Appetitive latent inhibition in rats: Now you see it (sign tracking), now you don't (goal tracking)

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Latent inhibition (LI), the retardation of Pavlovian acquisition after nonreinforced preexposure to the conditioned stimulus, is a popular paradigm for studying basic attentional and memory processes from both behavioral and neurobiological perspectives. It is argued that whether LI emerges depends on the behavioral measure used to index conditioning. An experiment with rats demonstrates that stimulus preexposure retards the development of sign-tracking responses directed at the stimulus, but not the development of goal-tracking responses directed at the site of food delivery. These results are consistent with models that explain LI in terms of a deficit in retrieval.

When a conditioned stimulus (CS) is repeatedly presented alone, its ability to induce a conditioned response when subsequently paired with an unconditioned stimulus (US) is reduced. This phenomenon, known as latent inhibition (LI; Lubow, 1989), is attracting substantial interest due in part to the proposal that it models some of the deficits observed in schizophrenic patients (J. A. Gray, 1998). For example, administration of amphetamine, a drug known to have psychotomimetic effects, has been shown to disrupt LI (Solomon & Staton, 1982), whereas haloperidol, an antipsychotic drug often used in the treatment of schizophrenia, enhances the likelihood of observing LI (Weiner & Feldon, 1987). Moreover, acute schizophrenics show a disruption of LI, but chronic schizophrenics who have been on neuroleptic treatment for at least 8 weeks show normal LI (Baruch, Hemsley, & J. A. Gray, 1988; N. S. Gray, Hemsley, & J. A. Gray, 1992).

In addition, LI continues to be a source of theoretical challenge. Two classes of theories have been proposed to explain LI—namely, those suggesting that nonreinforced CS preexposure interferes with subsequent acquisition of the CS–US association (acquisition-deficit models; e.g., Lubow, 1989), and those suggesting that CS preexposure interferes with the expression of the CS–US association (retrieval-deficit models; see Escobar, Oberling, & Miller, 2002). The issue of retrieval deficits in learning situations can be approached by broadening the behavioral observations in freely moving animals. Whereas LI experiments typically assess acquisition rate in terms of a single response measure, a growing body of evidence suggests that the specific response chosen to assess conditioning is a crucial determinant of the results obtained with any given set of

parameters (Domjan, 2000). For example, Akins, Domjan, and Gutiérrez (1994) varied the CS–US interval in an experiment with male Japanese quail in which the CS was a localized visual stimulus (a foam block) and the US was sexual reinforcement (access to a receptive female). The characteristic finding in experiments varying the CS–US interval is that conditioning is reduced as the CS–US interval increases from some optimal value (see Rescorla, 1988). Akins et al. (1994) found that conditioning was, in fact, present at long intervals (20 min), as assessed against unpaired controls, but the form of the response had changed relative to that observed with short intervals (1 min). Short intervals resulted in sign tracking (i.e., increased activity around the CS area), whereas long intervals promoted conditioned behavior that occurred farther away from the CS location. Similar results were obtained by Brown, Hemmes, Cabeza de Vaca, and Pagano (1993) in an autoshaping experiment with pigeons. They found that delay conditioning led to significantly greater sign-tracking responses than did trace conditioning, but that, in contrast, trace conditioning produced more goal-directed behavior than did delay conditioning.

In the present experiment, we examined the possibility that the CS–US association is indeed formed during conditioning after nonreinforced CS preexposure, as suggested by retrieval-deficit models, but that this association is expressed in terms of a behavior different from that observed in nonpreexposed controls. Sign tracking and goal tracking were measured in an appetitive Pavlovian situation and set against each other through spatial segregation. Both responses have been observed in rats trained under similar conditions (Papini & Brewer, 1994), although with a greater spatial proximity between the CS and US sites than what was used in the present experiment. Sign tracking tends to occur at the beginning of the CS; goal tracking, during the latter portion (Davey, Oakley, & Cleland, 1981). Typically, only goal tracking is reported in appetitive experiments on LI (e.g., Channell & Hall, 1984; Killcross & Balleine, 1996), although some experiments have pro-

vided information about more than one response system. For example, Holland and Gallagher (1993; Chiba, Bucci, Holland, & Gallagher, 1995) measured the effects of non-reinforced CS preexposure (either the house light or a panel light) on subsequent appetitive conditioning in terms of rear behavior and food cup behavior. Although evidence of LI was found with both response measures, the results are inconclusive for two reasons. First, rearing behavior was recorded during CS presentation, but it was not defined in terms of orientation toward the CS or proximity to the CS site. Thus, it is unclear whether this behavior reflected true sign tracking. Second, the panel light CS was located near the goal, whereas the house light CS was located inside the sound-attenuating chamber and it was "even with the end wall that contained the food cup" (Holland & Gallagher, 1993, p. 247). The relatively close distance between the CSs and the food cup probably allowed the rat to oscillate between the sign tracking and goal tracking (e.g., Papini & Brewer, 1994; Zener, 1937). These problems are understandable given that the goal of Holland and Gallagher's experiments was not to set sign- and goal-tracking responses against each other. Therefore, the issue of the potential differential sensitivity of various dependent measures to the effects of CS preexposure remains open for clarification, and it has both practical and theoretical implications for an understanding and application of the LI paradigm.

METHOD

Subjects

Thirteen male, experimentally naive 90-day-old Wistar rats served as subjects. Ad-libitum weights ranged from 350 to 450 g. The animals were maintained at 85% of this weight by limiting their daily access to food, and they were housed in individual cages with water available ad lib. The room was on a 12:12-h light:dark cycle (light on at 0700 h). Training sessions were administered between 1200 and 1700 h.

Apparatus

Training occurred in a 1.2-cm thick cardboard box, 120 cm long, 50 cm wide, and 60 cm high. An aluminum food cup was placed in the center of a 50-cm wall. A hole was cut in the wall of the box where the cup was placed. The food cup's orientation, then, was flush against the wall, as in a standard operant chamber. The CS was a light (60 W) located on a 120-cm wall, 15 cm above the floor and 37 cm from the food cup. The box was placed on a yellow tile floor that was cleaned after every session. A radio produced masking white noise. The sign and goal areas, each 10 × 6 cm in size (the longer dimension parallel to the closest wall), were marked off by red tape. A JVC VHS-C video camera recorded all the sessions. Illumination was provided by a lamp (40 W, 120 cm from the box) directed away from the conditioning box.

Procedure

Rats were randomly assigned to three groups: explicitly unpaired (Group EU; $n = 4$), context control (Group X; $n = 4$), and CS preexposed group (Group LI; $n = 5$). The experiment consisted of two phases, preexposure and acquisition. During preexposure, Group LI received 15 sessions (10 trials/session) of nonreinforced CS presentations. CS duration was 10 sec. Groups X and EU received the same amount of exposure to the conditioning box (18-min long sessions), without CSs or USs. During acquisition, Groups X and LI received

20 sessions (10 trials/session) in which the 10-sec CS ended with the delivery of the US (five 45-mg pellets, Noyes, rodent A/I formula). The five pellets were placed in a cup, and, at the appropriate time for food delivery, the cup was emptied into a funnel so that the pellets fell on the food cup inside the conditioning box. The mean intertrial interval was 90 sec (range: 60–120 sec). Group EU received a similar number of CSs and USs, but the mean interval between successive events was 45 sec (range: 30–60 sec). A die rolled before each session randomly determined the order of stimulus presentation.

The procedure used to collect information on sign- and goal-tracking responses was the same as that used by Burns and Domjan (2001). The main data were taken from videotapes of Sessions 1, 5, 10, and 15 of preexposure in Group LI, and from Sessions 1, 5, 10, 15, and 20 of acquisition in all the groups. Scoring was performed by three students unaware of the nature of the experiment and training conditions of each group. One student scored the preexposure sessions, and the other two scored the acquisition sessions. Observers measured the time spent in the sign and goal areas. A rat was scored as being either in the sign area or in the goal area on the basis of the location of its nose. The location of the animal's nose was recorded during the 10-sec CS and also during the 10 sec before CS onset. The primary measure was the percentage of trials in which a response (sign tracking or goal tracking) was scored. A sign-tracking response was defined as more time spent in the sign area during the CS than before the CS. A goal-tracking response was defined as more time spent in the goal area during the CS than before the CS. Notice that these definitions imply that the scoring of each of these behaviors occurred only when there was an increase in the amount of time allocated to each site from the period before the CS to the period during the CS. For example, a rat that spent the entire session in the goal area would receive a score of zero for goal tracking because the response did not increase from the period before the CS to that during the CS. Furthermore, notice that the absolute scores of these responses during the CS period would have little meaning without reference to what the animal was doing immediately before CS onset. Thus, a rat that spent the entire session in the goal area (as happened with some rats in Group EU), would have a high absolute score for goal tracking, but this would say nothing about the CS's ability to control this response. Scores were subjected to analysis of variance with a .05 alpha value. Post hoc pairwise tests were based on Ryan's procedure (Toothaker, 1992).

RESULTS

Interobserver reliability was calculated in terms of the percentage agreement for the presence or absence of both sign- and goal-tracking responses during the 10 sec prior to the CS and the 10 sec during the CS. Data from the two students scoring acquisition sessions were used to estimate reliability. These observers agreed on 90.1% of the trials. The data presented here come from one of the observers. The decision to use this observer's data was made prior to scoring.

Figure 1 shows the percentage of trials with a response for both sign- and goal-tracking behaviors during preexposure in Group LI. The degree of reduction in response frequency in the absence of reinforcement was greater for sign tracking than for goal tracking. In fact, a one-way analysis of each measure indicated that whereas the reduction in sign-tracking frequency across sessions was significant [$F(3,12) = 9.33$], the change in goal tracking did not reach significance [$F(3,12) = 2.38$]. The light was expected to induce an unconditioned orienting response
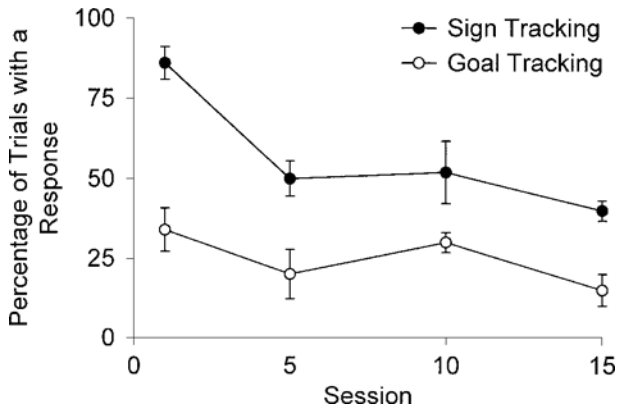
Figure 1. Percentage of sign tracking and goal tracking observed in four scored sessions during a phase of nonreinforced preexposure to the conditioned stimulus in Group LI.

$[F(8,40) = 1.40]$. Post hoc tests revealed that Group X responded to the CS on significantly more trials than did Groups LI and EU, which, in turn, did not differ from each other. The data from the first session were discarded for the second group × session analysis in order to determine whether the initial increase in sign tracking (presumably resulting from an unconditioned orienting response to the light CS; see the Discussion) was in any way contributing to the group effect. This analysis yielded a significant effect only for groups $[F(2,10) = 5.86]$. Post hoc comparisons confirmed that the source of this effect was the performance of Group X, which was significantly above that of Groups LI and EU. The latter groups did not differ from each other.

Figure 2b shows the percentage of trials with a goal-tracking response in each group and across sessions. These results reflect more conventional learning functions, be-

followed by habituation after repeated presentations. By contrast, the goal area does not provide the animal with any localized stimulus that may induce such an orienting response and thus its level should be relatively unchanged across sessions.

Figure 2 shows the percentage of trials with a response for each group during conditioning separately for sign tracking (top panel) and goal tracking (bottom panel). As expected, the frequency of sign tracking was relatively high early in training for Groups X and EU, neither of which was preexposed to the CS. These rats had no opportunity to habituate the orienting response. The sign-tracking level of Group LI was also high early in training and, although it was lower than that of the other groups, an analysis of first-session data indicated nonsignificant group differences $[F(2,10) = 1.83]$. Notice that the levels of responding of Group LI at the end of preexposure (Figure 1) and in the first conditioning session (Figure 2a) were very similar. Any increase in responding during the first conditioning session would be more parsimoniously attributable to food-induced dishabituation (cf. Thompson & Spencer, 1966), rather than to conditioning itself. By Session 5, the scores in all groups were lower than at the start of acquisition training. Sign tracking increased thereafter in Group X, which demonstrated the highest amount of responding. Group LI's response level was indistinguishable from the level of Group EU and clearly lower than that of Group X, thus demonstrating an LI effect. Although the response level of Group LI was rather low, there was a consistent trend to increase the frequency of sign tracking from Session 5 to 20. It is presumed that further conditioning training would have lead to a higher sign-tracking level in Group LI.

Two separate group × session analyses of the data supported these conclusions. The first, which involved all the sessions that were subject to observation and scoring, revealed a significant difference across groups $[F(2,10) = 5.73]$ and across sessions $[F(4,40) = 4.71]$. However, the group × session interaction did not reach significance
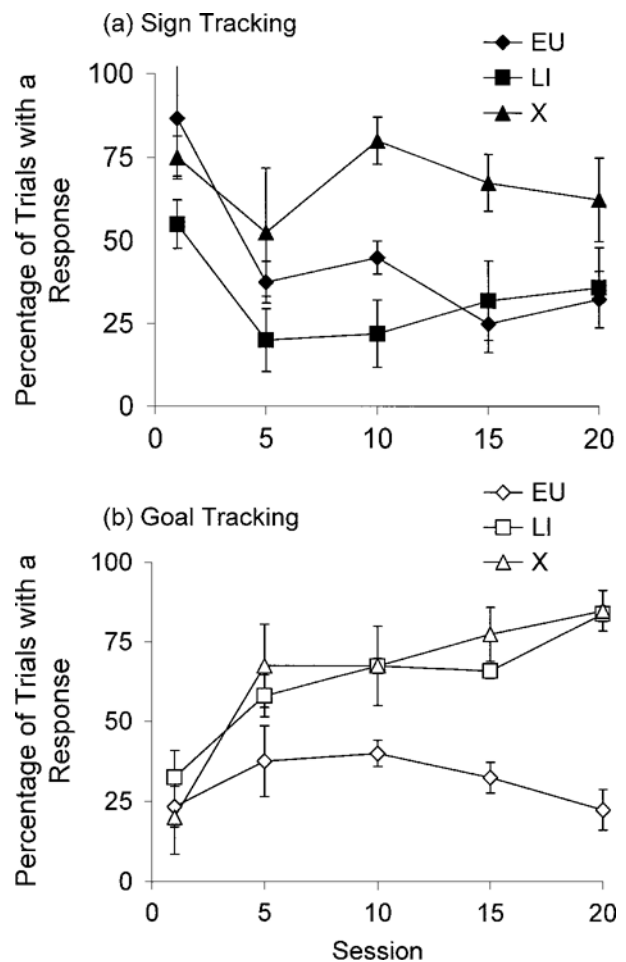

Figure 2. Percentage of (a) sign tracking and (b) goal tracking in five scored sessions during the conditioning phase of the experiment. Groups received previous nonreinforced preexposure to the conditioned stimulus (LI) or to the context (X) followed by paired training. Group EU received preexposure to the training context followed by explicitly unpaired presentations of the conditioned and unconditioned stimuli.

cause the light CS does not induce unconditioned approach to the goal during early trials. As was the case with the sign-tracking results, Group EU produced a relatively low level of behavior throughout the conditioning sessions. However, and unlike in sign tracking, Groups LI and X acquired goal tracking at roughly the same rate, thus providing no evidence of an LI effect. A group × session analysis supported these conclusions. The difference between groups was significant $[F(2,10) = 18.91]$, as was the increase in responding across sessions $[F(4,40) = 14.38]$. Furthermore, the group × session interaction also reached a significant level $[F(8,40) = 3.24]$. Post hoc comparisons revealed that Groups X and LI responded at the same level, and both were significantly higher than Group EU.

DISCUSSION

The results of this experiment suggest that the presence or absence of LI depends critically on whether the assessment of conditioning involves sign tracking or goal tracking, respectively. The greater acquisition level displayed by the context control group (Group X) relative to the CS-preexposed group (Group LI) in terms of sign tracking is the typical comparison used to demonstrate LI (see Lubow, 1989, for examples). At face value, such results suggest that nonreinforced preexposure to the CS causes an acquisition deficit during subsequent conditioning. This conventional interpretation is not applicable to the goal-tracking data obtained in the same rats. In this case, preexposed and control groups acquired goal tracking at nearly identical rates, and thus no acquisition deficit resulted from nonreinforced preexposure to the CS. It appears that rats learned to use the CS as a signal for the US whether or not they had been preexposed to the light. However, whereas the CS induced approach to both the signal and the goal areas in naive animals, the rats preexposed to the CS tended to use it as a signal to approach mainly the goal area. The discrepancy between the present results and the results reported by Holland and Gallagher (1993; Chiba et al., 1995) is unclear. As mentioned in the introduction, they reported LI effects in both rearing behavior to a light CS and food cup behavior; these responses could be understood, respectively, as representing sign tracking and goal tracking. One procedural difference lies in the relative distance of the CS and US sites: They were farther apart in the present situation than in Holland and Gallagher's experiments. Whether these differences can be attributed to the spatial separation of CS and US sites or to other procedural differences (e.g., within- vs. between-subjects design) cannot be determined with the available evidence. Whatever the case, one major implication of the present results is that single-measure studies of LI may lack sensitivity to detect the subtle effects of CS preexposure on the form of the conditioned response (see Domjan, 2000). The attribution of a deficit in acquisition or performance that is usually tagged to the LI phenomenon should be weighed carefully against the use of a particular response measure.

A glance at Figure 2a indicates that the sign-tracking data did not exhibit the typical negatively accelerated function of acquisition curves. Group X, for example, showed similar amounts of responding on the 1st session and in the 20th. This is largely due to a strong orienting response induced by the light CS, particularly during its initial presentations. Groups X and EU exhibited an approach response of similar strength early in the conditioning phase, but whereas sign-tracking declined in Group EU, it was maintained in Group X. One possible account for this finding suggests that the learning curve in Group X is the net result of two underlying functions, one describing habituation of the orienting response to the light (see Figure 1 for such a function in Group LI), and another describing the maintenance of the orienting response during CS–US pairings—which did not apply to Group EU.

These results are relevant to the theoretical distinction between acquisition-deficit and retrieval-deficit models of LI. Acquisition-deficit models (see, e.g., Lubow, 1989) predict that if LI is present, it should be evident in all forms of the conditioned response. LI is exhibited because conditioning to the CS does not occur. In contrast, retrieval-deficit models (e.g., Bouton, 1993; Miller & Matzel, 1988) propose that conditioning occurs, but that the association is not expressed. These models are consistent with the possibility that associative knowledge might be evidenced more readily in some responses than in others. The results of the present experiment clearly favor a retrieval-deficit explanation; LI was observed in one form of the response but not another.

There are at least three possible explanations of the observed results. The first possibility is that these results were restricted to the particular conditions used in the present experiment. For example, several experiments have shown that nonreinforced preexposure to the CS can indeed result in retarded acquisition assessed in terms of goal tracking (e.g., Channell & Hall, 1984; Killcross & Balleine, 1996). In these experiments, conditioning has typically involved pairings of an auditory CS (e.g., clicker, tone) or a visual CS (e.g., diffuse overhead light) with some appetitive reinforcer (e.g., food pellets, saline solution). Goal tracking is measured in terms of head entries into a recessed magazine in which reinforcers are delivered. Unfortunately, experiments in which such a goal-tracking measure is used have rarely provided sign-tracking data, so it is difficult to evaluate their relevance to the present argument.

The second hypothesis suggests that LI can be detected with both response measures, but that it affects sign tracking faster than it affects goal tracking. In aversive conditioning preparations, the measurement of concurrent responses typically demonstrates that acquisition is reflected faster in measures of arousal (e.g., heart rate) than in peripheral responses (e.g., eyelid closure; Schneiderman, 1972). It is possible that the detection of an LI effect with a goal-tracking measure may require, for example, more preexposure trials or longer CS durations than those that yielded evidence of this effect in the sign-tracking mea-

sure. The studies cited previously in which LI was assessed in terms of goal tracking are characterized by the use of relatively diffuse CSs, such as clickers, tones, and overhead lamps (Channell & Hall, 1984; Killcross & Balleine, 1996). Diffuse CSs fail to generate sign tracking, but they are known to induce substantial levels of conditioning, detectable, for example, when the CS is used as a secondary reinforcer in a second-order conditioning paradigm (Rescorla, 1980). The present failure of goal tracking to reveal an LI effect would thus be equivalent to any failure of a conditioning effect to emerge when inadequate training parameters are used. The fact that conditioning is translated into different response systems at different rates has long been recognized, but the notion that the mechanism of LI would show similar response diversity is novel.

The third hypothesis suggests that CS preexposure leads to a shift in the form of the conditioned response without disrupting acquisition. In the present experiment, acquisition in the control group (i.e., Group X) induced a combination of sign and goal tracking that is typical of conditioning situations (see, e.g., Zener, 1937). Such oscillation may have been reduced in rats preexposed to the CS. Preexposure then shifted the response-selection process toward goal tracking and away from sign tracking. Burns and Domjan (2001) reported a similar shift in response form in a sexual reinforcement experiment with quail. Extensive exposure to the training context relative to the duration of the CS induced high levels of sign tracking, whereas small amounts of exposure to the context relative to the duration of the CS induced high levels of goal tracking. Burns and Domjan suggested that the form of the conditioned response is determined by the temporal parameters of the conditioning situation. However, the mechanism underlying such a response shift could be phrased in terms of Skinner's (1966) variation-selection hypothesis of instrumental conditioning. According to this hypothesis, animals enter a situation with a wide repertoire of behaviors, from which reinforcement selects those that are instrumental in leading to the goal event. Applied to the present situation, the variation selection hypothesis suggests that the onset of the light CS in the first conditioning session elicits different responses as a function of CS preexposure experience. In nonpreexposed animals, the CS induces an orienting response involving approach to the CS, which is subsequently reinforced. Thus the sign-tracking response continues to occur at relatively high levels. By contrast, rats preexposed to the CS exhibit significant habituation of this orienting response. Such habituation changes the response offer of these animals at the outset of conditioning, reducing the strength of CS approach tendencies and increasing the chances that other responses would be reinforced, including goal approach. The CS is used as a signal for the US in both training conditions (i.e., Pavlovian conditioning occurs equally effectively in both conditions), but the response selected for expression differs because CS preexposure has modified the initial offer of response forms available for conditioning. This view

assumes that the behaviors observed in appetitive Pavlovian conditioning situations with rats are basically instrumental, a claim that finds support in the sensitivity of such responses to omission contingencies (Antip, 1977; Davey et al., 1981; Stiers & Silberberg, 1974).

Whichever of these possibilities may explain the present results, they strongly warn against an interpretation of LI in terms of acquisition failure. Under the present conditions, LI emerged when acquisition was measured in terms of sign tracking, but not when it was measured in terms of goal tracking. Therefore, the form of the response needs to be considered seriously when one is assessing the effects of nonreinforced preexposure to the CS on subsequent conditioning.

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