Latent inhibition as a function of CS intensity in taste aversion learning

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Abstract

An experiment is reported in which the relationship between the intensity of a preexposed stimulus and latent inhibition was investigated, using the taste aversion learning paradigm in rats. Two concentrations of a saline solution (high, 1%; and low, 0.25%) were used during preexposure and conditioning phases in a factorial design. Two control conditions without preexposure were added, one for each stimulus concentration during conditioning. The known effect of conditioned stimulus (CS) intensity during conditioning was confirmed: the more concentrated the solution used in conditioning, the higher the acquisition rate. A direct relationship was observed between the CS intensity used during preexposure and the latent inhibition effect: the more concentrated the solution during preexposure, the lower the acquisition rate of conditioning. The implications of these results for latent inhibition theories are considered.
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Keywords: Latent inhibition; Stimulus intensity; Taste aversion learning

1. Introduction

It is well known that nonreinforced preexposure to the to-be-conditioned stimulus (CS) retards the acquisition process of the conditioned response (CR) during subsequent conditioning. This phenomenon is termed *latent inhibition* (Lubow and Moore, 1959), and has, since its discovery, generated a great deal of research (see Lubow, 1989). Some of these efforts have focused on examining the effect of CS intensity on latent inhibition, although results from these studies have been mixed.

Crowell and Anderson (1972), Schnur and Lubow (1976) found that latent inhibition is a direct function of preexposed CS intensity, measuring the conditioned emotional response (CER) in rats. However, in experiments using rabbits as subjects, Lubow et al. (1968) conditioning the pinna response, and Solomon et al. (1974) conditioning the nictitating membrane response, failed to find this relationship between CS intensity and latent inhibition (see also Della Casa et al., 1999, using humans as subjects). Crowell and Anderson (1972) pointed out that this discrepancy between results may reflect an interaction between the mechanisms underlying the effects of CS preexpo-

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sure and the type of conditioning paradigm or response system employed. Hernández et al. (1981) found some evidence favoring this hypothesis in an experiment with rabbits. They found a direct relationship between CS intensity and latent inhibition when heart rate was the CR recorded, but not when the eyeblink response was registered. In light of these results, the authors suggested that the somatomotor (i.e. eyeblink) and autonomic (i.e. heart rate) systems may be affected in different ways by CS preexposure. The somatomotor system may be less sensitive to the effect of CS intensity on latent inhibition than the autonomic system. Besides explaining the results, obtained by these particular authors, this hypothesis may also explain discrepancies between the results of previous studies, i.e. the effect of stimulus intensity observed in studies in which an emotional, tonic, diffuse and autonomic response of fear is conditioned (Crowell and Anderson, 1972; Schnur and Lubow, 1976), and the absence of the effect in those studies in which the CR is discrete, punctual and somatomotor, as in the case of the nictitating membrane response (Solomon et al., 1974) and the pinna response (Lubow et al., 1968).

With the aim of confirming these results and extending them to other, different situations, the experiment presented here analyzed the relationship between the intensity of the preexposed stimulus and latent inhibition, using the taste aversion learning paradigm in rats. For this paradigm, the avoidance response (decrease in consumption) to the conditioned taste is considered operationally as an indication of a probably more complex CR. The taste aversion learning endows the taste with affective value by means of a conditioning procedure. The pairing procedure between the taste and the illness in this learning situation allows to the taste to acquire an emotional or motivational significance. The taste becomes an aversive stimulus that in turn will be rejected in the future. Therefore, the conditioned aversion, which is mediated by an emotional or motivational reaction, is likely to affect the autonomic system rather than the somatomotor system. So, according to Hernández et al.'s hypothesis, the higher the intensity of the pre-exposed taste, the greater latent inhibition we

would expect to find when a taste aversion is conditioned. The ultimate purpose of the study presented here was to analyze whether the effect of stimulus intensity on latent inhibition is parallel to its effect on other similar learning situations. The implications of these results for latent inhibition theories will be considered later.

Thus, the experiment tested the effect of pre-exposure to a salty taste with different intensities (concentrations) on the acquisition rate of aversive properties during conditioning. In order to assess the effect of CS intensity, during preexposure separately from the effect of CS intensity during conditioning, a factorial design was used with two taste concentration levels, high concentration (1%) and low concentration (0.25%), during both preexposure and conditioning (Group 1–1, Group 1–0.25, Group 0.25–1, and Group 0.25–0.25). Furthermore, two control groups without preexposure to the taste were added, one for each concentration level during conditioning (Group 0–1 and Group 0–0.25). This design also enabled the effect of preexposed CS intensity to be analyzed independently of any generalization decrement produced by a change in stimulus intensity. If a change in taste concentration between preexposure and conditioning produces a generalization decrement, then this will result in less latent inhibition than if no change had occurred. Therefore, in accordance with this generalization decrement hypothesis, latent inhibition should be lower for Group 1–0.25 than for Group 0.25–0.25, and for Group 0.25–1 than for Group 1–1. However, a different pattern of results may be expected in accordance with the preexposed CS intensity hypothesis. If the magnitude of latent inhibition is a direct function of preexposed CS intensity, then higher taste concentrations during preexposure will result in greater latent inhibition, regardless of what taste concentration was conditioned.

2. Method

2.1. Subjects and apparatus

Subjects were 48 naïve male Wistar rats with a mean weight of 369 g (range: 330–419 g) at the

beginning of the experiment. They were housed in individual cages located in an air-conditioned temperature-controlled room on a 12-h light: 12-h dark cycle with light on at 08:00 h. Dry food was available throughout the experiment, but access to water was limited. The deprivation schedule consisted of animals receiving free access to water for 30 min twice a day for 6 days prior to the start of the experiment. The first intake session was at 12:30 h and the second one at 18:30 h. These liquid intake sessions were maintained throughout the experiment. The experimental sessions were conducted in the subjects' home cages during the first session of each day.

Inverted 50 ml centrifuge tubes equipped with stainless steel ball-bearing-tipped spouts were used to present controlled amounts of flavored solutions and unflavored tap water. The stimulus employed was a saline solution (NaCl) with two concentrations: high (1% w/v) and low (0.25% w/v).

2.2. Procedure

The procedure was divided into two phases, preexposure and conditioning. The subjects were randomly assigned to one of six equal-sized groups ($n = 8$) in accordance with the factorial arrangement of three preexposure conditions (exposure to 1 or 0.25% saline solution, or not exposed) and two conditioning conditions (conditioned to 1 or 0.25% saline solution): Group 1–1, Group 1–0.25, Group 0.25–1, Group 0.25–0.25, Group 0–1, and Group 0–0.25.

2.2.1. Preexposure
The experiment included 16 sessions of preexposure. In each daily session, subjects were allowed access to 10 ml of a saline solution during 30 min. Subjects in Groups 1–1, and 1–0.25 received the 1% solution, whereas subjects in Groups 0.25–1 and 0.25–0.25 received the 0.25% solution. Subjects in Groups 0–1, and 0–0.25 received water rather than saline solution during the sessions of this phase.

2.2.2. Conditioning
All subjects received nine conditioning trials. During each trial, they were given access to 10 ml of saline solution for a 30 min period, immediately followed by an intraperitoneal injection of 10 ml/kg 0.2 M lithium chloride (LiCl). For subjects of Groups 1–1, 0.25–1, and 0–1, the 1% saline solution was conditioned, whereas for subjects of Groups 1–0.25, 0.25–0.25, and 0–0.25, the 0.25% saline solution was conditioned. Each conditioning day was followed by a recovery day in which subjects received free access to water twice, as before.

3. Results

Mean consumption of water on the day before the start of the experiment was 7.6, 10.3, 10.6, 10.6, 8.8, and 10.7 ml for subjects in Groups 1–1, 1–0.25, 0.25–1, 0.25–0.25, 0–1 and 0–0.25, respectively. A one-way analysis of variance (ANOVA) was conducted with these data and revealed that differences between groups were not statistically significant, $F(5, 42) = 1.29$, $P = 0.287$ (here and elsewhere a criterion of statistical significance of $P < 0.05$ was adopted). Subjects consumed practically all the amount supplied (10 ml) during each preexposure session.

Fig. 1 shows the mean amounts of saline solution consumed for each of the six groups over the nine conditioning trials. It is apparent that all groups came to suppress consumption of the conditioned solution, but there were differences in the rate at which the aversion was acquired. On the one hand, consumption of the more concentrated solution decreased more rapidly than consumption of the less concentrated one. On the other hand, preexposure appeared to retard the acquisition of the aversion, reflecting the latent inhibition effect. When the more concentrated solution was conditioned, it is clear that preexposure to the more concentrated solution (Group 1–1) retarded conditioning as compared with non-preexposure (Group 0–1), but preexposure to the less concentrated solution (Group 0.25–1) did not. However, when the less concentrated solution was conditioned, preexposure to
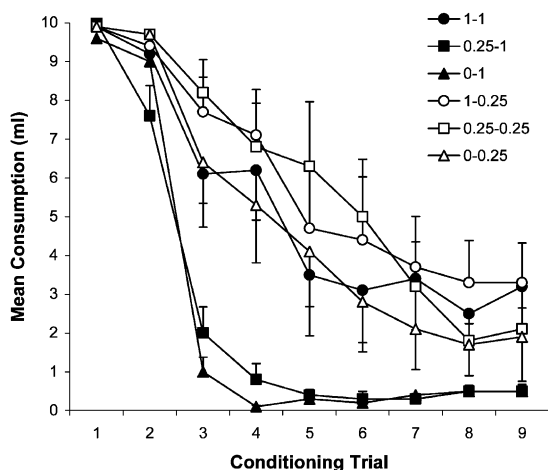
Fig. 1. Mean amounts of saline solution consumed by groups for the nine conditioning trials. For Groups 1–1, 0.25–1 and 0–1, a 1% saline solution was conditioned, and for Groups 1–0.25, 0.25–0.25 and 0–0.25, a 0.25% saline solution was conditioned. Groups 1–1 and 1–0.25 had been preexposed to a 1% saline solution. Groups 0.25–1 and 0.25–0.25 had been preexposed to a 0.25% saline solution. Groups 0–1 and 0–0.25 did not receive preexposure.

both the more concentrated solution (Group 1–0.25) and the less concentrated one (Group 0.25–0.25) retarded conditioning only slightly as compared with non-preexposure (Group 0–0.25). An ANOVA was conducted on these data with the between-subject variables of concentration during preexposure (1, 0.25, or 0) and concentration during conditioning (1 or 0.25), and the within-subject variable trial. This analysis revealed significant main effects of concentration during preexposure, $F(2, 42) = 4.25$, $P = 0.021$, and concentration during conditioning, $F(1, 42) = 15.35$, $P < 0.001$, but the interaction between the two variables was not significant, $F(2, 42) = 1.97$, $P = 0.153$. There was also a significant main effect of trial, $F(8, 336) = 151.07$, $P < 0.001$, as well as significant interactions between concentration during preexposure and trial, $F(16, 336) = 2.51$, $P = 0.001$, and between concentration during conditioning and trial, $F(8, 336) = 9.61$, $P < 0.001$. The three-way interaction was not significant, $F(16, 336) = 1.39$, $P = 0.142$. Subsequent tests of simple main effects examining the interaction between concentration during preexposure and trial revealed differences among preexposure conditions

in Trials 3, 4, 7, and 9, $Fs(2, 116) > 3.28$, $Ps \leq 0.041$. Pairwise comparisons using the Newman–Keuls test indicated that consumption by subjects preexposed to the more concentrated taste was significantly higher than consumption by non-preexposed subjects in Trials 3, 4, 7 and 9, and significantly higher than consumption by subjects preexposed to the less concentrated taste in Trials 4 and 9. This indicates that subjects preexposed to the more concentrated taste acquired the conditioned aversion more slowly than subjects preexposed to the less concentrated taste and non-preexposed subjects. In other words, a direct relationship was found between preexposed CS intensity and the magnitude of latent inhibition. A simple main effects analysis of the interaction between concentration during conditioning and trial revealed that consumption by subjects conditioned to the more concentrated taste was significantly lower than consumption by subjects conditioned to the less concentrated taste for Trials 3–7, $Fs(1, 116) > 4.95$, $Ps \leq 0.028$. Therefore, a direct relationship was observed between CS intensity during conditioning and the acquisition rate of conditioned aversion, confirming the well-documented effect of CS intensity during conditioning (Kamin, 1965).

4. Discussion

The results of this experiment indicate that latent inhibition is a direct function of preexposed stimulus intensity in the taste aversion learning paradigm with rats. This is evident in the fact that preexposure to the more concentrated taste retarded conditioning in comparison with preexposure to the less concentrated taste and non-preexposure when either concentration was used in acquisition. This means that the results cannot really be explained by the generalization decrement hypothesis. According to this hypothesis, preexposure to the taste with the same concentration as that used in acquisition should have produced greater latent inhibition than preexposure to the taste with a different concentration. Consequently, latent inhibition should have been greater for Group 1–1 than for Group 0.25–1, and

similarly, greater for Group 0.25–0.25 than for Group 1–0.25. However, the lack of interaction between the concentration used during preexposure and the concentration used during conditioning suggests that changing taste concentration from preexposure to conditioning did not reliably affect the preexposure effect obtained. So far we have assumed that the generalization between the more and the less concentrated tastes is symmetrical. But, if it were assumed that generalization between them is asymmetrical, could the generalization decrement explain these results? The weak stimulus might be considered a subset of the strong stimulus. Under this assumption the strong stimulus should be considered a compound stimulus (AX) formed by weak stimulus elements (X) and elements of the strong stimulus itself (A). When the weak stimulus is preexposed and the strong stimulus conditioned (Groups 0.25–1), only some of the elements of the to-be conditioned stimulus are preexposed. On the other hand, when the strong stimulus is preexposed and the weak stimulus conditioned (Groups 1–0.25), all elements of the to-be conditioned stimulus are preexposed. We may therefore expect a greater generalization decrement from the weak to the strong stimulus (Group 0.25–1) than from the strong to the weak stimulus (Group 1–0.25). Nevertheless, bearing in mind the overshadowing effect on latent inhibition (e.g. Lubow et al., 1982), the weak stimulus elements (X) may acquire lower latent inhibition during strong stimulus (AX) preexposure than during weak stimulus (X) pre-exposure. Thus in Group 1–0.25, elements X should compete with elements A during preexposure, and in turn should acquire lower latent inhibition than in Group 0.25–0.25, for which those elements are preexposed in isolation. Although this competition would occur in Group 1–1, both elements A and X are part of the to-be-conditioned stimulus in this case, and in consequence latent inhibition would be greater than in Group 0.25–1, for which only elements X are preexposed. Therefore, differences in the degree of generalization decrement may be compensated by differences in the amount of latent inhibition acquired. In other words, the pattern of results expected from the assumption of asymmetrical

generalization may not be so different from that expected from the assumption of symmetrical generalization. In conclusion, these results are difficult to explain in terms of generalization decrement, and seem to support the hypothesis that there is a direct relationship between latent inhibition and stimulus intensity.

Thus, these results coincide with those obtained by Crowell and Anderson (1972), Schnur and Lubow (1976) using the CER preparation with rats, and Hernández et al. (1981) employing the heart rate conditioning with rabbits, yet contradict those obtained through conditioning the pinna response (Lubow et al., 1968), the nictitating membrane response (Solomon et al., 1974) and the eyeblink response (Hernández et al., 1981) in rabbits. Even when we take into consideration the complexity of the CR involved in taste aversion learning, it seems reasonable to assume that the components of the CR in this situation are more likely to reflect the conditioning of an autonomic response than the conditioning of a somatomotor response, as we have seen before. In consequence, these results also coincide with Hernández et al.'s hypothesis, which states that the autonomic response system might be more sensitive to the effect of CS intensity on latent inhibition than the somatomotor system. Confirmation of this hypothesis through further research may be interesting since it may suggest that multiple mechanisms are at work in latent inhibition. Latent inhibition in autonomic system may be produced by mechanisms that are not involved in the somatomotor system. In any case, given the lack of additional data about the possible interaction between the effect of preexposed CS intensity and the response system employed, more research is required in order to investigate its causes. It is also possible that the absence of the effect of the stimulus intensity in those studies does not reflect an actual interaction, but only a specific parametric or operational effect.

Another purpose of this study was to examine the extent to which the effect of stimulus intensity on latent inhibition is similar to the known effect of the same variable on other paradigms of non-associative and associative learning, such as habituation or Pavlovian conditioning. Parallel find-

ings regarding the effects of stimulus intensity on these learning modalities serve to strengthen the hypothesis that these phenomena share common processes. When listing features of habituation, Thompson and Spencer (1966) stated that '*The weaker the stimulus, the more rapid and/or more pronounced is habituation. Strong stimuli may yield no significant habituation*' (p. 19). Indeed, if habituation is inversely related to stimulus intensity, then our results, together with the similar ones mentioned above, would support the hypothesis that the process responsible for latent inhibition is not the same as that which underlies habituation. However, although this inverse relationship between stimulus intensity and habituation has been reported for a wide variety of species and response systems (Thompson and Spencer, 1966), this general effect has been challenged by several studies (e.g. Davis and Wagner, 1968; Wickelgren, 1967) that have found the opposite effect. In any case, any comparison between results obtained in the latent inhibition paradigm and those obtained in the habituation paradigm should be considered very cautiously. Most of the studies that have investigated the effect of stimulus intensity on habituation have employed shorter intertrial intervals (ITIs) than those used when testing this effect in the latent inhibition paradigm. Bearing mind that different processes may occur depending on the length of the ITI (Wagner, 1976), it is therefore hardly surprising that different results are found for the two paradigms (see Hall, 1991; Lubow et al., 1981).

On the other hand, taking into account the well-documented direct relationship between stimulus intensity and learning rate in Pavlovian conditioning (Kamin, 1965), our results coincide with theories which see latent inhibition as the result of mechanisms similar to those that govern the conditioning itself (Lubow et al., 1981; Pearce and Hall, 1980; Wagner, 1976, 1981). These theories agree that latent inhibition effect reflects a loss of associability or attention to CS during preexposure. This loss will bring about a decrease in processing to CS that will result in a failure to acquire the CS-US association at the time of conditioning. These theories disagree, however, in the particular associative mechanisms postu-

lated to determine the changes in processing to CS. The conditioned attention theory proposed by Lubow et al. (1981) suggests that latent inhibition reflects the conditioning of an 'inattentional' response to the CS during preexposure. The theory predicts that acquisition of the inattentional response is governed by the same principles as the conditioning, and therefore latent inhibition will be a positive function of the preexposed stimulus intensity. Pearce and Hall (1980) theory assumes that the better predictor a given stimulus is of its consequences, the less attention is paid to it. This theory implicitly assumes that the stronger the preexposed stimulus, the faster the learning about 'no consequences' and the faster the decrease in attention that is responsible for latent inhibition during non-reinforced preexposure. Wagner's account (Wagner, 1976, 1981) suggests that long-term habituation (which occurs with long ITIs) and latent inhibition may be the product of the same associative learning. According to this account, both phenomena are a consequence of the formation of an association between the stimulus and the experimental context during preexposure. The theory postulates that the stronger the context-stimulus association, the less processing will be received by the stimulus, and consequently, the stimulus will be less likely to enter into a new association (latent inhibition) or to produce an unconditioned response (habituation). Assuming that the more intense a stimulus, the better the opportunity for the development and strengthening of this context-stimulus association, this theory may also explain the stimulus intensity effect observed in this study. More recently, it has been proposed that the latent inhibition effect may reflect a performance failure at the time of the retrieval of the CS-US association formed during acquisition (Bouton, 1993; Miller et al., 1986). This alternative account of latent inhibition focuses on interference mechanisms between contents learned during preexposure and conditioning. These theories emphasize an interference effect that occurs during performance rather than learning, thus leaving unexplained the effect of variables that are know to affect latent inhibition, such as for example the number of preexposures, duration of stimulus preexposure,

and, as in this study, stimulus intensity (see Lubow, 1989). Therefore, the results reported here support the traditional interpretation of latent inhibition, i.e. that it reflects a learning phenomenon rather than a retrieval failure.

Acknowledgements

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