DISCRIMINATION OF SERIAL AUDITORY PATTERNS IN RATS

- roles of configural and elemental associations

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ABSTRACT

In order to test whether rats could discriminate between tone sequences, food deprived rats were given appetitive discrimination conditioning with repeated ascending or descending series of musical notes serving as conditioned stimuli (CSs). The other type of tone sequence was reinforced as the other was followed by nothing. In Experiment 1, each series of 8 tones formed a 2 s cycle. The cycle was repeated six times so that the duration of the whole sequence was 12 s. In Experiment 2, the CSs were similar to those in Experiment 1 except that they started with a random note. As a result, rats could discriminate between the stimuli when the CS started systematically with the same note. When the starting note of the CS was randomized rats could not make the discrimination. Thus, according to this study, in a discrimination learning paradigm with serial auditory compounds rats probably form an association between the first tone and the US (or lack of it) but not with the serial pattern and the US.

Keywords: Pavlovian conditioning, discrimination learning, serial order learning, elemental, configural, stimulus compound, tone sequence, rat

INTRODUCTION

The problem of serial order has challenged researchers since a great long time. Serial order refers to the ways that the behavior of humans or nonhuman species is influenced by stimulus events that occur in temporal succession. In the history of associative learning theories the theoretical focus has been in considering the organism's reactions to given stimuli singly, instead of considering the effects that appear when stimuli is presented in some temporal order (Hulse, 1978). The early study of serial order concerned merely human learning and cognition, while the problem of serial order in animal learning was neglected for decades. Lashley (1951) brought up the physiology of the cerebral cortex and pointed out that the cerebral cortex operates as an actively excited and organized system in receiving inputs. In his analysis Lashley focused mainly on human verbal behavior since he argued that problems raised by the organization of language seem to be characteristic of almost all other cerebral activity. Early studies of human serial pattern learning usually concerned people's ability to learn to organize and remember various serially ordered patterns (Hulse, 1978). Broader theories of serial pattern learning emerged in the 1970's. Depending on the theory in question, collections of symbols from which patterns are constructed were called either alphabets (Jones, 1974) or element sets (Hulse, 1978). Theories of serial pattern learning (e.g. Jones, 1974; Restle, 1970) provide a set of combinatorial rules that operate on the element sets or alphabets. People then use these rules in generating corresponding cognitive structures. In his theory Restle (1970) presented a hierarchical model for sequential learning. Restle assumes that the cognitive representations of patterns become hierarchically organized in 'structural trees'. Hulse (1978) suggested that the almost 40 years of neglect of the problem of serial order in nonhuman species may have been caused by lack of an appropriate element set suitable for animals. However, appealing to later research, many potential element sets exist also for nonhuman subjects.

How to describe associations that are formed when an organism is conditioned to a compound stimulus has indeed been in interest of many researchers since a long time (e.g. Kehoe & Gormezano, 1980). Modern conditioning theories (e.g. Pearce, 1987; Rescorla & Wagner, 1972) view stimulus compounds essentially in two different ways. A stimulus compound "AB" is considered here as an example. If AB was treated as a divisible entity composed of two stimulus elements ("A+B"), it would be said to be coded *elementally*. In this case responding to AB would be equal to the algebraic sum of the response tendencies evoked by the elements A and B. On the other hand, if the elements A and B were assumed to interact with each other to create a new stimulus "X", which is treated as if it were unrelated to either A or B, then AB would be said to be

coded *configurally*. In this case AB would be seen as an unanalyzable and invisible whole (X) and responding to the compound would then be determined by the associative strenght of the new stimulus X. One way of defining the basic difference of the ways in which elemental and configural model view the standing of elements and compounds was described by Rescorla (1999). As Rescorla suggests, the elemental account views components and compounds fundamentally different, with the latter containing the former but not vice versa. Stimulus elements are the primary units whereas compounds are derivative of the joint presentation of multiple elements. According to the configural model, however, elements and compounds have a similar status. They are simply different stimuli that generalize to each other in a symmetrical way, but one does not contain the other.

An early elemental approach to the analysis of discrimination learning was introduced by Spence (1936, 1937) by postulating changes in the associative strength of particular component stimuli in a conditioning paradigm. An important feature of Spence's theory is that it contained an elemental characterization of the stimuli that are associated. Spence's quantitative, elemental approach has had a broad and impressive influence on the history of associative learning theories. According to a variety of later elemental theories of learning (e.g., Frey & Sears, 1978; Kehoe, 1988; Pearce & Hall, 1980; Rescorla & Wagner, 1972), a compound stimulus is seen to be composed of separable elements that individually have the potential for entering into an association with the US. The individual strengths of the elements combine to yield the strength of the whole compound. The algebraic sum of the associative strengths of the elements then determine the magnitude of the conditioned response (CR) in the presence of the compound. The elementalist approach of associative learning is especially obvious in the Rescorla-Wagner model (Rescorla & Wagner, 1972).

According to an alternative viewpoint of associative learning, the pattern of stimulation on a trial cannot be broken down in the way that elemental theories consider, but instead itself constitutes a unique CS. One of the earliest attempts to formalize such a configural view was by Gulliksen and Wolfle (1938). Thus unlike elemental theories, a variety of configural theories of learning (e.g., Friedman & Gelfand, 1964; Gulliksen & Wolfle, 1938a, 1938b; Heinemann & Chase, 1975; Pearce, 1987, 1994) assume, that if two or more stimuli are presented together for conditioning, then a representation of the stimulus compound will enter into a single association with the outcome of the trial. Responding in the presence of a compound is then considered to be determined by its own associative strenght. A configural model of conditioning was developed by Pearce (1987, 1994) as he rejected the elemental aspect in favor of a more wholly configural

representation. Pearce's model has had an influential role in the history of associative learning theories. A fundamental assumption of the configural model is that subjects trained with any stimulus configuration, are assumed to form an association between the memory representation of that particular configuration and the US. If trained with stimulus A, for example, subjects are presumed to form an association to the representation of that configuration. If subsequently tested with an AB compound, subjects should respond only because there is some similarity between AB and A. This similarity causes AB to activate the same memory representation as had been activated by A. Since this tendency should be less than unity, according to Pearce, there should be less responding to AB than to A.

The present research investigated discrimination learning in rats exposed to food delivery during a conditioned stimulus CS+. The purpose of this research was to examine if rats can learn to discriminate between serial auditory compounds. Two auditory stimulus compounds, the other consisting of a set of ascending tones and the other consisting of a set of descending tones, served as CSs. In the discrimination training phase the other compound was followed by food while the other was followed by nothing. The research consisted of two experiments. Experiment 1¹ examined a basic discrimination paradigm. The purpose of Experiment 1 was to examine if rats learn to make the discrimination between CS+ and CS-, that is, between the ascending and descending tone sequences. In Experiment 1 the two different auditory compounds were always the same, starting systematically with the same note. For this reason in the second part of the research, in Experiment 2, the starting notes of the auditory compounds were randomized. Thus in Experiment 2 the experimental design was reconstructed so that the tone sequences serving as CS+ and CS- started with a random note. As to the theories of associative learning presented earlier, the aim of the present research was to examine whether rats form the association between CS and US according to the principles of elemental versus configural theories. In case that rats were able to learn the configuration, they are expected to discriminate between the two auditory compounds not only in the basic discrimination paradigm (Experiment 1) but also when the CSs start with a random note (Experiment 2).

¹ The results of Experiment 1 are reported briefly in my Bachelor's thesis.

EXPERIMENT 1

Method

Subjects

The subjects were 8 experimentally naive Sprague-Dawley albino rats, approximately 120 days old at the beginning of the experiment. The mean free-feeding weight was 368 g (range 349-390 g). Before training the rats were gradually reduced to 85% of their ad libitum weights by food deprivation and maintained at those weights for the remainder of the experiment. During the experiment the rats were housed in couple cages, with free access to water at all the time, in a colony, which was illuminated between 6.00 a.m. and 6.00 p.m. The rats were tamed by daily handling. At the beginning of the experiment subjects were randomly assigned to two subgroups (n=4).

Apparatus

The experimental chamber consisted of four individual boxes (30 cm x 20 cm x 25 cm). The back wall and two side walls of each chamber were aluminium, the ceiling was white plastic, the front wall clear acrylic and the floor consisted of 20 steel rods, each 0,5 cm in diameter, spaced 1 cm apart. Each experimental chamber was enclosed in a sound- and light-resistant shell, and the four shells were arranged in a 2 x 2 matrix. The US was a single 45 mg food pellet that was delivered into a food magazine located 15 cm apart from the experimental chamber. Eating was supervised by an infrared photo beam that was directed across the aperture of the food magazine and automatically recorded magazine entries. The tone CS was delivered from a loudspeaker mounted 15 cm apart from the experimental chamber. The intensity of the auditory stimuli was 85 dB. Air circulation and background noise of 70 dB were provided by an exhaust fan located 9 cm above the experimental chamber. A 4W, 12V lamp in the ceiling of the shell provided continuous background illumination. A computer controlled programming of trials so that behaviour during every trial was recorded.

Procedure

Subjects first received 3 sessions of magazine training, each lasting 60 min, in which food pellets were delivered individually on a 60-s variable time schedule. The purpose of this food cup training was to ensure that the subjects learn to make an association between the food pellet and the sound

of the food magazine. Altogether 12 rats received the magazine training and the 8 best succeeded were chosen to take part to the actual experiment. These 8 rats were randomly assigned to one of the two subgroups with 4 subjects per group: Group down+ and Group up+. After magazine training subjects received 30 training sessions (1 session per day). In the training sessions a set of ascending / descending tones operated as a tone CS. The two sets consisted of 8 tones (each lasting 200 ms) that were musical notes from the 6th and 8th octave and that were played 6 times (at 50 ms intervals) so that the duration of the whole CS was 12 s. The interval between the CS's varied and was randomly selected of 135/150/165/180 or 195 s. The training sessions lasted 60 min and during the session both groups received the tone CS 20 times of which half were immediately followed by a food pellet (for Group down+ the descending CS was rewarded and for Group up+ the ascending CS was rewarded). The primary response measure used in this experiment was the rate of food cup entry, that is, the number of times the animal entered the magazine. This was deemed to have taken place whenever the infrared beam inside the magazine was broken.

Results and discussion

Figure 1 shows the mean number of magazine activity as a function of training. The 30 training sessions were merged into 10 blocks of three successive sessions. One rat was excluded from the statistical analysis because it showed negligible level of responding to both the pellet delivery and CSs.

In the beginning of the experiment the rate of responding to both CS –types increased rapidly. At first, the rate of responding was at a similar high level for both types of trial, but as training progressed, the rate of responding declined in all subjects. In the latter half of discrimination training, all subjects seemed to respond more vigorously on the reinforced than on the nonreinforced trials. A repeated measures ANOVA revealed that discriminative learning was evident based on significant Block x CS-type –interaction [F(9,54) = 3.03; p < .01]. Also the main effects of both Block [F(9,54) = 3.79; p < .001] and CS-type [F(1,6) = 8.85; p < .05] were significant.

The results indicate that stimulus discrimination has occurred and that learning has appeared also during a longer time period.

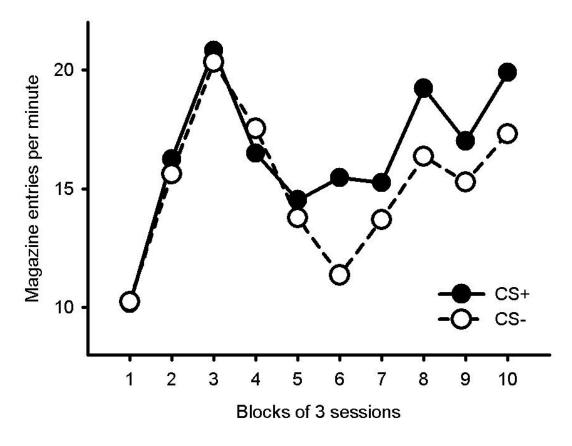


Figure 1. Mean number of magazine activity during Experiment 1.

EXPERIMENT 2

Method

Subjects

The subjects were 8 experimentally naive, male, Sprague-Dawley albino rats (*Rattus norvegicus*) supplied by National Centre for Animal Research in Kuopio, Finland. At the beginning of the experiment the rats were approximately 2 months old. The mean free-feeding weight was 435 g (range 400-484 g). Prior to the start of the experiment the rats were gradually reduced to 85% of their free-feeding weights and were maintained at these weights throughout the experiment by being fed a restricted amount after each experimental session. During the experiment the rats were housed in couple cages and had free access to water at all the time. The cages were placed in a light-proof room which was illuminated between 6.00 a.m. and 6.00 p.m. The subjects were tested at the same time on successive days during the period when the lights were on in their holding room.

Apparatus

Four identical conditioning chambers (24.5 x 23.0 x 20.0 cm) made of aluminium, were housed in separate chests stacked in a 2 x 2 matrix. Each chest was dimly lit by a 4W, 12V lamp in the ceiling of the chest, and independently ventilated by an exhaust fan providing also a background noise of 70 dB. One wall of each conditioning chamber was equipped with a pellet magazine into which 45-mg food pellets could be delivered. A speaker, located behind the magazine immediately outside the chamber, was used to present a 80 dB-tone (a scale) serving as auditory stimuli (CS). Infrared transmitter and receiver pair formed an infrared beam inside the pellet magazine and its breakage was measured. Interruptions of these beams were recorded by a self programmed software running on a PC clone. Control of the experimental events was done by E-Prime software.

Procedure

Before discrimination training all rats were given two 30-min sessions of magazine training. During these magazine training sessions two 45 mg food pellets were delivered by a pellet dispenser (MedAssociates) at regular 60-s intervals. After magazine training the 8 subjects were divided into two squads of four. The other squad was named Group up+ and the other Group down+. The discrimination training consisted of 30 sessions of conditioning, carried out as one session per day.

The duration of one session was 60 min and during this session both groups received the tone CS 20 times, that is, 10 presentations of a CS+ trial and 10 presentations of a CS- trial. For Group up+ the ascending tone sequence was used as a CS+ and the descending tone sequence as a CS-. For Group down+ the arrangement was the opposite, that is, the descending sequence operated as a CS+ and the ascending sequence as a CS-. The sequence of the trials was random. The CS+ trials were reinforced by delivery of two food pellets. The intertrial interval (ITI) had a mean duration of 165 s (range = 135-195 s). The measure of conditioning used in this experiment was the rate of food cup entry. The number of magazine responses was recorded for 12 s prior to every trial. CR was calculated by subtracting the mean number of magazine entries during the pre-CS period from the mean number of magazine entries during the CS period per session. A set of 8 tones operated as tone CS. The notes (and their frequencies in Hz) used in the training phase were C (262), C# (277), D (294), D# (311), E (330), F (349), F# (370) and G (392) in the 8th octave. Duration of each tone was 200 ms and they were separated by silent gap of 50 ms. One cycle lasted thus 2 s and was repeated 6 times making CS duration 12 s. The US in CS+ trials was delivered immediately at the offset of the CS.

Results and discussion

Experiment 2 was identical to Experiment 1 except that the CS sequence started at a random tone in the ascending / descending cycle. The mean rates of responding during the trials for the discrimination training stage are shown in Figure 2. The responses were merged into blocks of three successive sessions.

Responses to both CS –types evidently increased rapidly in the beginning of the experiment. As the conditioning trials progressed, however, the amount of responses evened out and all subjects showed similar levels of magazine activity regardless of whether the current stimulus signaled food or not. The data was analysed by repeated measures ANOVA. No significant main effects were found in the Block x CS-type ANOVA for repeated measures. However, a corresponding analysis was performed on the first four sessions of the experiment. In this case, a repeated measures ANOVA revealed a significant main effect of Session [F(3,21) = 9.92; p < .001]. The pattern is shown in the insert in Figure 2.

Thus, it could be inferred that learning proceeded very fast but no evidence for discrimination was found.

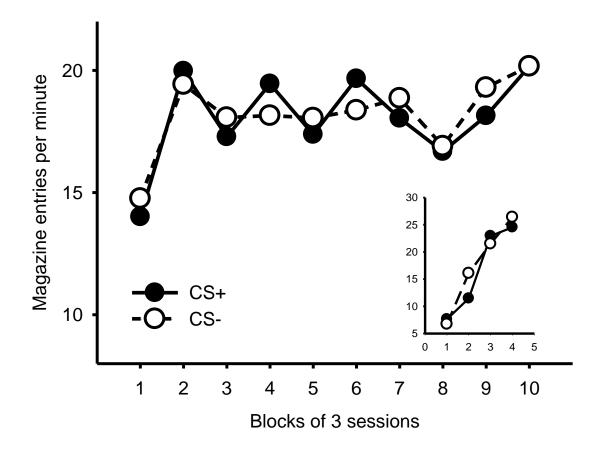


Figure 2. Mean number of magazine activity during Experiment 2.

GENERAL DISCUSSION

In present research two experiments investigated discrimination learning of serial auditory compound in rats. A basic discrimination paradigm (Experiment 1) examined if rats were able to discriminate between ascending and descending tone sequences as these sequences were constantly the same. After this, another test (Experiment 2) was performed in which the starting notes of CSs were randomized in order to rule out the possibility that successful learning in Experiment 1 would be due to association formation between the very first tone in a series (which was systematically different in CS+ and in CS-) and the reward. The results of Experiment 1 suggest that stimulus discrimination between the ascending and descending tone sequences occurred, which apparently gives promising evidence of the rats' ability to discriminate between serial auditory stimulus compounds. According to these findings rats should learn the configuration based on configural theories. Thus, Experiment 1 consequently gives support to the configural theories of associative learning. The results of this experiment evoke expectations for the rats' success also in the latter phase of the study. Against expectations, the results of Experiment 2 show that randomizing the starting note of the tone sequences makes it impossible for the rats to learn the discrimination between the ascending and descending tone sequence. Rats clearly learned the association between a tone sequence and a food pellet, but any discrimination between CS+ and CS- did not appear. As rats were not able to discriminate between the two auditory compounds starting with a random note, are they thus not able to learn the configuration as would be predicted by configural theories. Thus the results of Experiment 2 support the elemental approach to associative learning theories. As an afterward notion, considering the hearing sensibility of rats, the present research arrangement could be improved by choosing stronger auditory tones for the experiments.

As a review to the history of research in serial pattern learning, there seems to be many functional parallels between the way in which people and animals process serial information. Hulse's research (1978) suggests that rats are sensitive to rather complex structures and that useful theoretical models for the formal description of such structures can come from those developed for human pattern learning. Hulse and Dorsky (1979) ended up to the same result; rats seem to be sensitive to formally defined relations among sequences of stimuli in a manner that follows directly from cognitive principles of serial pattern learning. Furthermore, a research by Hulse, Cynx and Humpal (1984) examined starlings' ability to discriminate and generalize among acoustic patterns organized according to rules of human rhythm and pitch perception. The aim of the experiments was to identify the principles of serial information processing that animals and humans share, and

the principles they do not share. The results suggest that like humans, starlings generalize a rhythmic discrimination across tempos with great facility. On the other hand, unlike humans, starlings fail to generalize pitch pattern discriminations across range changes in frequency. Experimental evidence apparently suggests that cognitive models for human serial pattern learning provide a promising path for the study of comparable problems in animal behavior.

Also the topic of how animals represent sequences of events has been under research over the years. A study by Weisman, Wasserman, Dodd and Larew (1980) explored the possibility that pigeons may represent and remember the temporal order of two events. The study included three experiments, in which two-event sequences were presented as discriminative stimuli; one particular order of events as the positive discriminative stimulus (signaling reinforcement) and other possible sequences as negative discriminative stimuli (signaling nothing). The results suggest, that pigeons identified the items of the positive sequence and their temporal order and successfully demonstrated discriminative control by ordered stimuli. Still the results by Weisman et al. (1980) might be explained by configural learning, when the discrimination would have been solved simply on the basis of the summation of configural associations formed between pairs of stimuli. A more recent study about serial order learning in Pavlovian conditioning (Murphy, Mondragón, Murphy, & Fouquet, 2004) settled an experimental design that eliminated the possibility of solving the discrimination by configural learning without coding the order in which two stimuli are presented. The study by Murphy et al. (2004) included two experiments in which hungry rats were trained with successively presented pairs of auditory and visual stimuli. Certain serial orders of stimuli were paired with food and the reversals of these orders were extinguished. Responding to the second element of each pair was analyzed and as a result rats succeeded to discriminate trial types that preceded food from those that did not. The results of this study suggest that rats can use the serial order of two element sequences as the basis for discrimination.

Over the years, a large number of experimental comparisons has been made of the predictions of elemental and configural models. Usually attempts to evaluate these different theoretical accounts have led to conflicting results, as some studies have lent more support to configural than elemental theories and others vice versa (Pearce & Bouton, 2001). Configural and elemental theories of associative learning differ of each other in many ways. One of these ways according to Pearce and Bouton (2001) lies in the predictions they make concerning the influence of similarity on discrimination learning. A general prediction of configural theory is that a discrimination between two patterns of stimulation will be more difficult when they are similar than when they are different. Elemental theories do not always make this prediction. The present proposition was

confirmed in a study by Redhead and Pearce (1995), that examined the way in which similarity influences the ease with which a discrimination between compound stimuli is solved. The results suggest that when the similarity of the signals for reward and non-reward is enhanced by increasing the number of elements they share, then the discrimination between them becomes more difficult. Overall, the results of this study suggest that associations based on the entire pattern of stimulation that signals an US are acquired during conditioning. Alvarado and Rudy (1992) performed an interesting study, which suggests that animals use configural cues even to solve problems that can be solved with elemental associations. According to their study rats can, depending on past experience, respond to a compound stimulus as either a combination of elements or a unified whole. According to Sutherland and Rudy (1989), some animals even have two learning systems; a simple associative system that operates according to principles of elemental theories and a configural association system that enables animals to form a representation of the whole stimulus compound to solve problems that require configural solutions. Alvarado and Rudy (1992) stand up for configural theories also by implying that since animals can make solutions that cannot be deduced from the basic assuptions of elemental theories, they must be able to construct a unique representation of the pattern of stimulus elements present on a particular learning trial and use this representation to control behavior. Also Pearce and Wilson (1990) bring up evidence that support configural theories by demonstrating that animals can solve discriminations that theoretically would be insoluble in the absence of configural cues. A whole different and interesting viewpoint comes from Gallistel (1994), who points out that the primary variables in classical conditioning experiments are the temporal intervals separating the onsets and offsets of the stimuli (the CSs and USs). Gallistel brings up Pavlov's reports according to which animals had learned the intervals and that these intervals had been an important determinant of the conditioned response.

In summary, the results of the present experiments support the conclusion that in a discrimination learning paradigm of serial auditory compound rats form an association between the first tone and the US (or lack of it) but not with the serial pattern and the US. Consequently, this research suggests that in the present task rats are either unable to use configural coding of the auditory patterns or, for a reason or another, favour elemental learning strategy. The significance of the present experiments rests mainly with these implications they hold for currently influential theories of conditioning and discrimination learning. Since the core propositions of both configural and elementistic hypotheses have been empirically confirmed in numerous studies over the years, the major basis for evaluating the available theories seems to rest on their relative ability to derive empirical combination laws as well as permit the differentiation of a compound from its

components and still to generate testable consequences (Kehoe & Gormezano, 1980). On the other hand, since both the elemental and the configural approach can explain findings of Pavlovian conditioning experiments, it seems likely that theorizing will combine the best features of both configural and elemental models. Practically, each model has advantages in dealing with particular conditioning phenomena since the elemental model provides a more natural account of summation and the configural model is more natural in dealing with a range of discriminations in which compounds and their component elements are differentially treated (Rescorla, 1999).

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