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Serial order of conditional stimuli as a discriminative cue for Pavlovian conditioning

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The temporal or serial order in which events occur in the environment can signal different outcomes and therefore determine how an animal should respond. In this short report we propose a novel design for studying serial order learning in Pavlovian conditioning. In both Experiment 1a and 1b hungry rats were trained with successively presented pairs of auditory and visual stimuli (e.g., A->B). On half the trials the sequences were paired with food. A completely counterbalanced design was used such that each stimulus signalled both reinforced and non-reinforced trials with only the order of the pair signalling whether reinforcement would be delivered. Responding from the second element of each sequence showed that the rats discriminated trial types that preceded food from those that did not. This result suggests that rats can use the temporal order of two sequentially presented non-overlapping elements as the basis for discrimination.

The order in which sequential stimuli occur can have important consequences for action. Sequential learning has been identified as the ability to encode the temporal order in which stimuli occur (Conway & Christiansen, 2001). Examples of naturally occurring temporally ordered stimuli are found in the auditory stimuli of animal communication but also in visual stimuli for most events, as processing of visual events occurs over time and stimuli change even, for example with respect to the relative position of the viewer. Previous work that claimed to find evidence of encoding of temporal order might be explained by associations, the content of which has no temporal order information. We examine one such paper by Weisman, Wasserman, Dodd & Larew (1980) and propose a configural learning of their findings and propose a novel experimental design to test temporal order learning within Pavlovian conditioning.

There is in fact good evidence that within a standard CS-US conditioning procedure the order in which the two events are presented influences behaviour. Forward pairing of the neutral conditioned stimulus (CS) and the unconditioned stimulus (US) results in a conditioned response to the CS that reflects sensitivity to the duration of the CS or proximity relative to the US and the order in which the two events are presented. Backward pairing of the two events encourages learning, but of a somewhat different nature, suggesting the importance of the temporal order of the stimuli. For example, Moscovitch and Lolordo (1968) showed that unlike forward pairings of the CS prior to the US that produces excitatory conditioning, presenting the CS following the US resulted in inhibitory conditioning. Given the claims of the ubiquity of sequential learning it is somewhat surprising that many associative theories of conditioning fail to describe the nature of the temporal information that is available and might be acquired during conditioning involving sequentially presented non-overlapping stimuli. One possible reason for this neglect may be the fact that standard associative mechanisms can explain most conditioning phenomenon without requiring an explicit temporal coding.

There is somewhat less research showing that the temporal order of multiple sequentially presented non-overlapping CSs can be acquired. Some previous experimental designs have yielded results consistent with the hypothesis that animals can learn about temporal order during Pavlovian conditioning. One such design involves two orders of sequentially presented CSs. Seger and Sheur (1977) showed that responding was greater to the second CS of two successively presented CSs that preceded a US (A->B->US) than to the second stimulus when the reverse order was extinguished (B->A->no US). The solution of this simple discrimination however, does not provide convincing evidence that the animals have encoded or represented the temporal order of the two cues. As Weisman, Wasserman, Dodd & Larew (1980) have suggested, they might simply use a recency or primacy strategy and therefore learn for example, to respond to B if it occurs later in the compound trial.

Solving this discrimination involves encoding some aspect of the temporal delay between the beginning of the trial and the termination of the second CS. But it does not require that the animals represent or code the temporal order of A and B, although their performance might be consistent with this hypothesis. A similar account has been used by Terrace (1986) to explain a similar discrimination with pigeons.

Weisman et al. (1980) provided a more elaborate experimental discrimination and claimed to find evidence that pigeons could learn and represent the order of two-event sequences. They used a conditioned pecking procedure with pigeons in three experiments. Pigeons were reinforced with grain for pecking following successive presentation of a two-element stimulus sequence. In their Experiment 2 they showed that pigeons responded more at the end of a reinforced sequence ($A\text{->}B^+$) than after the nonreinforced sequences involving all other combinations of A and B ($A\text{->}A^-$, $B\text{->}A^-$ or $B\text{->}B^-$) and combinations of A and B with a novel third stimulus C ($A\text{->}C^-$, $B\text{->}C^-$, $C\text{->}A^-$, $C\text{->}B^-$ or $C\text{->}C^-$). They proposed that the pigeons could only solve this by representing the temporal order-A followed by B, and associating this order with food. However, a different strategy that does not involve temporal coding might have been possible. The highest rates of responding were found when B was preceded by A (i.e., the reinforced sequence). But, there was also strong responding whenever B occurred as the second stimulus, regardless of the preceding element (B->B, X->B). This might suggest a strong association between the element B and the US especially if it occurred later in the trial pair, much like the account described earlier for the experiment by Seger and Shuer. There was further evidence that response rates were high to the specific reversal of the A-B sequence (i.e., when B was followed by A). This might suggest sequential presentation may have resulted in the formation of a configural cue in spite of the fact that they had not been presented simultaneously and that this representation did not code the order of the stimuli (e.g., Holland, 1985). Two associations with the US may have formed and summed and resulted in the successful discrimination: One association of the configuration of A and B-the two elements that were reinforced- with the US, and a second association between the occurrence of B and the US. This would mean that other sequences that either contained the AB configuration, regardless of their temporal order, or B as the second element would also elicit relatively high rates of responding. This mechanism for solving the temporal order discrimination is entirely consistent with the pattern of responding observed and is also a relatively simple way to solve the discrimination without encoding the temporal order. Furthermore, summation of associative strengths is a major tenet of some associative theories (e.g., Rescorla and Wagner, 1972) and has been reported elsewhere (e.g., Murphy, Baker & Fouquet, 2001; Rescorla, 1997).

In their Experiment 3, Weisman et al. extended their findings using a conditional discrimination paradigm in which three element sequences were employed and forward and backward presentations of A and B were reinforced depending upon the value of the third stimulus (A->B->C^+ and B->A->D^+) but all other combinations were extinguished (AAC, AAD, ABD, BBC, BBD, BAC). Again animals were able to solve this discrimination in which C and D were presented simultaneously and pigeons chose the correct key. That is, they responded differentially to C and D depending upon the order in which A and B had been presented. However this result can also be explained based on the summation of two associations with the US involving configural cues. If the order in which the stimuli are presented is ignored, there were three different temporally contiguous pairs of stimuli in the two reinforced sequences: A and B, B and C and A and D. Each of these pairs may have generated configural cues that became associated with the US without coding the temporal. Both reinforced triplets (ABC and BAD) contain two of these configurations while the nonreinforced compounds contain only one (AAD,ABD, BBC, BAC) or none (AAC, BBD). If the associations that form between the compounds and the US sum, then the high level of responding to ABC and BAD would be straightforwardly predicted. Interestingly, this hypothesis also predicts that responding should be lowest during AAC and BBD, the two triplets that contain none of the two-element compounds present in the reinforced sequences, and an intermediate level of responding to the other non-reinforced sequences. Examination of the figures from the original paper is consistent with this hypothesis. One interpretation of performance during these experiments then, is that animals form configural cues for nonoverlapping sequentially presented stimuli and that these cues become associated with the US.

Experiment 1a and 1b

We propose an alternative experimental design to assess serial order learning during Pavlovian conditioning that cannot be solved simply on the basis of the summation of configural associations formed between pairs of stimuli. This design involves presenting pairs stimuli, both reinforcing and extinguishing each stimulus an equivalent number of times and having each element presented an equivalent number of times in the first and the second position. The design involved training with four different elements (A, B, C and D) arranged to generate four unique stimulus pairs, presented in two orders producing eight stimulus compounds. Four compounds resulted in food (A->B, B->C, C->D, D->A) and the reversals of these were extinguished (B->A, C->B, D->C, A->D). In addition, in order to minimize generalization between pairs of stimuli, each pair consisted of an auditory stimulus and a visual stimulus. Thus, all four pairs consisted of the same combination of stimulus modality. This design reduces the possibility that any stimulus generalization between pairs of stimuli from the same modality might facilitate configural learning, or that generalization between similar pairs of stimuli might aid discrimination.

Finally, this design also reduces the possibility of generalized occasion setting. Each stimulus (e.g., A) precedes both a reinforced stimulus (e.g., B) and nonreinforced stimulus (e.g., D; i.e., A->B+ and A->D-). Each stimulus (e.g., A) has a corresponding stimulus (e.g., C) that precedes the same two stimuli (B, D), however C signals the reverse reinforcement contingencies (B-, D+) from that of A. Therefore, it is unlikely that learning about A and its two associations for instance, would result in some form of acquired equivalence (e.g., Honey & Watt, 1998) that might facilitate discrimination of the corresponding stimulus C.

Experiment 1a

Method.

Subjects. 8 naïve male Wistar-derived rats (*Rattus norvegicus*) housed in pairs, obtained from the breeding colony at the University of Hertfordshire were used as subjects. They started the experiment approximately 90 days old and weighed between 400-450 grams. They were reduced to 85% of their free-feeding weight before the start of the experiment and remained at this level for the duration of the experiment.

Apparatus. Conditioning for both experiments took place in eight identical conditioning chambers (MED Associates, East Fairfield, VT.) with internal dimensions of 32 cm wide, 21 cm high and 26 cm deep. The chambers were housed in sound and light attenuating cubicles with background noise produced by ventilation fans (≈80 dB). In the middle of one wall was a food magazine tray into which 45mg food pellets (Noyes, Formula A) could be delivered. Head entries into the food tray were recorded by a single optical integrated circuit sensor and infrared LED, breaking the beam counted as a single entry. There were four conditional stimuli; two auditory (A and C) and two visual (B and D). A tone (Stimulus A; not sinusoidal) with a fundamental frequency of 2.8 kHz (86-87 db SPL) was generated by a piezo electric crystal (KPE-350; Farnell Electronics, Leeds, UK). The same tone was used for Stimulus C but pulsed at 5 times a second. For the light stimulus (Stimulus B), the 28-volt stimulus light located above the food magazine was illuminated or Darkness (Stimulus D) was produced by turning off the houselight. Between trials the chambers were illuminated by a dim house-light on the wall opposite the food tray.

Procedure. All animals were trained with a single 30 minute session of magazine training during which free pellets were delivered according to a variable interval 60 second schedule. Each conditioning session involved presenting 80 trials on a Variable time 68-s schedule. There were 10 presentations of each of the four reinforced pairs (A->B, B->C, C->D, D->A) and the reversals of these that were extinguished (B->A, C->B, D->C, A->D). Each trial comprised of a 10 second S_1 followed by a 1 second gap followed by onset of a 10 second S_2. Food pellets were programmed to coincide with the offset of S_2 at the end of reinforced trials. The four stimulus compounds (S_1->S_2) were assigned to ensure that each sequence included one auditory and one visual stimulus. The four sequences which were followed by food were Tone-Light, Light-Pulsing Tone, Dark-Tone and Pulsing Tone-Dark and the reverse order of these pairs were extinguished. Training continued for 21 consecutive sessions. Magazine tray entries were recorded during the first and second element of each sequence and are reported as the number of times that the animal introduced its head in the tray during the intervals. A .05 rejection criterion was used for all statistical tests.

Results and Discussion.

The dependent measure was the rates of head entries in the magazine tray per minute analysed in three session blocks. Initially head entries were distributed throughout the session but as training continued responding occurred more frequently during the second element (S_2). Importantly though, consistent with the hypothesis that rats would learn which two-element sequences were paired with the food, responding was greatest during (S_2) on the reinforced sequences.

Discrimination was assessed by analysis of responses during S_2 of each sequence. During the S_1 the rats could not know whether the trial was to be reinforced or not, and consistent with this there was no reliable difference in response rates during S_1 on reinforced compared with nonreinforced trials. The mean difference on the seven blocks of three sessions of training varied little from zero (-0.19, 0.04, 0.63, -1.61, -1.58, 0.49, –1.11 respectively for blocks 1-7). An ANOVA testing for the factor blocks failed to find any reliable effect, F(6,42)=1.52, partial ω^2=.053. However, as stated there was a reliable difference between responding on reinforced trial to nonreinforced trials during S_2. Since these were the same four stimuli on both reinforced and nonreinforced trial sequences and responses were recorded before the US was delivered the increase in responding on reinforced trials reflects the extent of discrimination learning in anticipation of the food. Figure 1 presents responding during S_2 as a difference score reflecting the difference in between responding to A, B, C and D on reinforced trials (S_2^+) from responding to the same four elements on non-reinforced trials (S_2^-). A repeated measures ANOVA across the 7 blocks of three sessions found a reliable main effect of Blocks, F(6,42)=3.84, partial ω^2=.233. This result supports the observation that the difference scores increased over the training blocks.

Insert Figure 1 about Here

The top panel of Figure 2 shows the levels of responding during reinforced and non-reinforced trials separately for the last block of training. This difference shows that rats responded more to A, B, C and D when they were part of the reinforced sequence than when they part of the non-reinforced sequence. A two factor ANOVA for trial type (S_2^+, S_2^-) and sequence (A-B, B-C, C-D and D-A) found a main effect for the difference between S_2^+ and S_2^- , F(1,7)=15.57, partial ω^2=.477, and a main effect for sequence indicating that there were differences in rates of responding to the four sequences F(3,21)=4.76 partial ω^2=.260, but importantly no interaction between these two factors, F(3,21)=1.30 partial ω^2=.014 was found, suggesting that the difference was consistent across the four sequences.

Insert Figure 2 about Here

The results of this experiment quite clearly show that rats could discriminate between instances of a stimulus when they were part of a reinforced pair. The effect size estimates confirm that the discrimination effect was quite large. These estimates are also useful for confirming that, in spite of the relatively small number of subjects, the nonreliable interaction is associated with a small effect. This is important for supporting the claim that the discrimination was not solved by only learning some of the sequences. The order in which the two stimuli of the pair were presented acted as a discriminative cue for reinforcement.

Although the same four stimuli were present on reinforced and non-reinforced trials the specific orders which were assigned as reinforced was not counterbalanced. For example Tone followed by Light was always reinforced and the reverse was extinguished. It is possible then that the assignment of reinforcement to the orders may mask some bias to learn about these specific orders. To rule out this explanation a second version of this experiment was carried out with half the animals receiving the same treatments as Experiment 1a and half the animals receiving the same stimulus pairs but now in which the order was counterbalanced. This design provides a replication of Experiment 1a and a test of the reverse orders.

In addition, in an attempt to increase the size of the discrimination two changes were made to the training procedure. The inter-trial-interval (ITI) was lengthened and the duration of the stimuli was shortened from 10 seconds to 6 seconds. Increasing the ITI duration might be expected to reduce interference between trials and thereby enhancing discrimination of reinforced from nonreinforced trials. Decreasing the stimulus duration was predicted to shorten the overall trial length and thereby reduce the chance of forgetting which stimulus was presented first during the course of the trial.

Experiment 1b

Subjects. 16 male Hooded Lister rats were obtained from a local breeder (Charles River). They were housed and maintained under the same conditions as Experiment 1a.

Apparatus. The same chambers and stimuli were used except that the pulsing tone was replaced with clicker. The click was produced with an electro-mechanical relay attached to the outside wall of the conditioning chamber, when operated at 7.5Hz it produced an audible click and vibration to the chamber.

Procedure. As in the previous Experiment, one session of magazine training was conducted prior to the conditioning sessions. The procedure involved the same training parameters except that the mean inter-trial-interval for the variable time schedule was 123-s. In addition each element of the pair was only presented for 6 seconds, with a 1 second gap between stimuli. Another difference between the two versions of the experiment was that in 1b the sequences were counterbalanced with respect to order and reinforcement. Half the animals received Tone->Light, Light->Click, Dark->Tone and Click->Dark as the order that were paired with the US while the other half received the US for the reversed orders (i.e., Light->Tone, Click->Light, Tone->Dark, Dark->Click). In spite of our attempts to strengthen the discrimination performance, discrimination was weaker following 26 days and there was no reliable evidence of that the rats had solved it. At this point we reduced the total number of trials per session from 80 to 48 while maintaining the session duration. Almost immediately discrimination performance improved. Since this change did not involve differential experience with the stimuli themselves the only effect was on the level of performance in each session . We do not report the training data because of this change to the trial number.

Results. Consistent with the results of Experiment 1a after the reduction in the number of trials per session rats demonstrated a higher level of responding to the second element of reinforced sequences than to the second element of non-reinforced sequences. There was little evidence of the discrimination however during the first 26 days, before the number of trials was reduced from 80 to 48. However following 6 days on the new trial schedule a reliable difference was observed, suggesting perhaps that the counterbalancing introduced extra error variance. The absolute rates are lower than Experiment 1a perhaps reflecting the shorter stimulus duration and/or the counterbalancing. The bottom panel of Figure 2 presents the rates of responding to S_2 from the last block of two sessions separated by whether it was part of a reinforced or nonreinforced stimulus pair. A two-way ANOVA for trial type (S_2^+, S_2^-) and stimulus (A, B, C and D) found a main effect for the difference between S^+ and S^- F(1,15)=6.09, partial ω^2=.137,and a main effect for sequence type indicating that there were differences in rates of responding to the four different elements F(3,45)=3.37, partial ω^2=.100 but importantly no interaction between the two main effects, F(3,21)=0.64 was found, partial ω^2=-.008 suggesting that the difference was consistent across the four sequences.

General Discussion

The results of these two experiments support the conclusion that rats can use the serial order of two element sequences as a discriminative cue for reinforcement. This is not the first demonstration that temporally ordered conditioned stimuli can influence responding (e.g., Weisman et al., 1980). However our experimental design does not rule-out an associative explanation but eliminates associative mechanisms that do not require coding in some way of the order in which two stimuli are presented. The current design involves comparing responding to the same physical stimulus presented at the end of either reinforced and non-reinforced stimulus pairs. This ensures that there are no specific differences between the reinforced and nonreinforced S_2 and therefore ruling out explanations based on some non-temporal configural associative learning.

Associative theories of learning generally assume that following CS-US pairings an association is formed between the CS and US (e.g., Rescorla-Wagner, 1972; Pearce, 1987). With multiple simultaneously presented CSs these theories assume that configural associations or within-compounds associations are formed. However, with sequentially presented CSs the assumption has been that animals learn individual chains of associations from CS1 to CS2 to the US (Terrace, 1986). We proposed that sequentially presented stimuli might also result in configural associations without coding the temporal order. Wagner and Brandon (2001) have recently developed a real-time model of Pavlovian conditioning that predicts configural learning with nonoverlapping sequentially presented stimuli. Not only does this model predict configural associations, but the model also predicts that these configural representations might contain information about stimulus onset and offset that might allow it to account for our data.

Previous configural models of animal learning involving the formation of associative units that code the entire stimulus configuration (Pearce, 1987) have been used successfully to account for learning in which multiple stimuli are presented simultaneously. However, a purely configural account without temporal order would have trouble explaining the results of our experiments since each stimulus pair that might result in the formation of a configural association was both reinforced and non-reinforced. Furthermore each of the four stimuli used in the experiment immediately preceded the US and therefore there was no unique stimulus that consistently preceded the US. Therefore, to solve the discrimination, animals would have to learn, in some way, the specific order of each stimulus pair. Recently, Pearce has extended his configural model to include units that code the spatial relationship between simultaneously presented cues (George and Pearce, 2001). Spatial units code the relative position in space of stimulus events. A similar strategy allowing coding of temporal information would be required to account for the present data.

There are non-configural accounts of learning involving sequentially presented stimuli in relation to the phenomenon of occasion setting. A simple occasion setting procedure involves sequentially presented stimuli in which the first element (the feature) determines responding to the second element of a two element sequence, the target (e.g., A->B->US and B->noUS). Although there is some controversy over the necessity of presenting the target alone for a feature to become an occasion setter, if we consider that its presence is not required (e.g.,Bonardi, 1989; Hall and Mondragón, 1998; Honey, 2000) it may be possible to develop an explanation of our results. In this case the signalling properties of B are determined by the immediately preceding stimulus. The assumption is that A modulates or facilitates the B->US link. On trials in which B signals the absence of the US (B->A->NoUS), it may becomes associated with a A->noUS link (Bonardi and Ward-Robinson, 2001; Honey, 2000), or may inhibit the link between B and the US. (Rescorla, 1985; Holland 1983; Bouton and Swartzentruber 1986). In this manner, there is no explicit coding of the temporal relationship except in the structure of the associated links. That is, the early presentation of A becomes associated with the later presentation of B and its consequences or vice versa. It would be possible to generalise this account to our discrimination in which each stimulus became associated with both an excitatory and inhibitory link. The associations that would form between each second stimulus and the US (S_2 links) would be related to S_1 activated links that would either activate or inhibit the S_2 links. In this way, the temporal order is encoded by the structure of the hierarchy rather than by specific units that code the temporal position of the elements. Further research will be required to assess whether the stimuli in these experiments act like occasion setters or whether during occasion setting animals encode temporal information in manner not predicted by hierarchical structures.

It is interesting that in spite of the ubiquity of temporal sequences in experience that relatively little work has been conducted to demonstrate this learning with neutral stimuli. It might not be surprising that many animals have the ability to discriminate auditory sequences given the nature of the auditory stimuli used in communication. Our experiments used both auditory and visual stimuli pairs suggest a general ability to learn temporal order is not restricted to communication but may represent a general cognitive capacity. Furthermore any attempt to characterize serial learning in associative terms will require that the model codes the temporal course of the stimulus trace.

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Figure Captions

Figure1. The mean difference scores (S_2^+ - S_2^-) reflecting acquisition of the discrimination during training in blocks of 3 sessions in Experiment 1a.

Figure 2. The mean rates of head entries during the second element (S_2) for reinforced and non-reinforced trials on the final block of training in Experiment 1a (top panel) and Experiment 1b (bottom panel)