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# Transfer of Memory Retrieval Cues Attenuates the Context Specificity of Latent Inhibition

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Previous studies have demonstrated that the transfer of retrieval cues for original acquisition memories, old 'reactivated' memories, and extinction memories attenuated the context shift effect. This study examined whether latent inhibition (CS preexposure) cues would also transfer, thus alleviating the context specificity. Rats preexposed to a particular context were immediately exposed to a different, novel context. When these rats were trained and tested in the shifted context following preexposure/exposure they showed the latent inhibition effect, i.e., retarded learning in the context that differed from preexposure. That the rats treated the shifted context as the preexposure context demonstrates that the preexposure retrieval cues transferred. These results are consistent with other findings that a novel context can serve as retrieval cues for an event learned in a different setting.

*Keywords: rat, latent inhibition, transfer retrieval cues, context shift effect*

It is well established that shortly after acquisition, while the learned event is being processed and stored, a memory is malleable, thus leaving an active memory susceptible to a variety of manipulations (Spear & Riccio, 1994) and post event information (Roediger & McDermott, 2000). During this labile consolidation process, the target information, as well as the context cues, are encoded (Dudai, 2004; McGaugh, 2000).

Recent research has demonstrated that exposure to different contextual cues while the memory is actively being encoded incorporates the novel cues with the original memory. This research takes advantage of the context shift effect, the observation that performance is impaired when subjects are trained and tested in distinctly different contexts. The context shift effect has been attributed to a memory deficit resulting from the lack of appropriate retrieval cues and has been observed in studies using both human and animal subjects (Godden & Baddeley, 1975; Gordon, McCracken, Dess-Beech, & Mowrer, 1981; Smith, 1979; Zhou & Riccio, 1996). In an early study focusing on the transfer of retrieval cues, Boller and Rovee-Collier (1992) trained 6-month-old infants to kick a leg to activate a mobile in a crib with a distinct liner. Immediately following training, the infants were exposed to a novel context (different crib liner). When later tested in the new context the infants

responded as if they were in the original training context, thus the novel crib liner cues were encoded into the original memory and gained control over responding (see also Boller & Rovee-Collier, 1994; Cuevas, Rovee-Collier, & Learmonth, 2006).

Along the lines of Boller and Rovee-Collier's (1992) research investigating the transfer of retrieval cues but using rats as subjects, Briggs, Fitz, and Riccio (2007) investigated whether novel contextual cues introduced shortly after acquisition could gain retrieval control over responding. In their study, rats exposed to a novel environment shortly after fear conditioning showed less memory impairment than non-exposed controls when tested in the new context. Moreover, the alleviation of the context shift effect was less effective with longer training-to-exposure delays. The time dependent function of the transfer of cues demonstrates that the memory must be in an active state for the information to transfer, which is consistent with evidence from the retrograde amnesia literature (Duncan, 1949; McGaugh, 1966). Related to the importance of the activity level of a memory for transferring cues, Briggs and Riccio (2008b) later demonstrated that contextual cues for an old, 'reactivated' memory could be transferred to a new context by reactivating a previously stored memory prior to exposure to the new context. A subsequent study by Briggs and Riccio (2009) found a similar transfer effect using an

extinction memory. In extinction, the cues previously paired with a biologically relevant reinforcer (e.g., food or shock) are presented without the outcome, leading to a reduction in responding. Taking advantage of the fact that extinction is new learning and context specific (see Bouton, 2004), Briggs and Riccio (2009) demonstrated that exposing the rats to the fear-conditioning context following extinction training in a different context reduced fear, i.e., the extinction cues transferred to the training context.

Given that the transfer of contextual retrieval cues has been demonstrated with original acquisition memories and for extinction memories, the present experiment was designed to investigate whether contextual retrieval cues for latent inhibition could also come under control of cues not present at the time of preexposure learning. Latent inhibition (also known as the CS preexposure effect) is a deficit in the association between a to-be-conditioned stimulus (conditioned stimulus) and a biologically relevant event (unconditioned stimulus) as the result of having been previously exposed to the conditioned stimulus (i.e., preexposure retards learning) (Lubow, 1973; Lubow & Moore, 1959). The term latent inhibition refers to the inhibition of the conditioned responding produced by the prior exposure to the conditioned stimulus without the reinforcer. Latent inhibition is similar to extinction in that learning takes place without an explicit reinforcer, however the cues-only exposure occurs before training in latent inhibition, rather than following training in extinction. Moreover, similar to extinction, a limitation of latent inhibition is that it is highly dependent on the context or setting in which the preexposure occurs (Hall & Honey, 1989; see also Westbrook & Bouton, 2010). This context specificity demonstrates that the latent inhibition effect is not due to a prevention of conditioning or learning, but a separate learned event. To evaluate the transfer of preexposure cues in the present study, the context specificity of latent inhibition will be utilized. Thus, if the transfer of preexposure retrieval cues to a new context does take place, the context specificity of latent inhibition should be attenuated.

## Method

### Subjects

Forty experimentally naive, adult male Long-Evans hooded rats, obtained from Susquehanna University's animal facility breeding colony, served as subjects. The rats were approximately 160 days old at the start of the experiment with an average weight of 570 grams. The animals were housed

individually with free access to food and water, and were maintained on a 12:12 hour light:dark cycle. All experimental sessions took place during the light portion of the photocycle and at the same time each day. Approval of the experimental protocol was obtained by the Susquehanna University Institutional Animal Care and Use Committee prior to data collection.

### Apparatus and Contexts

Preexposure, training, and testing were conducted in two identical 48 X 21 X 22 cm passive avoidance shuttle boxes (Ugo Basile model 7551) with metal grid floors (grids spaced 1.2 cm apart) that were connected to a shock source. Each shuttle box was divided by a sliding door into two compartments—one black side and one white side—of equal size. The exposure chamber was a clear 21 X 21 X 21 cm Plexiglas cube with a sliding lid. The exposure chamber was placed near the shuttle box in each context during exposure.

The two shuttle boxes were located in two separate rooms that served as contexts. Context A was a 4.88 X 3.66 m well-lit room with white walls. Context B was a 1.83 X 3.05 m room that was lit with a 25 W red light bulb placed near the shuttle box. White noise was present in Context B (70 dB) and the room was scented with an Air-Wick Magnolia & Cherry Blossom scented oil air freshener.

### Procedure

Prior to the beginning of the experiment, all subjects were handled for 5 minutes on two consecutive days. Groups of 10 rats were randomly assigned to one of four conditions before receiving preexposure in either Context A or Context B. Assignment to the contexts were counterbalanced in such a way that within each group five rats were preexposed in Context A and five in Context B. For simplicity, we refer to the shifts generically (A to B or B to A). The design of the experiment is summarized in Table 1.

Following handling, three groups received preexposure (Fear, LI, and Transfer). Preexposure began with bringing the rat in its home cage into the context and placing the cage on a table for 15 seconds to allow for brief context exposure. After 15 seconds, the animal was removed from its home cage and placed on the experimenter's arm for 15 seconds near the apparatus, again allowing for context exposure. The rat was then placed in the white side of the shuttle box and the lid was closed. Fifteen

Table 1: Experimental Design

Group	Preexposure	Expose	- 24 hr -	Training	- 24 hr -	Testing
Fear	Context B	----		Context A		Context A
LI	Context A	----		Context A		Context A
Transfer	Context B	Context A		Context A		Context A
Expose	----	Context A		Context A		Context A

Note: Contexts A and B were counterbalanced within each group.

seconds after the lid was closed, the door automatically opened and the latency to cross into the black compartment (tilted floor connects a circuit) was automatically recorded. One second after the animal crossed to the black side, the door automatically closed. The rat remained in the black compartment of the shuttle box for 12 minutes, preexposing the rat to the black side cues. There was no foot-shock delivered to the animal during preexposure. A fourth exposure-only control group (Expose) did not receive preexposure training, rather was merely exposed to the training/testing context.

Exposure consisted of bringing the rat into the context and immediately placing the rat into the clear exposure chamber for 5 minutes. As the experimental treatment of interest, the Transfer group was immediately exposed to the shifted context that differed from preexposure following the preexposure treatment. Two groups, the Fear control group and the latent inhibition control group (LI), did not receive exposure. These groups were returned to the colony room following preexposure.

Twenty-four hours after preexposure/exposure, all animals (four groups) received punishment training. Punishment training was similar to preexposure. For training, the rat was brought into the context in its home cage and was placed on a table near the apparatus for 15 seconds. The animal was then removed from its home cage and placed on the experimenter's arm for 15 seconds, then placed into the white compartment. After 15 seconds in the white side, the door automatically opened allowing the rat to cross to the black side and the latency to cross was recorded. One second after the rat crossed into the black compartment the door automatically closed. Two seconds after the door closed a single inescapable 1-second, .8 mA footshock was delivered via the grid floor. This fear conditioning procedure produces fear of the black compartment (conditioned stimulus) by being paired with the shock (unconditioned stimulus). Fifteen seconds after crossing into the black side, the animal was removed and returned to its home cage.

Testing occurred 24 hours after training in the same context as training. This 5-minute passive avoidance test was identical to training except that no shocks were delivered and the animal was removed

immediately after crossing into the black compartment. The latency to cross to the black side was recorded as the dependent measure.

## Results

*Preexposure.* All three preexposure groups exhibited short cross latencies with group means ranging from 30.0 to 62.7 seconds. An ANOVA performed on the preexposure cross latencies revealed no differences among the three groups,  $F(2, 27) = 1.45, p = .25$ .

*Training.* Rats in all four groups also exhibited short training cross latencies ranging from 16.5 to 29.0 seconds. An ANOVA comparing all groups training cross latencies revealed no differences among the four groups,  $F(3, 36) = 1.15, p = .34$ .

*Counterbalancing.* There were no differences among cross latencies at preexposure ( $p = .08$ ), training ( $p = .15$ ), and testing in either context ( $p = .28$ ). Accordingly, the contexts were collapsed within each group for all analyses.

*Testing.* Figure 1 shows the mean cross latency scores for all four groups at test. An ANOVA revealed that the groups differed significantly,  $F(3, 36) = 3.78, p = .02$ . Fisher's LSD post hoc tests were conducted to compare group differences.

As can be seen, the Fear group exhibited a considerable amount of fear (longer cross latencies) compared to the latent inhibition (LI) group, which demonstrates that the preexposure is context specific and that the preexposure was sufficient to reduce fear. Post hoc tests confirmed a significant difference between groups Fear and LI ( $p = .01$ ). Thus, preexposure retarded learning when conducted in the same context as training, but not when preexposure and training occurred in distinctly different contexts. The context specificity of the preexposure was attenuated by the transfer of retrieval cues, since the group that was exposed to the shifted context immediately after preexposure (Transfer) displayed as much fear as the preexposure (LI) group ( $p = .98$ )

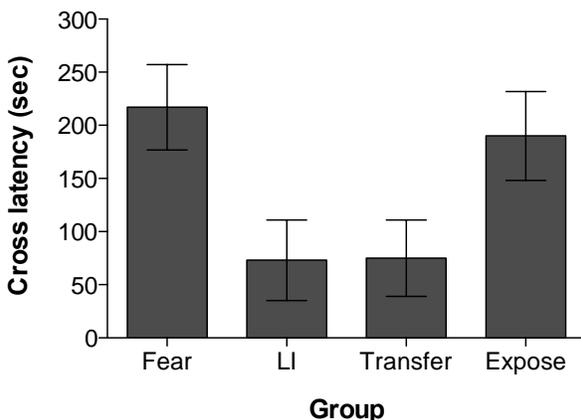


Figure 1. Mean latency to cross from the white (safe) side to the black side for all groups. Error bars represent the standard error of the means. Groups Fear and LI demonstrate that latent inhibition (CS preexposure) is context specific and that the preexposure was sufficient to reduce fear. The Transfer group demonstrates that exposure to the shifted context following preexposure attenuates the context specificity (i.e., transfer of preexposure retrieval cues). Group Expose demonstrates that the exposure alone was not sufficient to produce the reduction of fear.

and significantly less than the Fear group ( $p = .01$ ). The exposure-only control group (Expose) demonstrated that the exposure to the training/testing context alone did not contribute to the reduction of fear, as this group showed as much fear as the Fear group ( $p = .62$ ) and significantly more fear (longer cross latencies) than the LI group ( $p = .04$ ) and Transfer group ( $p = .04$ ).

### Discussion

The findings presented here provide evidence that retrieval cues for latent inhibition can become associated with a new context by mere exposure to the context immediately following preexposure, thus reducing the context specificity of the latent inhibition effect. These results are consistent with and extend other findings demonstrating a transfer of retrieval cues for original memories (Boller & Rovee-Collier, 1992, 1994; Briggs, Fitz, & Riccio, 2007), reactivated memories (Briggs & Riccio, 2008b; Tronel, Milekic, & Alberini, 2005), and memories for extinction learning (Briggs & Riccio, 2009). Thus, it appears that this characteristic of a latent inhibition memory is similar to other memories, in regards to the ability of neutral cues gaining retrieval control, while extending the

more contemporary view that latent inhibition is a separate learned event, similar to extinction learning.

The current results are also consistent with research demonstrating that the context specificity of latent inhibition can be attenuated by cueing the CS preexposure in the to-be-conditioned context prior to training. In a series of studies, Gordon and Weaver (1989) showed that by providing a cue that was present during preexposure while the subjects underwent conditioning in a separate context weakened the context specificity of latent inhibition. The authors described this attenuation of the context specificity as a transfer of the preexposure effect to a different context; however, the cueing treatment was effective "...only when the cueing treatment involved a stimulus that was present during CS-alone presentations and only when the cueing treatment was administered in the conditioning context" (p. 415). Thus, it appears that the preexposure effect was reinstated in the conditioning context causing the decrement in performance, rather than a transfer of retrieval cues. The present results reported here appear more likely due to the transfer of memory retrieval cues because there were no specific cueing stimuli presented during the exposure treatment, rather the animals were merely exposed to the shifted context for a brief period of time (not long enough to induce latent inhibition, as demonstrated by the Expose only control group). In explaining our results, we favor the notion that during the exposure session, an active representation of the preexposure memory becomes associated with or encoded in the new context, thus allowing the animals to treat both contexts as functionally similar.

Although there is evidence of weakening the context specificity of latent inhibition effect using a cueing treatment, the important finding here is that retrieval cues never associated with a preexposure session can serve as retrieval cues for the episode. What has yet to be determined is whether the transfer of latent inhibition cues is consistent with the characteristics of the transfer of other memories. That is, would longer preexposure to exposure delays prevent the transfer of retrieval cues as seen with original and reactivated memories? The current investigation did not assess the temporal gradient of the transfer. In addition, we also did not test whether the transfer of memory for preexposure demonstrated here had any effect on the loss of the preexposure effect if tested back in the preexposure context (see Briggs & Riccio, 2008a). Would the exposure cause the preexposure cues to transfer as an "erase and update" effect, or would the preexposure cues transfer and remain in both contexts? These and other important questions regarding the transfer of

memory retrieval cues phenomenon deserve further investigation to determine the mechanisms involved.

#### Authors Note

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