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The Role of Ambiguous Expectancy in Differential Inhibition: a Different Role for Context from direct US association

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Two experiments using the conditioned suppression procedure were carried out in order to test the role of direct context-US association in differential inhibition. In Experiment 1, experimental groups differed in inter-trial interval (ITI) and shock density. The results showed that only the short ITI group (higher density shock) passed both retardation and summation tests. Experiment 2 was designed to test whether differences in several kind of ITIs and type of trial presentation could explain differences among groups undergoing the summation test. Results indicated that ITI is the critical variable implicated, but its contribution to inhibitory control of response is modulated by the type of trial presentation. Only the group with short ITIs and random presentation of trials passed both tests. The critical result was that there were no differences in contextual conditioning compared with its yoked group (trials in alternation). The results are discussed within the framework of the ambiguous expectancy hypothesis for differential inhibition proposed in this paper.

Key words: Ambiguous Expectancy, Differential Inhibition, Expectancy of Reinforcement

Differential inhibition (DI) was first described by Pavlov (1927). The procedure was simple: the presentation of two CSs, one of them always followed

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by the US (CS+) and the other not (CS-). During the course of differential conditioning, the CS+ begins to elicit a conditioned response, while the CS-, under some conditions, gains inhibitory control of the response. However, some authors have used it as control for other inhibitory procedures, presumably due to the difficulties of getting inhibitory control of the response in the laboratory (Cunningham, 1979; Delamater, Kruse, Marlin & Lolordo, 1986; Hoffman & Fitzgerald, 1982; Holland, 1984; Mahoney, Kwaterski & Moore, 1975; Rescorla, 1976, 1985). Thus, the status of DI is somehow ambiguous: it is often included among the inhibitory procedures, but is only marginally utilized as such a procedure (Lolordo & Fairless, 1985; Mackintosh, 1983).

Since inhibition was defined as the cancellation of the expectancy of reinforcement (Konorski, 1948), DI has presented a slight challenge for this definition. Indeed, it is not clear at all where this expectancy comes from, since the putative excitatory cue (CS+) is not present during the presentation of the CS-. This is the main difference between DI and other inhibitory procedures. Thus, in the conditioned inhibition procedure, the CS- is presented within an extinction compound with the CS+ (A+, AB-). In the negative correlation procedure, the CS- is presented in the context which is assumed to be the excitatory cue (+, B-). In order to resolve this question, Konorski (1948) proposed the first conceptual explanation of the phenomenon: generalisation of excitatory value from CS+ to CS-. If the CS- is similar to the CS+, it is sensible to think that the CS- could gain some excitatory value and would behave as a generalised excitatory cue. The expectancy of reinforcement would come from the CS- itself, and would be cancelled when the US is not presented. Unfortunately this was contrary both to Pavlov’s observations and to Konorski´s own results (Konorski & Szwejkowska, 1952). The similarity between the CS+ and CS- made it more difficult to obtain DI. Thomas and Basbaum (1972) found the same result: DI was observed only if the CS- was of a different sensory modality from the CS+. The reason why increasing similarity between the two stimuli reduces DI seemed to be, in fact, the generalisation of the excitation from CS+ to CS-. Williams and Overmier (1988) pointed out that generalisation of the excitation prevented the expression of inhibition in several procedures, and that inhibitory control might be more readily obtained if the CS- were extinguished before testing.

Konorski (1967) proposed a second explanation for DI. The expectancy of reinforcement came from the context of conditioning itself, which would enter into association with the US in the reinforced trials. Context conditioning was assessed by Odling-Smee (1975a, 1975b, 1978), using an escape preparation. The Rescorla-Wagner model (1972) offers a similar explanation of the phenomenon. Context enters into competition with other cues in order to gain associative strength just like any other stimulus present during the conditioning session. From this point of view, DI can be regarded as a special case of the negative correlation (NC) procedure in which CS- is presented in an excitatory context. However, it seems logical to think that context gains much more associative strength in the NC than in the DI procedure. In the latter case, the US is always predicted by the CS+, which presumably overshadows the context in a few sessions. Thus, it is quite possible that context has little excitatory value during conditioning sessions and very little, if any, at the time of testing. Wagner and Rescorla (1972) predicted the loss of differential inhibition with a sufficient number of trials. Consistent with this prediction, Hammond (1966, 1967) observed a progressive decrease of the CS- suppression ratio. The author interpreted this data as a progressive lack of excitatory strength of the context. Nevertheless, the CS- was still able to pass the summation test. So it seemed that the CS- could become an inhibitory stimulus in spite of the lack of context excitation. Yadin and Thomas (1981) showed that the context in DI did not elicit a fear response by using the lateral septal nucleus activity as a measure of fear, but they did find this fear response in the NC procedure. The authors interpreted this result as stemming from the more predictive cue for shock (CS) in the DI than in the NC procedure.

Another attempt to establish the underlying associative structure of DI comes from the comparator hypothesis (Miller, Hallam, Hong & Dufore, 1991). These authors suggest a parallel between DI and conditioned inhibition (CI). The context would act as an excitatory cue, which is reinforced when the US appears after CS+ presentation. The CS- would be presented in the context within an extinction compound. Thus, at the time of testing, the excitatory value of the CS- is compared with the comparator stimulus; the context. CS- could act as an inhibitor only if the context is excitatory. Nevertheless, one fact at least makes this parallel inadequate. In the DI, the CS+ is always followed by the US: it is never presented alone in extinction, while context is. It seems hard to believe that context can retain enough excitatory value at testing time (see Hammond, 1966). Nevertheless, Millet et al. (1991) found that CS- was able to pass both the summation and the retardation tests using conditioned lick suppression.

One of the proposals of this paper is to show how DI can be obtained without appealing to a direct context-US association at the time of testing. Other experiments conducted in our lab showed DI even after context extinction (González, 1999, Exp. 1). The hypothesis presented in this paper is that, following this initial direct association between context and US, the context enters into associations with both CSs. The context would be a cue, in the presence of which, two different stimuli can be presented: one is always followed by the shock (CS+), whereas the other one is never followed by the shock (CS-). If this is the case, the context in DI could be the source of an ambiguous expectancy of reinforcement, signalling the Pavlovian associations maintained with both CSs (excitatory and inhibitory). The expectancy of reinforcement cancelled would come from the association context-CS+, which is active during the inter-trial interval. Our thesis is that the inter-trial interval (ITI) plays an important role in DI, acting as a retention interval for information. Under some circumstances, multi-trial learning can be considered as a retention test for information acquired during prior trials, so the inter-trial interval can be envisioned as a retention period (Spear, 1978). Animals can codify information in a prospective way, that is to say, in order to be used in future trials (Hulse, 1978; Capaldi, Verry & Davison, 1980). During DI training, animals learn that one out of two stimuli there is going to appear: a CS+ that is always followed by the US, shock, and a CS- that is a safety signal. When the CS- is presented, the expectancy of reinforcement maintained by the context-CS+ association is cancelled, and the CS- becomes an inhibitor (González, 1996). When the CS+ is presented, the expectancy of reinforcement is fulfilled and the conditioned excitatory response occurs. This learning depends on temporal parameters: if the ITI (retention interval) is too long, this expectancy cannot be maintained: the two associations would not be active at the same time during the ITI period. Thus, the CS- would act merely as a stimulus that has no important consequence for the animal and would behave as a pre-exposed stimulus undergoing latent inhibition, whereas the CS+ would remain as an excitatory stimulus. The following experiments try to obtain empirical support for this hypothesis.

EXPERIMENT 1

If we accept that the ambiguous expectancy hypothesis is a plausible explanation for DI, a critical variable would be the inter-trial interval (ITI), since the hypothesis proposes that the two Pavlovian associations remain active for a short time during this period. Long ITIs would increase the probability of the monotonic decrement in retrieval that occurs with the passage of time (Spear, 1973). On the other hand, ITI has been identified as an important variable for inhibition: the shorter the ITI, the greater the probability of context conditioning, i.e. greater reinforcement density (Lolordo & Fairless, 1985). Nevertheless, the ITI role we try to investigate here is not related to reinforcement density. ITI is seen instead as a retention interval for animals to maintain the representation of the context-CSs associations active during non-events periods (ITI).

The present experiments use the conditioned suppression method. Experiment 1 was designed to test whether ITI affects DI. The groups were equated with respect to number of positive and negative trials, but differed in the interval between stimuli. As a consequence, they differed in session duration and, furthermore, in shock density. Standard tests for inhibition, summation and retardation tests, were used in both experiments.

METHOD

Subjects. Thirty-six, naive,adult, male Wistar rats with a mean ad lib weight of 304 g (range = 286-335 g) were housed in pairs with unlimited access to water and food in their home cages during the first week. At the end of this period, they were progressively reduced to 80% of their ad lib weights and were maintained at this level during the rest of the experiment by being fed a restricted amount of food at the end of each session.

Apparatus. Baseline, differential conditioning training, and tests were conducted in six Campden Instruments operant chambers. Each of the boxes had three walls of sheet aluminium, with a transparent plastic door as the fourth wall and an aluminium ceiling. Each of the boxes contained a recessed food tray where 45 mg of mixed composition food pellets could be delivered; this was situated in the centre of the left wall, adjacent to the door. Access to food tray was by means of a rectangular aperture 6 cm high x 5 cm wide, which was covered by a transparent plastic flap of the same dimensions. Each of the chambers was equipped with a lever, which was mounted on the right of the food tray. Two speakers were mounted on the ceiling of the chamber; through one of these a 30-Hz clicker and a 900 Hz tone, both at 82 dB (A), could be delivered from a Campdem Instruments tone generator (Model 258). A 60-W light was mounted on the ceiling of the chamber. The floor was constructed of stainless-steel rods and could be electrified by a Campdem Instruments shock generator (Model 521C). Shocks were 0.5-s in duration with an intensity of 0.5-mA. The boxes were housed in sound and light-attenuating shells. Masking noise was provided by the operation of ventilating fans contained in these shells. The apparatus was controlled by a PC programmed in a version of C.

Procedure. *Baseline: Lever-press and magazine training.* During the first 10-min session, animals were given magazine and lever-press training. Pellets were delivered according to a variable time (VT) 30-s schedule, and, in addition, every lever-press was rewarded by the delivery of a single food pellet. In the second session, animals were again rewarded for lever-pressing according to a continuous reinforcement schedule (CRF), until they either had achieved a total of 50 responses or had spent 30 min in the box. One similar additional session was given to animals when necessary. No response-independent food deliveries occurred during this session. Sessions 3 to 10 were 40 min in duration. In the third session, lever-pressing was reinforced in the first 10 min according to a variable interval (VI) 10-s schedule, in the second 10 min according to a VI 20-s schedule, in the third according to a VI 30-s schedule, and in the final 10 min according to a VI 40-s schedule. In the fourth session, lever pressing was reinforced in the first 10 min according to a VI 40-s schedule, in the second 10 min according to a VI 50-s schedule and during the rest of the session (20 min) according to a VI 60-s schedule. In the remaining six sessions of this stage, lever-pressing was rewarded according to a VI 60-s schedule. This schedule was maintained during the rest of the experiment.

Design of Experiment 1

Groups	Shock density	ITI	DI training	Summation	Retardation
Short	10+/h	140 s	52L+, 52T-	4L-, 4LT-	8 T+
Long	6+/h	260 s	52L+, 52T-	4L-, 4LT-	8 T+
Control	10+/h	140 s	52L+, 52C-	2T-, 4L, 4LT-	8 T+

Note. L (light); T (Tone); C (Clicker); += shock; ITI= intertrial interval.

Differential conditioning training. After these 10 baseline training sessions, animals were given differential conditioning training for the next 13 sessions. Animals were randomly assigned to one of three groups: Short, Long, and Control. In all groups, animals received four CS+ and four CS- presentations in random sequence in each session. CS+ was a 40-s and 60-W light (L) provided by a lamp mounted on the ceiling of the experimental chamber. CS+ was followed by a 0.5-s 0.5-mA shock . CS- was a 40-s, 900 Hz., 82 dB tone (T) (range: 80-85 dB) in groups Short and Long and a 40-s, 30Hzs, 80 dB clicker (C) in Control group. Sessions lasted different periods of time for every group: Short and Control, 24 min; Long 40 min. These differences in session duration made the groups differ in two other variables: shock density (SD) and inter-trial interval (ITI).

Summation test. The summation test, in a single session, consisted of four extinction trials in which the light (CS+) was on during 40 s. In the last half of this period, the tone (20 s.) was superimposed to the light. Tone was presented only twice in the Control group, at the beginning of the session, in order to avoid a decrement in the response due to the novelty of the stimulus. Both periods (L, LT) were compared with the number of responses conducted during the 20 s.

before the onset of the light, using a traditional suppression ratio (Annau & Kamin, 1961). Sessions were similar in duration to differential training sessions for every group, but because there were just four trials, ITIs were 280 s for Short and Control , and 520 s for Long.

Retardation test. Two retardation sessions followed, each consisting of four 40-s tone presentations followed by shock (shock parameters identical to excitatory trials in DI training). ITIs were the same as for differential conditioning training.

RESULTS AND DISCUSSION

An alpha level of .05 was used for all statistical tests.

Baseline data. Before assigning rats to experimental groups, one-way ANOVA was conducted using the average number of responses per minute during the last session in order to assess the equivalence among groups. The groups did not differ prior to differential conditioning training ($F<1$).

Differential conditioning training course: comparison between experimental groups (Short and Long) was conducted. A three-way ANOVA (stimuli, groups and sessions) revealed differences with respect to stimuli (CS+ vs. CS-), $F(1,19)=269.4$, group x stimuli, $F(1,19)=5.79$, and stimuli x session interactions, $F(12,228)=44$. A subsequent two-way ANOVAS applied to CS+ responding did not show any difference between the groups, CS+ $F(1,19)=1.27$, or a group x session interaction ($F<1$). However, the same analysis applied to CS- responding revealed a group effect, $F(1,19)=13.75$, and session effect, $F(12,240)=5.27$, but no group x session interaction, ($F<1$). A comparison between CS+ and CS- in every group showed a strong discrimination effect in groups Short, $F(1,19)=185.94$, and Long, $F(1,19)=93.64$. Suppression ratio means for groups and stimuli: Short: CS+ 0.09;CS- 0.58; Long: CS+ 0.14; CS- 0.50. (Fig. 1).

Context conditioning measure during DI training. Indirect context fear measure was calculated for every DI session by using a baseline suppression ratio (Baker, Mercier, Gabel & Baker,1981; Bouton & Swartzentruber, 1986). The baseline suppression ratio in this experiment was calculated according to the formula, Bsr= $x/(x+y)$, where x is the average number of responses for every animal during the minute prior to the 1st , 4th and 8th trial in every session and y the average response number per minute during the last baseline session. A two-way ANOVA (groups and sessions) found a group effect, $F(2,32)=4.97$, means: Short =0.42, Long= 0.50, Control=0.43. Comparisons by pairs showed that

Long group differed from Short (p< 0.01) and Control (p<0.05). No other differences were reliable. There was a session effect, $F(12,384)=21.61$, $p < 0.001$, but no group x session interaction, $F(24,384)=1.17$.

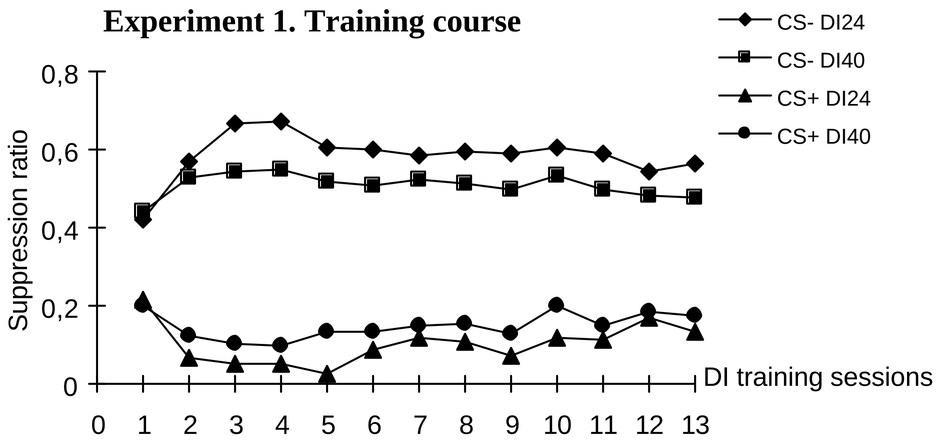

Figure 1. Experiment 1: Differential inhibition training. Group mean suppression ratio to every CS throughout training sessions for experimental groups.

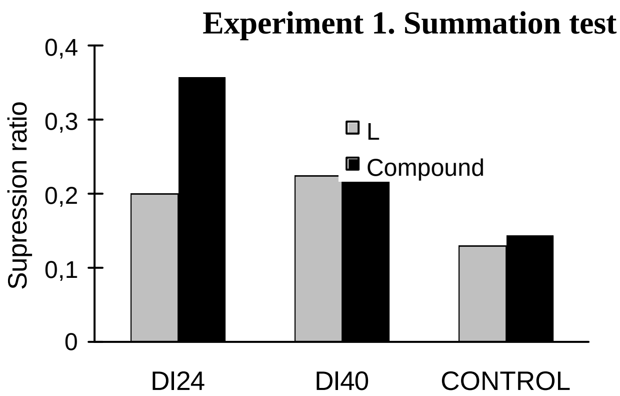

Figure 2. Experiment 1. Summation test. Group mean suppression ratios to the light (L) and to the compound.

Summation test. A three-way ANOVA, group (Short, Long, Control), summation (L vs. LT) and trial factors, showed both summation, $F(1,30)=7.6$, trial, $F(3,90)=5.52$, effects as well as a summation x group interaction, $F(2,30)=6.15$. Simple effects analysis showed a summation effect for Short group, $F(1,25)=17.02$, $p < 0.005$, but not for Long, $F< 1$, or Control $F(1,25)=$

2.39 groups. Means Short, 0.20 vs. 0.35; Long, 0.22 vs. 0.22; Control, 0.21 vs. 0.14 (Fig. 2).

Retardation test. The results of the two-way ANOVA, group and trials factors, showed both group, $F(2,29)=6.84$, $p<0.005$, and trial, $F(7,203)=17.54$, $p < 0.005$, effects as well as a group x trial interaction, $F(14,203)=1.83$. A simple effects analysis showed differences among groups in the 2^{nd} ,3^{rd} ,4^{th} ,5^{th} and 6^{th} trials. A contrast analysis throughout all sessions shows that both Short, $F(1,29)=13.12$, $p < 0.005$, and Long, $F(1,29)=7.67$, differed from Control, but not from each other ($F< 1$). Means: Short: 0.433; Long: 0.414; Control: 0.221. Means for every group and session are depicted in Fig. 3.

Experiment 1. Retardation test

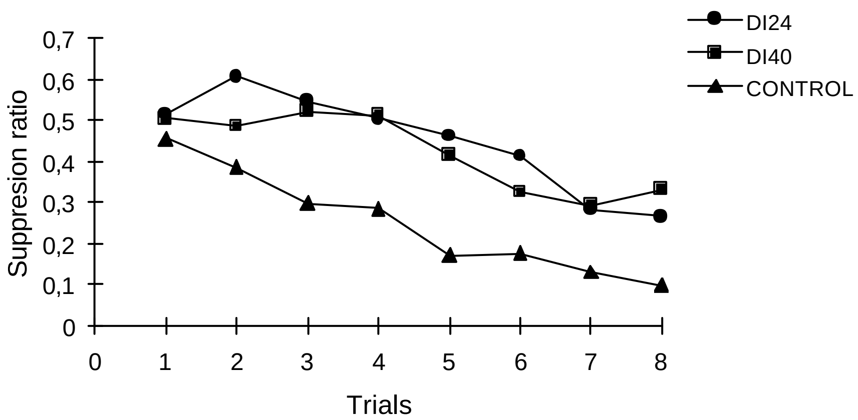

Figure 3. Experiment 1. Retardation test. Group mean suppression ratios to the Tone along retardation trials.

Differential conditioning course analysis allows the assessment of several facts. First, both experimental groups showed clear discrimination between CS+ and CS- during training. However, acquisition of a discrimination does not seem to be sufficient for a stimulus to become a differential inhibitor. The difference between the suppression ratios of the CSs- in both groups during training suggests that something else is occurring. Only the CS- in the Short group can be considered an inhibitor, since it passes both the summation and the retardation tests with respect to Control group. The retardation test alone seems to be insufficient for the assessment of DI, since the CS- in Long group is able to pass it, but does not differ from Control group in the summation test (see Papini & Bitterman, 1993, for a discussion about inhibition testing). A likely explanation for this result is that CS- in Long group behaves as a latent inhibitor; that is, pre-exposure during DI training allows it to pass the retardation test, but not the summation test (Brugada & García-Hoz, 1996). The rationale for this comparison arises from the fact that CS- in Long group would be presented in the absence of any expectancy of reinforcement. Pre-exposing a stimulus retards both inhibitory and excitatory conditioning (Baker & Mackintosh, 1977). An interesting result came from the analysis of the baseline suppression ratio. There was a difference between the experimental groups (Short and Long) in the direction of larger baseline suppression in Short group. This result makes the explanation of a higher level of context conditioning in Short group very appealing, which would enable it to get inhibitory control of the response. However, this result can be explained in another way. Experimental groups are quite different with respect to the training parameters. Long group is over-trained, since it gets 16 min of additional training during each session in the differential conditioning training stage. It is likely that the baseline suppression ratio is sensitive to this situation, making it difficult to determine the reason for the difference. A proper comparison between equivalent groups is offered in Experiment 2, in which groups with the same training are compared.

EXPERIMENT 2

ITI could explain differences between experimental groups results in Experiment 1. Shorter ITI in group Short would make CS- into an inhibitor. If so, an explanation in terms of context conditioning is still possible. In effect, the shorter the ITI, the greater the possibility of context retaining excitatory value through this extinction context conditioning period (Fanselow & Tighe, 1988; Rescorla & Wagner, 1972; Williams, Frame & Lolordo, 1991). Nevertheless, this is not the only explanation that can fit the data from Experiment 1. The ambiguous hypothesis suggests that ITI plays an important role in DI, acting as an retention interval for information. During DI training with short ITI, an ambiguous expectancy of reinforcement remains active. This information is temporally dependent. If the ITI (retention interval) is too long, this expectancy cannot be maintained. That is presumably what occurs in Long group. So ITI should not be very long. Another important feature in the logic of the hypothesis presented is that the expectancy of reinforcement has to be, in fact, ambiguous. That means that trials have to be presented randomly. Serial anticipation pattern learning has been demonstrated in instrumental learning (Capaldi et al., 1980; Hulse & Campbell, 1975). With serial presentation of trials (in alternation) it is sensible to think that an animal could learn the serial pattern of presentation. If this is the case, animals would have positive or negative expectancies of reinforcement according to the content of the next trial. There would not be any expectancy of reinforcement at the time CS- is presented.

In order to make different predictions for direct context-US theories and the hypothesis of ambiguous expectancy, groups Short-Short, S-S, (similar to group Short in Experiment 1) are equated with respect to ITIs but differ in type of presentation of trials: random (R) or in alternation (A). Direct context-US theories would predict no differences in the test for S-S(R) and S-S(A) groups, since shock density is kept constant for both groups. Ambiguous expectancy hypothesis predicts inhibition only in S-S(R) group.

In addition, if ITI can be seen as a retention period, it would be important to keep all ITIs short: CS+ to CS+, CS- to CS-, CS- to CS+ and CS+ to CS-. The two latter periods would have a basic role in direct context-US association explanation (Lolordo & Fairless, 1985). CS- to CS+ ITI would be relevant since the CS- could be a signal for a shock-free period: the longer this period, the greater the power of the safety signal, CS-. In addition, CS+ to CS- ITI would be relevant since CS- would have more possibilities of being presented when context still retains some of its excitatory value after US presentation. In Experiment 2, groups Short-Long, S-L, and Long-Short, L-S, were designed in order to test that all ITIs were relevant and not just the CS+/CS- or CS-/CS+ ones. So S-L groups have one short ITI, (CS+ to CS-), and the other long, (CS- to CS+), whereas this pattern is reversed for L-S groups. Our hypothesis predicts no inhibition for S-L and L-S groups because they have some long ITIs, making the retention interval longer in some trials. For direct context-US association theories, groups S-L should pass inhibition tests.

METHOD

Subjects. Thirty-six, adult, male Wistar rats with a mean ad lib weight of 417 g (range = 369-471 g.) were housed in pairs with unlimited access to water in their home cages during the first week. At the end of this period, they were reduced to 80% of their ad lib weights, and were maintained at this level during the rest of the experiment by being fed a restricted amount of food at the end of each session.

Apparatus. Identical to that used in Experiment 1.

Procedure. All aspects of the procedure that are not specified below were the same as those used for Experiment 1.

Table 2 shows the 2 x 3 design for this experiment, the first factor being type of trials presentation (random or alternation, R and A), whereas the second factor refers to arrangement with respect to CS+/CS- and CS-/CS+ intervals (short-

short, S-S, short-long, S-L, and long-short, L-S). The short interval (S) was 140 s, whereas the long interval (L) was 260 s, the durations being those used in Experiment 1. Six groups of animals are the products of the design. Half of them were given presentation of trials in alternation (groups A) whereas the rest of them received random presentation of trials (groups R). In addition, one third have a short-short arrangement of trial intervals (groups S-S), another third short-long (groups S-L) and the last third long-short (groups L-S). For A groups, the order of presentation was always CS+, CS-, CS+,.... and so on. For R groups, a random sequence of trials without restriction was provided by the PC program. In S-L and L-S groups, CS+/CS+ and CS-/CS- were 260 s when they were selected by the program. CS+ and CS- stimuli were identical to that used in the experimental groups in Experiment 1.

Design of Experiment 2

Groups		EC+/EC-	EC-/EC+	Training Sum.	Ret.
S-S (R)	140 s	140 s	52L+, 52T-	4L-, 4LT-	6 T+
S-S (S)	140 s	140 s	52L+, 52T-	4L-, 4LT-	6 T+
S-L (R)	140 s	260 s	52L+, 52T-	4L-, 4LT-	6 T+
S-L (S)	140 s	260 s	52L+, 52T-	4L-, 4LT-	6 T+
L-S (R)	260 s	140 s	52L+, 52T-	4L-, 4LT-	6 T+
L-S (S)	260 s	140 s	52L+, 52T-	4L-, 4LT-	6 T+

Note. R/S (random/serial presentation of trials); EC+/EC- (duration of the interval); EC-/EC+ (duration of the interval); L (light); T (tone); + (shock)

Summation and Retardation test sessions for each group were identical in duration to those of differential conditioning training. Summation trials were identical to those described in Experiment 1. Retardation test consisted of a single session in which six tone-shock trials were presented.

RESULTS AND DISCUSSION

Baseline. Baseline data measured as average number of responses per minute during the last baseline session did not show differences among groups. Animals were randomly assigned to groups (F< 1).

Summation test. Results for every group are depicted in Figure 4. A four-way ANOVA was performed with factors: kind of presentation of trials (random, alternation); ITI (short-short, short-long and long-short); summation (L, LT) and trials. The only main effect was found for trials, $F(3,27)=20.67$. Interactions occurred for summation x presentation x trials, $F(3,27)=6.87$, and summation x

ITI, F (2.29)=3.35. Several simple effects analyses were conducted in order to explore these interactions. Regarding summation x ITI interaction, the summation effect was reliable for short-short groups F (1,29)=7.48 as well as for the summation x trials interaction, F (3,27)=3.05. A marginally reliable interaction of summation x ITI x random was observed F (2,29)= 3.14, p=0.0581. It seems that there was an effect in the summation test for short-short interval groups that differs from serial to random conditions. A three-way ANOVA for summation in S-S groups was conducted. Summation effect was reliable, F (1,9)= 8.66, as well as a summation x groups x trials interaction, F (3,27)=3.56. A simple effect analysis, keeping presentations and intervals constant, showed effect of summation only in S-S(R) (F 1,29)=6.99. Trial by trial analysis showed summation on 1St trial, F (1,14)=16.73, 2nd F (1,14)=5.97, and 3rd, F (1,14)= 4.34. Inspection of Fig. 4 can be misleading with respect to S-S(A) group. Although the inspection of the figure seems to suggest a summation effect, that was not the case. Animals from S-S(A) group showed a sudden recuperation of suppression to the light in the last trial for all animals. The light was being extinguished during prior trials. This paradoxical recovery of the suppression could be due to extra experimental events which were not identified. Figure 4 captures this fact, since it shows the average along summation trials. With respect to short-long groups, there was no effect of summation (F <1) nor interactions, Fs(3,27)<2.63. For long-short, there was no summation effect nor interaction with presentation or trials, (Fs <1).

Retardation test. Results are depicted in Figure 5. A three-way ANOVA was conducted (presentation, ITI and trial factors). There was a presentation effect, F (1,30)=5. Trial effect was reliable, F (5,50)=7.73, p < 0.0001, as well as the presentation x trials interaction, F (5,150)=2.36. Other interactions were not reliable. A simple effects analysis exploring presentation factor showed a trial x random interaction, F (5,150)=5.26, p <0.005, that was focused on 5th and 6th trials, probably showing that S-L(R) and L-S(R) groups, which up to this moment had an identical course, differ. There were no differences among groups with respect to S-S(R) group (which is identical to Short in Exp. 1 which passed retardation test against Control group) nor suppression ratios below 0.5 before 4th trial.

Experiment 2. Summation Test

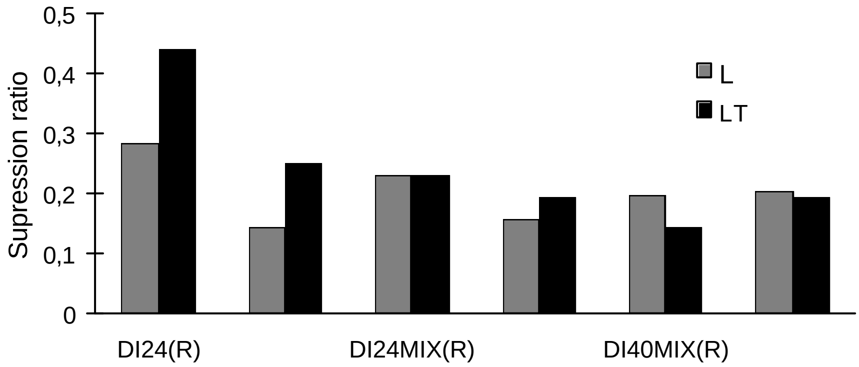

Figure 4. Experiment 2. Summation test. Group mean suppression ratios to the light (L) and to the compound light-tone (LT).

Experiment 2. Retardation test

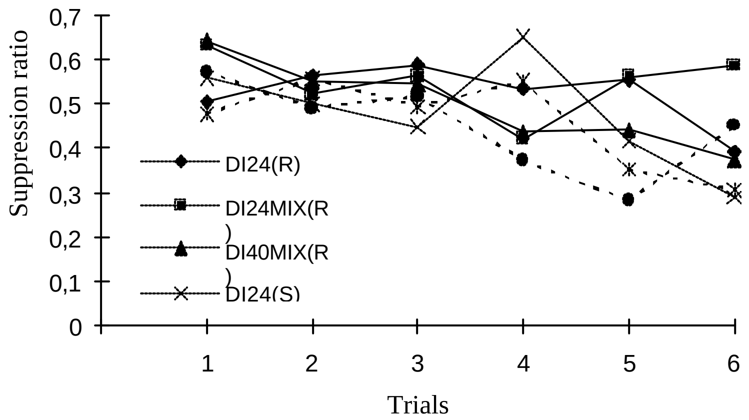

Figure 5. Experiment 2. Retardation test. Group mean suppression ratios to the Tone along retardation trials.

The results suggested that there was a summation effect only for S-S(R) group. The effect was located on 1^{st}, 2^{nd} and 3^{rd} trials. This group was able to pass the retardation test. However, the rest of the groups also passed the retardation test, but not the summation test, suggesting a latent inhibition effect rather than inhibition.

Regarding the different predictions arising from direct context-US theories for DI and ours, two results are relevant. First, there is no evidence for summation in short-long groups. The result is specially relevant with respect to S-L(A) group, which had the same opportunity for context-US association at the time CS- is presented after CS+ trials as had short-short groups, and had a long shock-free period signalled by the CS-. It seems that the critical feature of the procedure is to keep all ITIs short. Second, in this case, only random trial presentation enables the CS- to became an inhibitor since S-S(R) was the only group in which the CS- passed both tests for inhibition. There were no differences between S-S(A) and S-S(R) groups with respect to ITI duration or shock density. Still a direct context-US explanation could argue that, although both groups had been designed in order to produce the same amount of context conditioning, S-S(R) in fact produced more fear to the context. An alternation presentation of trial could give animals a cue to produce serial learning in S-S(A). Animals would learn to expect a CS+, then a CS-, and so on. There would not be any expectancy of reinforcement when CS- is presented, but there would be for CS+. In order to test this alternative explanation, comparison between ITI periods with respect to baseline performance should show more suppression in pre-CS+ periods than in pre-CS- for S-S(A) group. An analysis of variance showed differences between both periods in this sense, F (1,5)=10.80. A significant fact was that the first trial in all sessions was excitatory. So animals learned to expect the shock shortly after they were put into the experimental boxes. If this trial is eliminated for all sessions, there are no differences at all between periods, $F < 1$. It seems sensible to argue that the initial suppression on first trial was a conditioned response to being carried from home cages to experimental room and being placed in experimental boxes. This was a more salient cue than CS+. If this fear of context were produced by the CS+, it would occur later in the session in all pre-CS+ periods. So there is no reason to believe that this first appearance of context conditioning is due to the training cues themselves, but rather to extra training cues. Periods pre-CS+ and pre-CS- were identical in S-S(A) group so the alternative explanation from direct context-US association does not fit the data. There is no evidence for serial learning that could explain differences between group in the summation test. Context seems to be a place where both CSs occur, but context does not necessary maintain excitatory value from US presentation following CS+. Furthermore, an ANOVA using baseline suppression ratio mean from the minute prior to all trials over all sessions for S-S(A) and S-S(R) groups (except the first one in both groups) did not show group effect, F <1. There was session effect, F (12,120)=21.7, p<0.0001, and interaction between factors, F (12,120)=3.24, p <0.001. Simple effect analysis showed effects on 1st session, F (1,10)=8.24, means: S-S(A), 0.1074; S-S(R)

,0.3194; and 9th - *F* (1,10)=6.06; means S-S(A), 0.4977; S-S(R) ,0.3188 (fig 6). This measure would account for differences in contextual conditioning between groups. It is important to note that the result on first session is contrary to a direct context-US association in S-S(R), because this group has a higher suppression ratio than S-S(A). The isolated and late result in 9th session could hardly explain the reliable differences in summation test between both groups.

Experiment 2. Contextual conditioning for groups S-S(R) and S-S(A).

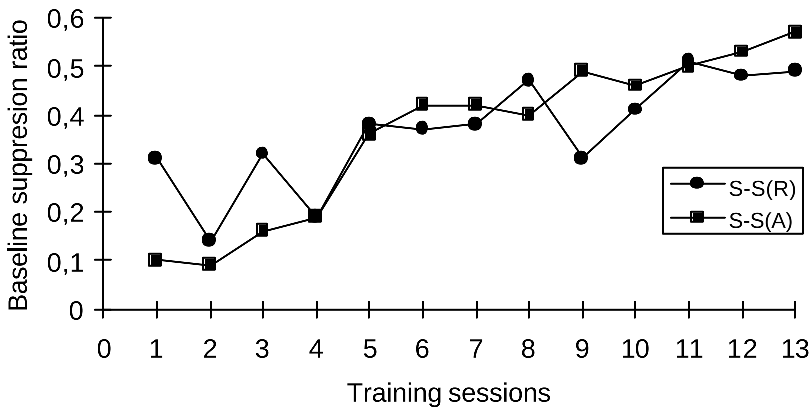

Figure 6. Experiment 2: Baseline suppression ratio by sessions for groups S-S(R) and S-S(A).

So far, direct context-US association cannot explain these patterns of results. With respect to the so-called critical intervals (CS+/CS- and CS-/CS+ ITIs), it is not enough to keep them short and long, respectively. S-L groups, with random or in alternation presentation of trials, did not pass the summation tests. It seems to be important to keep all ITIs short. Besides, it can not explain the important role of type of trial presentation. Groups S-S did not differ in contextual conditioning, but they did in summation test. Both factors find accommodation in the ambiguous expectancy hypothesis. Only with short intervals are animals able to integrate the presentations of the two CSs throughout the session in a prospective way. Context-CS+ association provides the expectancy of reinforcement needed for inhibition to occur, an expectancy that is cancelled at the time of the presentation of CS-. Further research is needed in order to understand the temporal dimension and the mechanism of formation of the ambiguous expectancy. So far, the temporal limitation and random presentation of trials seem to be critical factors for DI to occur according to these results. A critical result is that, even if we accept that context-US association is maintained at the very beginning of training in S-S(A), making it possible that CS- acquires inhibitory control of the response, the CS- is not able to pass summation test. So it is sensible to say that this initial raising of excitatory value of context is not sufficient to make the CS- into an inhibitor in DI procedure. Results published by the first author of this paper suggest that extinction of context cues before testing has no negative effect on summation test (González, 1998, 1999).

GENERAL DISCUSSION

The main proposal of this paper was to investigate how the context can play an important role in the DI procedure, different from the direct association with the US. Theories mentioned in the introduction focused on context conditioning. Nevertheless, it seems that, even if context gains excitatory strength at the very onset of training, it would not be very useful for maintaining this excitatory value. Animals need to detect signals in the environment that enable them to predict and avoid dangerous stimulus as well as recognise safety signals. What does occur when both signals are present in the same context but at different times? Probably animals look for the most predictive signals in this ambiguous context. Ambiguous expectancy hypothesis tries to account for this situation.

Results from the preceding experiments show that direct context-US association cannot explain a variety of phenomena. First, the relevance of short ITI in DI cannot be reduced to short CS+/CS- or CS-/CS+ intervals, the so-called critical periods. Groups S-L(A) and S-S(A) were not able to pass summation test, even if both have a short CS+/CS- period. Second, differences between Short and Long groups in Experiment 1 cannot be explained merely by a greater density shock in the first one. Experiment 2 showed how groups with the same reinforcement density, S-S(A) and S-S(R), differed in summation test. Moreover, these two groups were identical with respect to ITI and even to context conditioning, according to the measure used in this work. Direct context-US association theories would predict the same results on tests, since they have the same shock density and the same opportunity for context to be conditioned. Only the group in which trials are presented randomly is able to pass summation test. This result highlights the importance of the ambiguity or lack of predictability with respect to the context of trials in DI. Only if an expectancy of this sort can be maintained (ambiguous), would the CS- behave as an inhibitor. Otherwise, if we take into account the results of these experiments, CS- would act as a pre-exposed stimulus, a latent inhibitor, passing the retardation but not the summation test. This fact would make the retardation test trivial for DI.

RESUMEN

The Role of Ambiguous Expectancy in Differential Inhibition: a Different Role for Context from direct US association. Se llevaron a cabo dos experimentos utilizando una preparación de supresión condicionada con el fin de explorar el papel que la asociación directa contexto-EI puede tener sobre la inhibición diferencial. En el Experimento 1 los dos grupos experimentales, Short y Long, difirieron en la duración del intervalo entre ensayo (IEE) y en la densidad de descarga. Los resultados mostraron que solamente el grupo Short es capaz de pasar las dos pruebas de sumación y retraso, mientras el grupo Long solamente pasa la de retraso, pudiendo reflejar este dato el efecto de la preexposición durante el entrenamiento. El Experimento 2 pretendía explorar el efecto de la duración y tipo de IEE, así como del tipo de presentación de los ensayos, aleatorio o en alternancia, sobre la inhibición diferencial. Los resultados indican que la duración del IEE es la variable crítica implicada, pero que su contribución al control inhibitorio de la respuesta está modulada por el tipo de presentación de los ensayos. Solamente el grupo donde se mantienen la duración corta de todos los tipos de IEE y en el que se presentan los ensayos de forma aleatoria, grupo S-S(R), consigue pasar las prueba de sumación y retraso. El resultado crítico es que el grupo S-S(A), idéntico al anterior pero con presentación en alternancia de los ensayos, no pasa la prueba de sumación y sí, de nuevo, la de retraso, no habiendo diferencias entre ambos grupos con respecto al condicionamiento contextual. Los resultados se discuten dentro de la hipótesis de la expectativa ambigua para la inhibición diferencial propuesta en este trabajo, al mismo tiempo que se discuten las explicaciones en términos de asociación directa contexto-EI para este procedimiento.

Palabras clave: Expectativa Ambigua, Expectativa de Refuerzo, Inhibición Diferencial

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