behavioural data observed in rat serial pattern learning, the foregoing seven 3-element sequences were selected for study in part because SPAM made some predictions not anticipated by any of the early hypotheses alone. One particularly striking example demonstrates the importance of pairwise associations and generalization; the SPAM model predicted a priori that rats in the 16–1–0, 1–16–0, and 1–1–0 pattern groups should all run slowly for the terminal 0-pellet

element. That is, they should have approximately equally good anticipation of "0". The pairwise associations determine the predicted quantity, whereas the generalization determines the accuracy of the predictions. Specifically, in group 16–1–0 associations will form between 16 → 1 and 1 → 0; as the components of these associations (1 and 16) are highly discriminable, the second element (1) will predict 0 with little ambiguity; performance in group 1–16–0 will obey similar principles. In group 1–1–0, on the other hand, associations will form between 1 → 1 and 1 → 0. This means that on the basis of the second element (1) the animal will predict both 1 and 0 as Element 3. But as the net prediction will be of a small quantity (between 1 and 0), the resulting performance will differ little from that in groups 16–1–0 and 1–16–0. These results are not expected based solely on the element discriminability hypothesis because of differential levels of discriminability between Elements 1 and 2 (high discriminability for 16 vs. 1 pellets in 16–1–0 and 1–16–0, and low discriminability for 1 vs. 1 pellets in 1–1–0). Discriminability alone would predict that "1" as Element 2 in 1–1–0 should be a poor cue for anticipating "0", whereas "1" in 16–1–0 and "16" in 1–16–0 should be good cues for anticipating "0". Likewise, the result predicted by SPAM is not expected based solely on response enhancement because of expected differential enhancement from Element 2 in the three sequences; "1" as Element 2 in 16–1–0 and 1–1–0 should produce slower speeds on the following "0" than the effect of "16" on "0" in 1–16–0. Thus, this experiment directly pits these earlier hypotheses against the SPAM model. Both computer simulations and behavioural testing were conducted with these sequences to evaluate the correspondence of the behavioural data with both earlier theoretical ideas and the predictions of the SPAM model.

# METHOD

## Behavioural study

### Subjects

Initially there were 68 naïve female Long-Evans hooded rats. Six animals refused to consume food pellets on the runway, and they were excluded from the study. The remaining 62 rats were maintained at 85% of the ad libitum weight for the duration of the experiment. The subjects were distributed among the groups as follows: 1–1–0 ($n = 9$), 1–4–0 ($n = 9$), 1–16–0 ($n = 9$), 2–2–0 ($n = 9$), 4–1–0 ($n = 8$), 4–4–0 ($n = 9$), and 16–1–0 ($n = 9$). Rats were housed in individual cages on a 14:10 light/dark cycle and were tested during the light portion of the cycle. They were approximately 90 days of age at the start of the experiment.

### Apparatus

The apparatus was a straight enclosed runway, 134.6 cm long by 10.2 cm wide by 14.0 cm high finished with polyurethane. The start and goal areas were separated from the alley by two guillotine doors. The goal area contained a 7.6-cm niche at a right angle to the runway in which a food dish was located. A microswitch was located at the first guillotine door, which, when activated by the opening of the door, started a timer. When the photo-beam, located in the goal area 25.4 cm from the start box, was broken, the timer stopped, and the corresponding number of 45.0-mg Noyes pellets was dispensed. The food pellets were delivered to the dish via a food pellet dispenser. The runway was located in a testing room (approximately 2 × 2.6 m) illuminated throughout the test by fluorescent lighting. All aspects of timing and food pellet delivery were controlled from an adjoining room using a microcomputer and interface (interface and Med-State Software; Med Associates Inc., Fairfield, VT, USA).

### Pretraining

Upon removal from the breeding colony, rats were single caged and given ad lib access to food and water. On the first 7 days of pretraining, rats were handled for 15 min each. On Day 8 of pretraining, each rat was put in the runway and allowed to explore each section to find six food pellets (i.e., 45.0-mg Noyes pellets), three in the runway and three in the goal area, for 15 min. On Day 9 of pretraining, each rat explored the runway for two 7-min time periods in which each rat could find three food pellets per time period (i.e., one in the runway and two in the goal area).

### Experimental training

Rats were randomly assigned to one of the seven groups employed in this study. Each group received a fixed sequence of food pellets. Groups differed in the number of food pellets received on any trial: 1–1–0, 1–4–0, 1–16–0, 2–2–0, 4–1–0, 4–4–0, and 16–1–0. One rat became sick during the course of the experiment, and its data were excluded from the study. Rats received four sequences per day for 20 days. Rats were run in squads of four. Squads were run such that no rat received its second sequence until all rats completed their first sequence. This procedure produced an intersequence interval of 7 min. A daily session began with removing the rat from the home cage and placing it into the start box. The guillotine doors were raised, allowing the rat to run towards the goal area. When the rat broke the photo-beam located in the goal area, the scheduled number of food pellets was delivered. After eating all of the food pellets, the rat was returned to the start-box for the next trial, and the procedure was repeated until one sequence was completed. During the intersequence interval, rats were returned to their home cage. Rats were given 30 s to traverse the runway, otherwise the guillotine doors were closed, and the rat was placed in the goal area. Rats were excluded from the study if they refused to eat pellets in the runway. Six rats were excluded from the study for this reason (see above).

## Computer simulations

The SPAM program was written in C (Turbo C, Borland International, Scotts Valley, CA) for PC-compatible hardware. The SPAM model has been described in more detail elsewhere (for a mathematical description of the SPAM, see Wallace & Fountain, 2002). The following sections provide brief detail of the model's assumptions.

### Item representation and generalization

The sequences presented to each group of rats varied in the number of food pellets encountered during the first, second, and third trials. The number of food pellets encountered on any given trial was assumed to be a stimulus drawn from a dimension that systematically varied in similarity. The stimulus dimensions were constructed like the one used by Metcalfe (1990) in her simulation of colour-shift phenomena in memory (so-called "memory blends"). We selected three possible mappings of the similarity between food quantities (see Table 1). Stimulus Coding 1 assumed maximal stimulus discriminability between food quantities. Stimulus Coding 2 assumed a log-linear type of mapping between food quantities. A log-linear mapping would be most consistent with Weber's law, observed in other stimulus dimensions. Coding 3 assumed minimal stimulus discriminability between food quantities. Each of these coding schemes assumed a different amount of similarity between items, and the amount of generalization that can occur between items also varies across the coding schemes.

Temporal, spatial, or other unidentified cues or some combinations of cues may control responding on the first trial of a sequence. For this reason, "Start" represents an item independent of the stimulus dimension. The nature of the stimulus or stimuli that cue responding to the first sequence item is

TABLE 1
Stimulus coding schemes

| Stimulus coding | Stimulus dimension | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | 0 | 1 | | 2 | | 4 | | | | 16 | |
| 2 | 0 | 1 | 2 | | 4 | | | 16 | | | |
| 3 | 0 | 1 | 2 | 4 | 16 | | | | | | |

typically not identified in behavioural studies. We have included "Start" as a possible cue for the first item of sequences.

### Item association storage

Each item in a sequence was associated with items adjacent in the sequence, and then the associations were stored in a common memory trace (see Figure 1, Steps 1 and 2). For example, to represent the sequence 1–4–0, the associations Start*1, 1*4, and 4*0, would be made. The process of convolution was used to associate items (for a computational example in matrix algebra, see Appendix).

After an association has been made between two items, it is weighted according to strength of encoding. Setting the encoding parameter equal to 1 assumes complete encoding of the association. Decreasing the encoding parameter decreases the effect of the association on the composite memory trace. This weighted association is then added to a composite trace that contains all of the prior associations. The composite memory trace can also be weighted prior to the addition of the new association, which produces increased forgetting for more remote associations relative to more recent ones, thereby producing a recency effect. Setting the forgetting parameter at 1.0 assumes no forgetting. Reducing the forgetting parameter to .5 increases the amount of forgetting observed on remote associations relative to recent associations.

### Item recall and item anticipation

Items are recalled by probing the common memory trace with an item associated with the "to be recalled" item (see Figure 1, step 3). For example, to determine how well the final 0-item is recalled in the sequence 1–4–0, 4 is used to probe the common memory trace. The recalled item is then compared with each item in the stimulus dimension. The item in the stimulus dimension with the highest degree of similarity to the recalled item was selected as the model's anticipated food item for that probe on that iteration (see Figure 1, step 4). To get a representative sample of the model's performance for an anticipated food item under specific experimental conditions, the model was run for 1000 iterations. The percentage in which each item in the stimulus dimension was selected as the anticipated item during the 1000 iterations was used to calculate a weighted mean of the model's performance (see Figure 1, steps 5 and 6). The weighted mean represents the model's predicted or "anticipated" food quantity for a group on a single trial of the sequence. These values are directly related to the runway speeds obtained from the behavioural data. Larger anticipated food quantities from the SPAM model correspond to faster runway speeds.
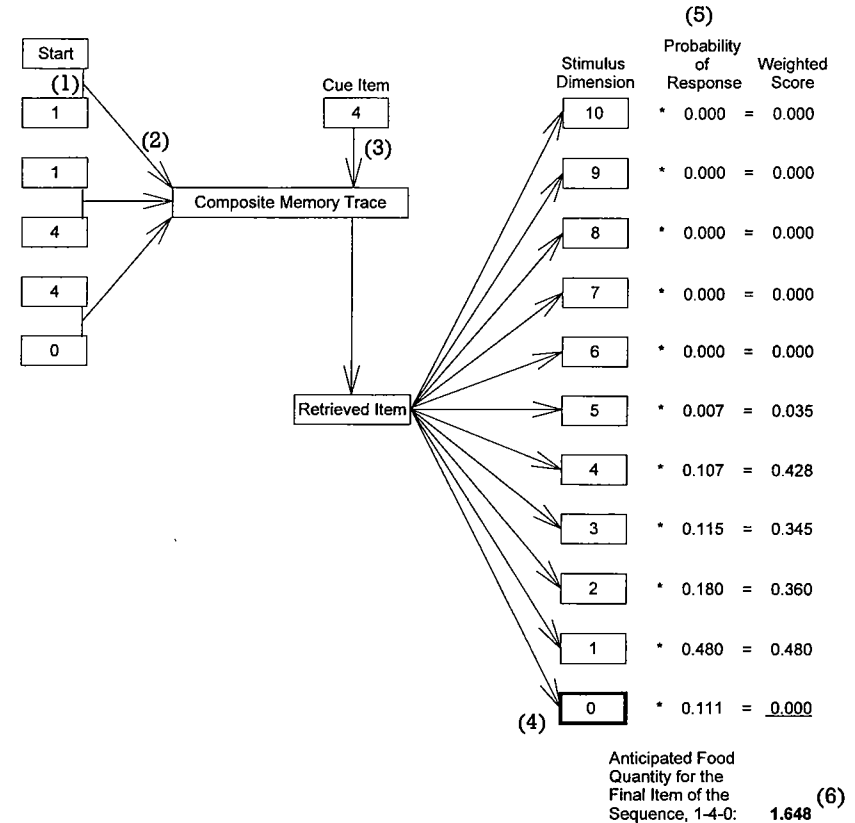
**Figure 1.** The SPAM model for the sequence 1–4–0, with "4" as a cue for the anticipated item. The schematic depicts the following steps: (1) association by convolution; (2) storage in a composite memory trace; (3) retrieval by correlation of a cue item with the composite memory trace; (4) recognition by selecting the lexicon item with the highest similarity to the retrieval item; (5) probability of responding to an item of the lexicon across 1000 iterations of SPAM; and (6) calculation of an anticipated item score for the third element of the sequence.

### Simulation parameters

Table 2 outlines the procedures employed for each of the simulated sequences: 1–1–0, 1–4–0, 1–16–0, 2–2–0, 4–1–0, 4–4–0, and 16–1–0. The model's performance was evaluated with the encoding parameter set to 1.0; therefore, all associations had maximal impact when added to the composite memory trace. Simulations were run with the forgetting parameter set at 1.0 or .5; therefore, the model was assessed with no recency effect or a mild recency effect. Item vector weights were set to zero throughout because adding information about individual items increases noise in the trace without affecting the general outcome of simulations.

TABLE 2
SPAM model simulations of selected three-element
sequences

| Group | Associations | Probe items |
|-------|--------------|-------------|
| 1–1–0 | Start–1, 1–1, and 1–0 | Start, 1 and 1 |
| 1–4–0 | Start–1, 1–4, and 4–0 | Start, 1 and 4 |
| 1–16–0 | Start–1, 1–16, and 16–0 | Start, 1 and 16 |
| 2–2–0 | Start–2, 2–2, and 2–0 | Start, 2 and 2 |
| 4–1–0 | Start–4, 4–1, and 1–0 | Start, 4 and 1 |
| 4–4–0 | Start–4, 4–4, and 4–0 | Start, 4 and 4 |
| 16–1–0 | Start–16, 16–1, and 1–0 | Start, 16 and 1 |

*Note:* "Start" represents an item independent of the stimulus dimension.

## RESULTS

The top, middle, and bottom panels of Figure 2 plot each group's mean runway speeds per 5-day block for the first, second, and third sequence elements, respectively. In all reported analyses, main effects and interactions were considered significant if $p < .05$. Analysis of variance on each group's mean runway speeds per 5-day block for the first, second, and third sequence elements indicated significant main effects for group, $F(6, 55) = 7.03$, block, $F(3, 165) = 68.28$, and element, $F(2, 110) = 148.23$. Each of the following interactions were found to be significant: Element × Group, $F(12, 110) = 16.37$, Block × Element, $F(6, 330) = 30.65$, and Block × Element × Group, $F(36, 330) = 4.424$. The Block × Group interaction was not found to be significant. The significant three-way interaction permitted planned comparisons (Tukey LSD) based on performance observed in the third block of training and showed that groups responded differentially to sequence elements. The third block of training was selected for further analysis because the average correlations between the behavioural data and the model predictions were the highest for this segment of training.

Panels of Figure 3 plot a group's mean running speed for each element observed during Block 3 of training. Groups 4–4–0 and 16–1–0 ran significantly faster on the first element than did the other groups but did not significantly differ from each other. Group 1–16–0 was significantly faster than groups 1–1–0, 1–4–0, 2–2–0, and 4–1–0. Groups 1–1–0, 1–4–0, 2–2–0, and 4–1–0 did not significantly differ in their running speeds for the first element. Group 1–16–0 responded significantly faster than all other groups on Element 2 of the sequence. While groups 4–4–0 and 1–4–0 did not respond differentially from each other on Element 2 of the sequence, both responded significantly faster than groups 2–2–0, 4–1–0, 1–1–0, and 16–1–0. Other differences in responding to Element 2 of sequences were not significant. Group 4–4–0 responded significantly faster on Element 3 than did the other six groups. Group 1–4–0 also responded significantly faster than groups 2–2–0, 4–1–0, 1–1–0, 1–16–0, and 16–1–0. Groups 4–1–0 and 2–2–0 did not respond significantly different from each other on Element 3; however, both groups responded significantly faster than groups 1–16–0 and 16–1–0. All other differences in responding to Element 3 were not significant.

Figures 3–5 compare rats' behavioural data and the SPAM model's predictions. Shown are the behavioural data for Block 3 of training (vertical bars) and the SPAM model's actual
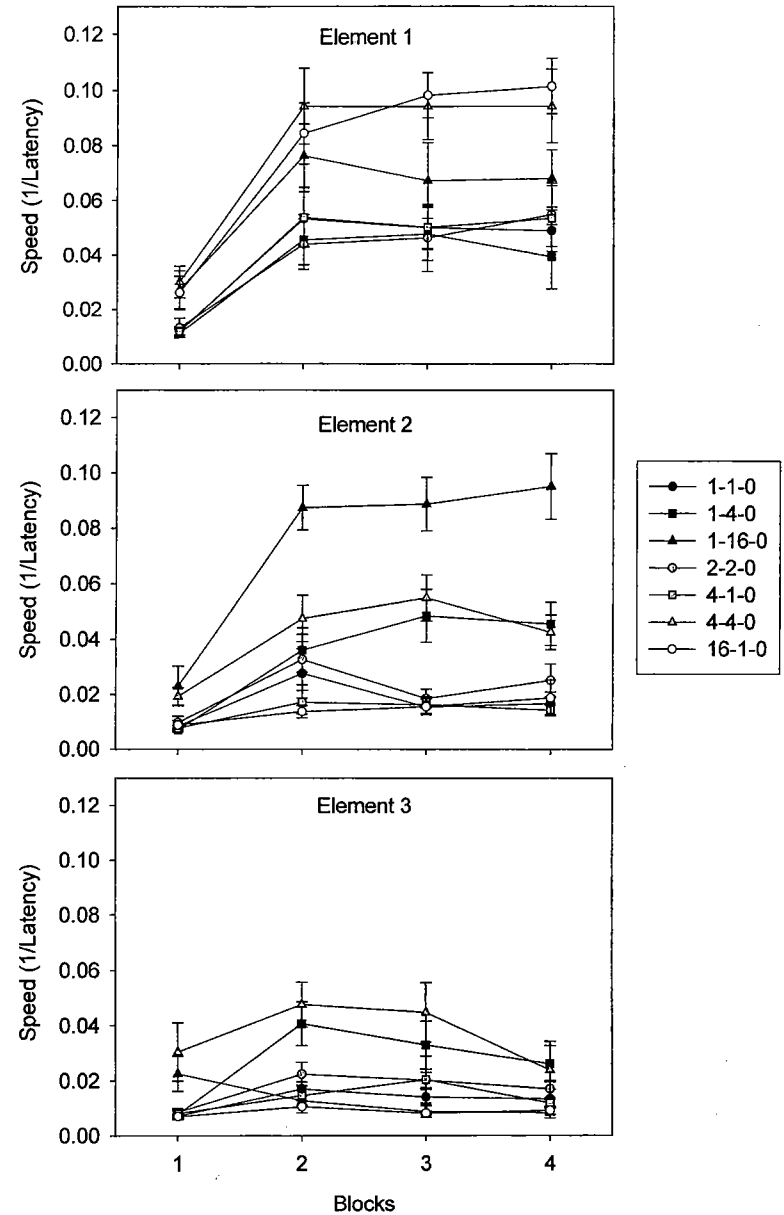


Figure 2. The top, middle, and bottom panels plot each group's mean running latency for the first, second, and third elements, respectively, across blocks of training.
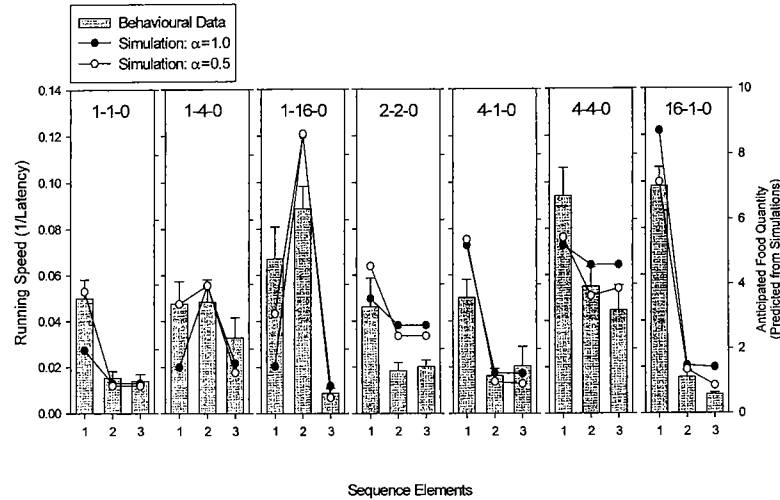
Figure 3.   Each panel plots a group's mean running speeds observed on sequence elements for Block 3 of training (vertical bars with *SEM* error bars). Predictions from the SPAM model are plotted for simulations in which elements were drawn from Stimulus Coding 1. This coding produced an item dimension with high discriminability of food quantities. The retention parameter, $\alpha$, was set to 1.0 and .5 in different sets of simulations.
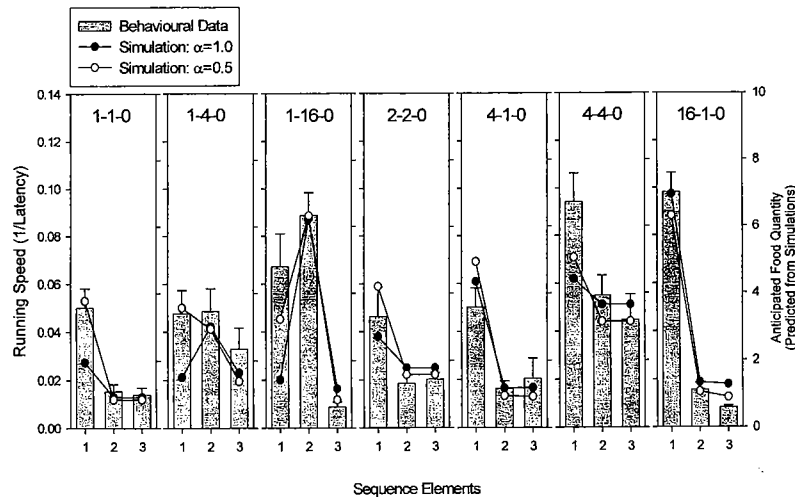


Figure 4.   Each panel plots a group's mean running speeds observed on sequence elements for Block 3 of training (vertical bars with *SEM* error bars). Predictions from the SPAM model are plotted for simulations in which elements were drawn from Stimulus Coding 2. This coding produced an item dimension with high discriminability of food quantities. The retention parameter, $\alpha$, was set to 1.0 and .5 in different sets of simulations. It should be noted that rats' behaviour data are reproduced from Figure 5 for ease of comparison across figures.
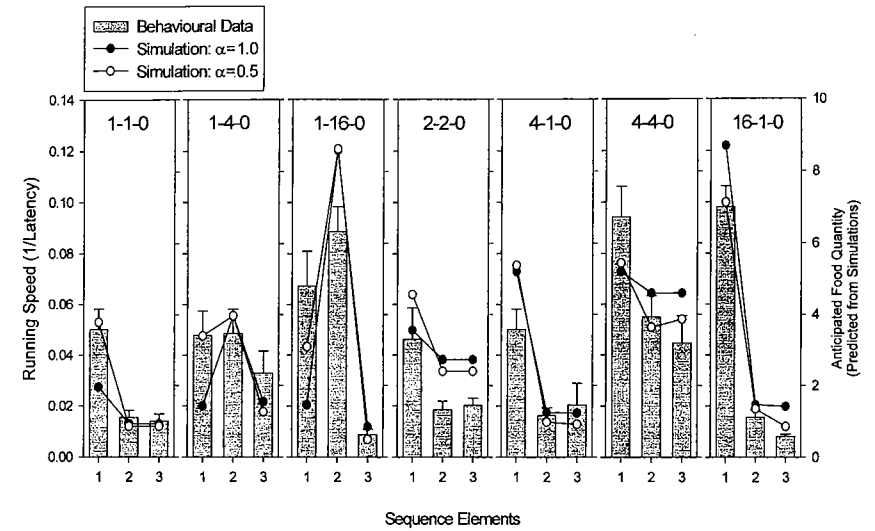
Figure 5.   Each panel plots a group's mean running speeds observed on sequence elements for Block 3 of training (vertical bars with *SEM* error bars). Predictions from the SPAM model are plotted for simulations in which elements were drawn from Stimulus Coding 3. This coding produced an item dimension with high discriminability of food quantities. The retention parameter, $\alpha$, was set to 1.0 and .5 in different sets of simulations. It should be noted that rats' behaviour data are reproduced from Figure 5 and 6 for ease of comparison across figures.

predictions for each training sequence. It should be noted that rats' behavioural data are reproduced in each figure for ease of comparison to the various simulation results. Figures 3–5 show simulation predictions for Stimulus Codings 1–3, respectively, with the retention parameter, $\alpha$, set to 1.0 and .5.

To assess the ability of the SPAM model to predict the obtained behavioural data, we examined the correlations between rats' behavioural data and predictions of the model. Table 3 shows the predictions of the model for each stimulus coding and level of the retention parameters, $\alpha$, correlated with behavioural data for each block of training and collapsed across blocks (overall). The correlations are reported for Elements 1, 2, and 3 separately and pooled across all elements. The simulation conditions were significantly correlated with the behaviour observed across training blocks when all sequence elements were considered. In general, when correlations were broken down on an element-by-element basis, the model continued to significantly correlate with performance observed during training. The highest correlations were observed between the model's predictions and the behavioural data from Block 3. Correlations in Block 3 ranged from .604 to .990. The highest set of correlations between the model and behavioural data from Block 3 were found under Stimulus Coding 2. Independent of stimulus coding schemes, correlations between the model and behavioural data were found to be highest when the retention parameter, $\alpha$, was set to .5.

TABLE 3
Correlations between rats' behavioural data and the SPAM model's prediction under Stimulus Codings 1–3

| Stimulus Coding | Alpha | Element | n | Block | | | | |
| | | | | 1 | 2 | 3 | 4 | Overall |
|---|---|---|---|---|---|---|---|---|
| 1 | 1.0 | All | 21 | .560** | .748** | .813** | .808** | .799** |
| | | 1 | 7 | .398 | .520 | .698* | .766* | .652 |
| | | 2 | 7 | .859** | .966** | .977** | .987** | .990** |
| | | 3 | 7 | .616 | .747* | .794* | .623 | .806** |
| | .5 | All | 21 | .565** | .864** | .903** | .909** | .896** |
| | | 1 | 7 | .341 | .478 | .665 | .733* | .613 |
| | | 2 | 7 | .811** | .961** | .965** | .997** | .985** |
| | | 3 | 7 | .577 | .766* | .812* | .663 | .816* |
| 2 | 1.0 | All | 21 | .602** | .780** | .847** | .833** | .832** |
| | | 1 | 7 | .409 | .546 | .718* | .772* | .669* |
| | | 2 | 7 | .876** | .960** | .990** | .985** | .993** |
| | | 3 | 7 | .733* | .825** | .854** | .666** | .891** |
| | .5 | All | 21 | .604** | .901** | .935** | .935** | .929** |
| | | 1 | 7 | .355 | .501 | .688* | .741* | .631 |
| | | 2 | 7 | .847** | .967** | .986** | .996** | .995** |
| | | 3 | 7 | .695* | .849** | .878** | .711* | .907** |
| 3 | 1.0 | All | 21 | .637** | .774** | .827** | .809** | .819** |
| | | 1 | 7 | .347 | .487 | .641 | .720* | .604 |
| | | 2 | 7 | .841** | .872** | .930** | .877** | .910** |
| | | 3 | 7 | .828** | .768* | .759* | .597 | .848** |
| | .5 | All | 21 | .568** | .829** | .838** | .843** | .843** |
| | | 1 | 7 | .319 | .454 | .604 | .693* | .572 |
| | | 2 | 7 | .818** | .905** | .955** | .917** | .939** |
| | | 3 | 7 | .808** | .796* | .778* | .640 | .868** |

*Correlation is significant at the .05 level (2-tailed). **Correlation is significant at the .01 level (2-tailed).

## DISCUSSION

The goal of the study was to examine the extent to which predictions from a variety of subsymbolic and symbolic hypotheses and a subsymbolic associative computational model account for behavioural data observed under systematic manipulation of element discriminability, reward magnitude, and serial order. We examine each in turn with regard to how well they handle the behavioural data.

## Element discriminability and response-enhancing properties of reward as determinants of serial pattern learning

Greater discriminability between an S+ (i.e., stimulus predicting reinforcement) and S– (i.e., stimulus predicting nonreinforcement) results in faster acquisition of discriminative control of responding in instrumental conditioning paradigms (Capaldi, Alptekin, & Birmingham, 1997). Capaldi and colleagues have generalized this phenomenon to serial pattern learning. Capaldi's element discriminability hypothesis posits that, as sequence elements become more discriminable, learning and asymptotic tracking of pattern elements should improve (Capaldi & Molina, 1979). The sequences 1–1–0, 4–1–0, and 16–1–0 have progressively more discriminability between Elements 1 and 2. Similarly, the sequences 1–1–0, 1–4–0, and 1–16–0 also have progressively more discriminability between Elements 1 and 2. The element discriminability hypothesis predicts that anticipation of Element 3, the final 0-pellet element, should be progressively better in each of these sets of sequences. This prediction was not confirmed by the behavioural data nor was it consistent with SPAM's predictions from simulations (see Figures 2 through 5): Although groups 1–4–0 and 4–1–0 ran faster than groups 1–16–0 and 16–1–0, showing poorer anticipation of 0, they also ran faster than group 1–1–0.

Earlier behavioural studies have frequently focused on how rats anticipate the 0-pellet element of sequences with much less attention paid to other elements. In addition, the 0-pellet element is often positioned as the terminal element of the sequence. Our experiment produced results for Element 2, which was never the 0-pellet element, that are at least as provocative and revealing as the Element 3 results. Element 2 anticipation was found to be a direct function of the quantity to be received as Element 2; it was not related to element discriminability. That is, patterns 1–1–0, 4–1–0, 16–1–0, and 2–2–0 produced the slowest running times on the 1-pellet Element 2, whereas 4–4–0 and 1–4–0 produced higher but equivalent speeds, and 1–16–0 produced the fastest running. Taken together with the Element 3 results, large differences in element discriminability, but equivalent value of Element 2 of 3 for specific subsets of these patterns, do not support predictions from the element discriminability hypothesis. Future work will examine under which conditions element discriminability plays a role in element anticipation.

One possible explanation of the foregoing effects is that response-enhancing mechanisms modulate anticipation. Capaldi (1998) reported that response-enhancing properties of larger reinforcements are a plausible mechanism for varying levels of element anticipation in serial patterns. Response enhancement refers to the observed effect that large food quantities enhance responding (increase running speed in runways) on trials that follow the large reward. The progressively poorer anticipation of the Element 3 0-pellet quantity, despite equivalent element discriminability in the sequences 1–1–0, 2–2–0, and 4–4–0, fits with a response enhancement explanation. Response enhancement predicts poor anticipation of "0" in these patterns because as Element 2 increases in quantity, producing more response enhancement on Element 3, the resulting response-enhancing effect is progressively incongruent with running slowly in anticipation of the 0-pellet quantity that is Element 3. But this argument fails to account for the lack of a progressive increase in responding and hence lack of a

progressive failure to correctly anticipate the 0-pellet Element 3 observed across sequences 1–1–0, 1–4–0, and 1–16–0; instead animals responded more on Element 3 in sequence 1–4–0 than they did in sequences 1–1–0 and 1–16–0.

It is possible that the constellation of results described above could be accounted for by some interaction of element discriminability and response enhancement factors. Unfortunately, no clear integration of element discriminability and response enhancement mechanisms has yet to emerge.

## Rule learning and serial position as determinates of serial pattern learning

At the risk of entertaining a patently "straw man" hypothesis or two, we momentarily consider the rule-learning and serial position hypotheses of serial pattern learning as explanations of our data. Hulse and colleagues (Fountain, Evensen, & Hulse, 1983; Fountain & Hulse, 1981; Hulse, 1978; Hulse & Dorsky, 1977, 1979) have theorized that serial learning is the result of the symbolic process of abstracting a rule that relates successive elements in a sequence. According to this view, the number of rules necessary to relate successive elements in the sequence determines the level of sequence tracking and extrapolation (Fountain & Hulse, 1981; Hulse & Dorsky, 1977, 1979). Rule-learning theory predicts that sequences like 16–1–0 and 1–16–0 should produce dramatically different anticipation of the final element. This stems from the fact that only one rule is needed to anticipate successive elements in the sequence 16–1–0 (viz., a single "less than" rule) in contrast to 1–16–0 that requires two rules (viz., both "greater than" and "less than" rules). This same argument holds for other sequences in the current study—for example, 4–1–0 versus 1–4–0—though in all these cases, little difference in anticipation was observed. Other data violating rule-learning predictions include the progressively worse 0-pellet anticipation observed for the sequences 1–1–0, 2–2–0, and 4–4–0. Each of these three sequences can be described by the same general rule structure, yet different levels of anticipation of the 0-pellet quantity were observed for these sequences. It should be noted, however, that applying rule-learning theory in this situation is controversial at best. Hulse (1980) suggested that the processes that control responding in longer sequences may not mediate anticipation in short sequences, and much evidence already exists to support a subsymbolic associative view of serial learning in two- and three-element series (e.g., Capaldi & Molina, 1979; Weisman, Wasserman, Dodd, & Larew, 1980).

Still other researchers have investigated the possibility that sequential behaviour is the result of learning that certain serial positions are associated with specific food quantities (Burns, Dunkman, & Detloff, 1999; Roitblat et al., 1983). Roitblat et al. demonstrated that sequence tracking was independent of reward magnitude. Rats were overtrained on the five-element sequence, 14–7–3–1–0. In transfer, different groups experienced the sequence with a different element replaced with a nonrewarded trial: 0–7–3–1–0, 14–0–3–1–0, 14–7–0–1–0, or 14–7–3–0–0. These transfers had little effect on pattern tracking, suggesting that serial position, not rules or other cues, controlled responding (Roitblat et al., 1983). Although similar probes were not included in the present study, our results challenge a prediction derived from the serial position theory. Specifically, if the same quantity is presented at the same serial position in different patterns, then anticipation of that quantity should be equal between groups. For example, the serial position theory would predict that all three-element

patterns that have 0 pellets as Element 3 should have equal anticipation of Element 3. This follows from the argument that rats use ordinal position in the sequence to predict the food quantity; therefore, quantities on trials before and after the target serial position should have no effect on anticipation (Burns et al., 1999; Roitblat et al., 1983). The serial position theory is hard pressed to account for the differential anticipation of 0-pellets that we observed for various sequences under these conditions. As a further test of the serial position theory, we calculated the correlations between the behavioural data and the food quantity presented at each serial position for all groups. Predictions from the serial position theory never account for more than 60% of the variance observed in the behavioural data across all blocks of training. Under certain parameter conditions, the SPAM model accounts for 80% of the variance of the behavioural data for the last three blocks of training. The predictions from the SPAM model are a better account of behaviour observed on each block, relative to predictions from the serial position theory.

## The sequential pairwise associative memory (SPAM) model: Pairwise association and generalization as determinants of serial pattern learning

The element discriminability and response enhancement ideas fail, individually, to account for the behavioural data. Rule learning and serial position accounts of serial pattern learning also fail to account for the obtained results. In contrast, predictions from the SPAM model under Stimulus Coding 2 and the retention parameter set to .5 correlated well with the observed behavioural data, with correlations ranging from .850 to .995 across Blocks 2 and 3 and collapsed across all blocks. What are the processes instantiated in SPAM that produced accurate prediction of the behavioural data? We propose that pairwise associations and generalization are the necessary mechanisms with stimulus coding scheme and retention rate as parameters that influence the predictions of the model quantitatively rather than qualitatively. In this case, sequential behaviour in tracking three-element sequences is largely accounted for by pairwise associations between successive elements and generalization between event memories. For example, the sequence 1–16–0 is represented as the two associations 1–16 and 16–0. Anticipation of a given element is then determined by the amount of generalization that occurs between the Elements 1 and 2. Considering that 1 and 16 food pellets are very discriminable, little generalization occurs between the different signalling food quantities. Therefore, anticipation of the terminal 0-pellet element is relatively easy, and the same argument holds for the 16–1–0 sequence. For the 4–4–0 sequence, "4" signals both "4" for Element 2 and "0" for Element 3. Consequently, maximal generalization of Elements 1 and 2 (because they were the same quantity) as cues for Elements 2 and 3, respectively, leads to anticipation of a larger quantity on Element 3 than with other conditions and, thus, poorer anticipation reflected in faster running speeds as observed in both the behavioural and simulation data. As might be expected, because of complete generalization between Elements 1 and 2 as cues in the 4–4–0 sequence, running speeds on Elements 2 and 3 were observed to be very similar, as predicted by the SPAM simulations. According to SPAM, the progressively worse anticipation of the terminal element found in the sequences 1–1–0, 2–2–0, and 4–4–0 is the result of maximal generalization of signals for "0" and progressively larger food quantities. Across sequences, Element 1 cues progressively larger food quantities, whereas Element 2

always cues the terminal 0-pellet element. Because the Elements 1 and 2 are identical in each sequence, maximum generalization is observed, and the net result is progressively poorer anticipation of the terminal element. In fact, this case reflects the results of the classic "branching" problem, where the same stimulus signals different events at different times and leads to performance based on anticipating both outcomes simultaneously. This idea should be compared to similar phenomena described by the term "memory blends" in the human memory literature by Metcalfe (1990) and to Capaldi's idea of generalized reward signal capacity in rat serial learning (Capaldi, Verry, & Davidson, 1980a). Thus, SPAM accounts for differential element anticipation in different sequences by appealing to pairwise association of sequence events and generalization between cues as the principal factors mediating pattern tracking.

Two interesting points can be made here. First, the sequences 1–1–0, 2–2–0, and 4–4–0 share equivalent amounts of discriminability between Elements 1 and 2; therefore, Capaldi and Molina's (1979) idea of discriminability alone would tend to incorrectly predict no differences between sequences in terms of anticipation of 0-pellets on Element 3; however, the sequences 1–1–0, 2–2–0, and 4–4–0 presumably have successively increasing amounts of response-enhancing properties of larger rewards on the anticipation of 0-pellets. Therefore, differences in anticipation of the final element could be attributed to increasing levels of response-enhancing properties of the stimuli preceding 0-pellets. Do the data support the notion of response enhancement as a separate behavioural process? The SPAM model has no separate response enhancement processes, and thus, to the extent that response enhancement is a separate process, SPAM should fail to account for the data. The fact that SPAM can predict effects attributed to response enhancement indicates that response enhancement is probably an epiphenomenon resulting from pairwise association and generalization; it is not a separate process or independent factor.

A second point is that a similar argument applies to the idea that multiple hedonic memories are required for serial pattern learning. Because SPAM does not include "remote associations" or similar multiple-association processes, the model would be expected to fail to account for the behavioural data to the extent that these are necessary for serial pattern learning. Given the high correlation between the SPAM simulation data and the observed learning, the results are consistent with the idea that rats did not use multiple hedonic behaviour in this task. This is not to say that rats cannot use multiple hedonic memories when it is necessary to do so, only that this construct is not necessary to account for the present data.

SPAM captures the relationship between reward magnitude and generalization in the context of pairwise association that has eluded other theories. As reward magnitude increases in sequences with low discriminability held constant, anticipation of the terminal, 0-pellet, element is progressively more difficult due to generalization from increasingly larger rewards. Reducing generalization by increasing discriminability between sequence elements can overcome the disruptive effects of large reward magnitude on anticipation of nonreward. Finally, intermediate levels of reward magnitude and generalization produce intermediate levels of anticipation. The correspondence between the predictions from SPAM simulations and the behavioural data identify the processes that mediate serial behaviour in three-element sequences: namely, pairwise association and generalization. These ideas have been foreshadowed by earlier investigators, particularly by Capaldi, Verry, and Davidson's (1980a) idea of generalized reward signal capacity. The SPAM model is the first to formalize the ideas of

pairwise association and generalization in such a way as to make possible novel predictions regarding pattern tracking in serial patterns and to account for effects such as response enhancement without appealing to independent processes.

## Conclusion

Pairwise and remote associations of stimuli and responses, stimulus discriminability, stimulus generalization, response enhancement, multiple hedonic memories, and other associative factors and effects have been studied extensively in rat serial pattern learning, but a synthesis of the extant data that would identify the critical mechanisms has been elusive. The present behavioural study and computational simulations provide a good start in this direction by identifying two factors, pairwise association and stimulus generalization (as a function of discriminability), as sufficient to account for rat serial pattern learning in three-element sequences. The results support the idea that response enhancement phenomena are likely epiphenomena resulting from pairwise association and generalization; they do not result from a separate process or independent factor. The results also strongly suggest that multiple hedonic memory as an independent factor plays little role in learning of the sort we studied, though it is quite possible that multiple hedonic memory may be critically important in other serial learning problems that are unsolvable for the rat without it.

The SPAM model (Wallace & Fountain, 2002) has already been shown to be sufficient to account for food quantity serial pattern tracking for some monotonic and nonmonotonic patterns of three to five items (Capaldi & Molina, 1979), serial pattern "extrapolation" (Haggbloom & Brooks, 1985), and "rule generalization" (Haggbloom, 1985) motivated by both the symbolic rule-learning hypothesis of Hulse (1980) and the subsymbolic element memory hypothesis of Capaldi, Verry, and Davidson (1980b). Interestingly, in this earlier work, Wallace and Fountain (2002) took as an assumption of the model that food quantity was perceived as a log-linear dimension. This assumption, based on the view that Weber's Law should apply to the perception of food quantity as it does to the perception of quantity in other stimulus dimensions, is common to theories of generalization and traditional notions of discrimination learning (Blough, 1975; Spence, 1937). This assumption was also implicitly accepted by Roitblat (1982) who attempted to apply Blough's (1975) model of generalization to the serial-pattern learning phenomena reported by Hulse and Dorsky (1979). The results of the current studies seem to further justify this assumption; Stimulus Coding 2, with its log-linear dimension of food quantities that adheres to Weber's law, produced a better fit with the behavioural results than did stimulus codings that produced either more or less discriminability in the resulting dimensions of food quantities.

Given the range of earlier phenomena and data for which the SPAM model has already accounted, empirical tests of novel predictions from the model were the next logical step in evaluating the validity of the model. Behavioural tests of a computational model are useful on two accounts. First, a close correspondence between a model's predictions and the behavioural data collected from the model-driven experiment increases one's confidence in the validity of the assumptions that serve as the foundation for the model. The SPAM model assumes that pairwise associations and generalization mediate serial pattern learning in sequences composed of a series of food quantities. The close correspondence between the SPAM model's predictions and the behavioural data reported here support this claim.

Second, careful use of the model to select appropriate conditions to be evaluated behaviourally can also result in data capable of discounting other possible mediating mechanisms. While computational modelling alone can demonstrate the sufficiency of psychological concepts instantiated in a model as an explanation of the target behaviour, behavioural tests of unique or novel predictions of a model can determine the sufficiency of competing psychological concepts. Computational modelling and behavioural studies guided by the modelling together provide a powerful framework for evaluating and characterizing the processes that mediate serial behaviour.

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## APPENDIX 1

### A computational example of convolution and correlation for one iteration of SPAM stated in matrix algebra

For simplicity and elegance of calculation, the processes of convolution and correlation can also be described in terms of specific types of vector multiplication. To simplify the matrices and calculations involved, our example illustrates convolution and correlation involving three-element vectors, but the vectors and resulting matrices can easily be expanded to any desired dimensions. Let us start with items $A = (\ldots a_{-1}, a_0, a_1 \ldots)$, $B = (\ldots b_{-1}, b_0, b_1 \ldots)$, and $C = (\ldots c_{-1}, c_0, c_1 \ldots)$.

$$A = \begin{bmatrix} 0.30 \\ -1.20 \\ 0.90 \\ 0.0 \\ 0.0 \end{bmatrix}_{5 \times 1} \quad B = \begin{bmatrix} -0.56 \\ 1.50 \\ -0.80 \\ 0.0 \\ 0.0 \end{bmatrix}_{5 \times 1} \quad C = \begin{bmatrix} -1.20 \\ -0.34 \\ 0.30 \\ 0.0 \\ 0.0 \end{bmatrix}_{5 \times 1}$$

The following procedures will associate items A and B through the process of convolution. The first step involves vector initialization of one of the vectors to be associated. This can be accomplished by initializing either A or B items in a $w \times w$ matrix, where $w = (2 * \text{number of vector features}) - 1$, then multiplying by the remaining item vector. In the example, Vector A is initialized, then the resulting matrix is multiplied by Vector B, as follows:

$$\begin{bmatrix} a_{-1} & 0 & 0 & 0 & 0 \\ a_0 & a_{-1} & 0 & 0 & 0 \\ a_1 & a_0 & a_{-1} & 0 & 0 \\ 0 & a_1 & a_0 & a_{-1} & 0 \\ 0 & 0 & a_1 & a_0 & a_{-1} \end{bmatrix}_{5 \times 1} * \begin{bmatrix} b_{-1} \\ b_0 \\ b_1 \\ 0 \\ 0 \end{bmatrix}_{5 \times 1} = \begin{bmatrix} a_{-1}b_{-1} \\ a_{-1}b_0 + a_0b_{-1} \\ a_{-1}b_1 + a_0b_0 + a_1b_{-1} \\ a_0a_1 + a_1b_0 \\ a_1b \end{bmatrix}_{5 \times 1}$$

That is, the initialized $[A]_{5\times5}$ matrix is multiplied by the $[B]_{5\times1}$ vector, thereby producing the convoluted vector, $[A*B]_{5\times1}$, representing the association of A and B items. Generally, the vector initialization procedure always produces a matrix that, when multiplied by the other item vector to be associated, produces a memory trace vector equivalent to that resulting from the procedures of Metcalfe (1982). It should also be noted that the same result is obtained independent of which item vector, A or B, is chosen for initialization. A numerical example follows.

$$
\begin{bmatrix}
0.3 & 0 & 0 & 0 & 0 \\
-1.3 & 0.3 & 0 & 0 & 0 \\
0.9 & -1.2 & 0.3 & 0 & 0 \\
0 & 0.9 & -1.2 & 0.3 & 0 \\
0 & 0 & 0.9 & -1.2 & 0.3
\end{bmatrix}_{5\times5}
*
\begin{bmatrix}
-0.168 \\
1.5 \\
-0.8 \\
0 \\
0
\end{bmatrix}_{5\times5}
=
\begin{bmatrix}
-0.168 \\
1.122 \\
-2.544 \\
2.31 \\
-0.72
\end{bmatrix}_{5\times1}
$$

Convolved vectors are then added to the composite memory trace vector, $[T]_{5\times1}$, until all associations (convolved vectors) to be learned are included.

Correlation is the process of retrieval that involves multiplication of the transpose of the cueing item $[A]^t_{5\times1}$. The resulting vector $[R]_{5\times1}$ represents the retrieve information given A associated with B and cueing with A.

$$
\begin{bmatrix}
0.3 & -1.2 & 0.9 & 0 & 0 \\
0 & 0.2 & -1.2 & 0.9 & 0 \\
0 & 0 & 0.3 & -1.2 & 0.9 \\
0 & 0 & 0 & 0.3 & -1.2 \\
0 & 0 & 0 & 0 & 0.3
\end{bmatrix}_{5\times5}
*
\begin{bmatrix}
-1.68 \\
1.122 \\
-2.544 \\
2.31 \\
-0.72
\end{bmatrix}_{5\times1}
=
\begin{bmatrix}
-3.686 \\
5.468 \\
-4.183 \\
1.557 \\
-0.216
\end{bmatrix}_{5\times5}
$$

Therefore, $[R]_{5\times1}$ should be more similar to the B item than to the other items in the lexicon, A and C. The similarity of $[R]_{5\times1}$ to items of the lexicon is gauged by calculating the inner produce between the R and A, R and B, and R and C vectors. The pair with the largest inner product represents the item recalled on that iteration of the program. From our numerical example above, it follows: $R \cdot A = -11.342$; $R \cdot B = -13.65$; $R \cdot C = -1.31$. Because the inner product for the $R \cdot A$ pair is the largest, B would be selected as the item recalled for one iteration of the program given A associated with B and cueing with A.

If one wants to include more associations into the composite memory trace, the following equation details that processes:

$$T_n = \alpha T_{n-1} + \gamma_1 A + \gamma_2 B + \omega AB$$

in which $\alpha$, $\gamma_1$, $\gamma_2$, and $\omega$ are encoding and memory parameters. The gamma and the omega parameters determine the amount of new information that is added to the composite memory trace. These parameters range from 0 to 1.0, where 0 indicates no encoding, and 1.0 indicates maximum encoding of item and associative information. Alpha is a memory parameters, also varying from 0 to 1.0, where 0 indicates no memory for prior information, and 1.0 indicates perfect memory for prior information. $T_{n-1}$ corresponds to the composite memory trace prior to the addition of the current association. It should be noted that the processes of adding more associations parallel Hebbian learning found in neural networks.

Anticipated item scores are based on the weighted average of 1000 interactions of the model with identical associations and cueing conditions. The proportion recall for each lexicon is calculated over all 1000 iterations. The following equation is then used to generate the anticipated item score:

$$Anticipated\ Item_i = \sum_{j=1}^{k} (proportion\ recall_j * lexicon\ value_j)$$

where $k$ is the number of items in the lexicon. Assuming that Vectors A, B, and C correspond to the food quantities 0, 5, and 10, and proportion recall for each vector was .20, .50, and .30, respectively, it follows:

$$Anticipated\ item = (0*.20 + 5*.50 + 10*.30) = 5.5$$

Therefore, the model predicts an anticipated item of 5.5 when 0 is associated with 5, and 0 is used as a cue for recall.

### PREPARATION OF FIGURE ARTWORK

Please submit the best possible figure artwork, i.e., an original or disk version and hard copy.

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