Biological Significance as a Determinant of Cue Competition

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ABSTRACT

Many researchers have noted the similarities between causal judgment in humans and Pavlovian conditioning in animals. One recently noted discrepancy between these two forms of learning is the absence of backward blocking in animals, in contrast with its occurrence in human causality judgment. Here we report two experiments that investigated the role of biological significance in backward Mocking as a potential explanation of this discrepancy. With rats as subjects, we used sensory preconditioning and second-order conditioning procedures, which allowed the to-be-blocked cue to retain low biological significance during training for some animals, but not for others. Backward blocking was observed only when the target cue was of low biological significance during training. These results suggest that the apparent discrepancy between human causal judgment and animal Pavlovian conditioning arises not because of a species difference, but because human causality studies ordinarily use stimuli of low biological significance, whereas animal Pavlovian studies ordinarily use stimuli of high biological significance, which are apparently protected against cue competition.
Similarities between the acquisition of causal relations by humans and Pavlovian conditioning of animals have recently attracted attention (e.g., Allan, 1993; Shanks, 1993; Wasserman, 1993; Young, 1995). These similarities suggest that similar or identical processes underlie these two forms of learning. Young (1995) compared animal learning and human causal attribution in a neo-Humean framework. In this view, causal and Pavlovian learning both depend on (a) temporal and spatial contiguity between events (i.e., causes and effects or conditioned stimuli [CSs] and unconditioned stimuli [USs] must be proximate), (b) temporal priority of the cause or CS (i.e., causes or CSs must precede effects or USs), (c) perceived contingency (i.e., one event must be perceived as a necessary and sufficient condition for the other event), and (d) a lack of cue competition (i.e., absence of an alternate cause or CS for the effect or US). The first three of these factors have received support from research in both fields of investigation; however, discrepancies have arisen from studies of cue competition in animal Pavlovian conditioning and human causality judgment.

One example of cue competition is forward blocking (Kamin, 1968). In forward blocking, a CS (A) precedes a US in Phase 1 (i.e., A → US), followed in Phase 2 by presentations of a simultaneous compound of A and another stimulus (X) preceding the US (i.e., AX → US). Forward blocking is evidenced by less conditioned responding to X in a subsequent test than is seen in subjects who did not receive the initial A ^ US pairings. Forward blocking has been explained through the initial A → US association interfering with the acquisition or expression of the X ^ US association, and has been observed in both human causal judgment and animal Pavlovian conditioning. In contrast, a typical backward blocking procedure consists of AX ^ US training in Phase 1 and A → US training in Phase 2. Backward blocking (i.e., reduced responding to X resulting from the A → US trials) is seen in human causal judgment (e.g., Chapman, 1991; Shanks, 1985, Van Hamme, 1994; Williams, Sagness, & McPhee, 1994), but not in animal Pavlovian conditioning (e.g., Miller. Hallam, & Grahame, 1990; Schweitzer & Green, 1982). This discrepancy may arise from animals and humans processing information in different manners, from fundamentally different processes underlying causal judgment and Pavlovian conditioning, or from procedural differences between causal judgment and conditioning experiments.

In an effort toward resolving this discrepancy, we (Miller & Matute, in press) identified biological significance as a variable that may be responsible for the conflicting findings. We defined biologically significant cues as cues that elicit responding. Furthermore, we distinguished cues of inherent biological significance (e.g., food, sex, painful stimuli, and intense stimuli) from cues of acquired biological significance (initially neutral stimuli that have acquired biological significance through association.
with events of inherent biological significance). In previous studies of backward blocking in animals, the outcomes (USs) have always been biologically significant (food, water, or footshock), whereas in studies of causal judgment in humans, the outcomes (effects) have typically been biologically insignificant (e.g., verbal descriptions of allergic reactions in hypothetical patients).

In order to assess this difference in procedures, we (Miller & Matute, in press) manipulated the biological significance of the cues during the backward blocking procedure using rats as subjects. We used a procedure in which A and X (auditory stimuli of moderate intensity) retained their initial low biological significance during Phases 1 and 2 because they were not paired with a biologically significant US. We accomplished this through the use of sensory preconditioning (SPC; Brogden, 1939). In our backward blocking procedure, A and X were followed by a third auditory stimulus of low biological significance (i.e., AX → B) in order to make the procedure analogous to the one typically used in studies of human causal judgment. Then, A alone was paired with the outcome in Phase 2 (i.e., A → B). Finally, B was made biologically significant by pairing it with footshock (i.e., B → US). This phase of training provided a motivational basis for responding, so that backward blocking could be assessed. Thus, Phase 1 served as the first phase of an SPC procedure for X and as the first phase of backward blocking; Phase 2 served as the second phase of backward blocking; and Phase 3 served as the second phase of SPC. These studies yielded backward blocking in animals, presumably because X never became biologically significant. We concluded that biologically significant cues are partially protected against cue competition and that in prior studies of backward blocking in animals, the to-be-blocked cue had acquired biological significance in Phase 1 (i.e., AX → US).

However, it is possible that the SPC procedure per se was responsible for the occurrence of backward blocking because all of our groups exhibiting backward blocking received SPC treatment with biologically insignificant stimuli. Therefore, in the present research, we investigated whether the occurrence of backward blocking depends on the use of an SPC procedure or on the low biological significance of the cues. In Experiment 1, we operationalized biological significance as inherent biological significance (in the form of stimulus intensity). In Experiment 2, we sought to elevate the concept of biological significance above being synonymous with stimulus intensity by manipulating acquired biological significance (in the form of the cues being a signal for a US) as a second means of operationalizing biological significance.
EXPERIMENT 1

Experiment 1 used an SPC procedure and manipulated the intensity (inherent biological significance) of the stimuli to see if backward blocking was influenced by the biological significance of the cues despite the consistent use of an SPC procedure (see Table 1). For Groups BB-M and CON1-M, A and X were auditory cues of moderate intensity (low biological significance); for Groups BB-H and CON 1-H, A' and X' were identical to A and X but of high intensity (high biological significance). To prevent A and X from acquiring biological significance during Phase 1, a moderate flashing light (B) served as a surrogate for the US. In Phase 2, A or A' alone was paired with B for the BB groups, whereas the CON1 groups received comparable training that lacked the critical A → B or A' → B presentations (i.e., C → B or C → B). In Phase 3, B was made biologically significant for all groups through B → US pairings. To control for the possibility of unconditioned responding to X' because of its high intensity, another control group (CON2-H) received training equivalent to that of Group BB-H except that A'X' and B were explicitly unpaired during Phase 1.

<table>
<thead>
<tr>
<th>Group</th>
<th>Phase 1</th>
<th>Phase 2</th>
<th>Phase 3</th>
<th>Tests</th>
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<tbody>
<tr>
<td>CON1-M</td>
<td>AX → B</td>
<td>C → B</td>
<td>B → US</td>
<td>X? A?</td>
</tr>
<tr>
<td>BB-H</td>
<td>A'X' → B</td>
<td>A' → B</td>
<td>B → US</td>
<td>X'? A'?</td>
</tr>
<tr>
<td>CON1-H</td>
<td>A'X' → B</td>
<td>C' → B</td>
<td>B → US</td>
<td>X'? A'?</td>
</tr>
<tr>
<td>CON2-H</td>
<td>A'X'/ B</td>
<td>A' → B</td>
<td>B → US</td>
<td>X'? A'?</td>
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Note. A and C were a complex tone and white noise, counterbalanced; X was a click train. A, C, and X without the prime were 10 dB(C) above background (moderate-intensity groups, M) and with the prime were 30 dB(C) above background (high-intensity groups, H). B was a flashing light; US was a footshock. → = followed by; / = unpaired. The BB groups were backward blocking groups, whereas the CON1 groups were their respective controls, which lacked A → B (or A' → B) pairings in Phase 2. The critical backward blocking phases are indicated in italicized boldface. See the text for an explanation of the distinction between the CON1-H and CON2-H groups.
Method

Subjects

The subjects were 30 male (230 g to 385 g) and 30 female (190 g to 270 g) experimentally naive Sprague-Dawley rats. Subjects were allowed free access to food in their home cages, whereas access to water was limited to 10 min/day. Subjects were randomly assigned to one of five groups (n = 12), counterbalanced for sex.

Apparatus

Twelve chambers housed in separate sound- and light-attenuating enclosures were used. Each chamber could be equipped with a water-filled lick tube that extended into a cylindrical drinking recess. An infrared photobeam was projected across the recess, so that subjects had to interrupt the photobeam in order to drink. Thus, durations for which subjects accessed the lick tube were recorded. Speakers in each enclosure could deliver the following auditory cues; a train of six clicks per second (X), a tone (compound of 3000 and 3200 Hz), and a white noise. The tone and white noise served as A and C, counterbalanced within groups. A flashing light of moderate intensity (25 W) served as B. All CSs were 5 s in duration; the US was a 5-s, 0.5-mA footshock.
Procedure

All training sessions were 60 min long. On Day 1, all subjects were acclimated to their experimental chambers for one 60-min session. For Groups BB-M and CON1-M, A and X were of moderate intensity (10 dB[C] above background), whereas for Groups BB-H, CON1-H, and CON2-H, A' and X' were of high intensity (30 dB[C] above background). Phase 1 training (Day 2) for all subjects consisted of four presentations (at 10, 20, 37, and 50 min into a single session) of the AX (or A'X') compound followed immediately by B, except for Group CON2-H, which received the A'X' compound and B consistently unpaired. Thus, A' and X' were not signals for B in Group CON2-H. Phase 2 training (Days 3-7) consisted of four daily A → B (or A' → B) pairings for Groups BB-M, BB-H, and CON2-H; for Groups CON1-M and CON1-H, C and C were substituted for
A and A', respectively. Onset of B coincided with the termination of either A, A', C, or C. Thus, A (or A') alone continued to serve as a signal for B in Groups BB-M and BB-H. In Phase 3 (Day 8), all subjects were exposed to four pairings of B followed immediately by the US. In order to restabilize baseline drinking from the disruption in drinking that ordinarily results from footshock during training, on Days 9 and 10 we reacclimated subjects to the chambers. During these two sessions, the lick tubes were returned to the chambers and no nominal stimuli were presented.

Backward blocking was assessed using conditioned suppression of drinking as an index of the associative status of X and X'. In a lick-suppression paradigm, robust conditioned responding is seen as suppression of drinking, and backward blocking would be expressed as reduced suppression to X or X'. On Day 11, all subjects were tested for suppression to the blocked stimulus (X or X'). The blocked stimulus was presented to each subject upon completion of an initial 5 cumulative seconds of drinking in the absence of any CS, and was terminated 10 min thereafter. Thus, each subject was drinking at the onset of the test stimulus, and the time required to complete an additional 5 cumulative seconds of drinking in its presence was measured. On Day 12, each subject was tested in the same fashion for suppression to the blocking stimulus (A or A').

One subject from Group CON1-H died during the experiment. Suppression scores for all remaining subjects were converted to log seconds in order to improve the normality of the within-groups data, thereby enhancing the appropriateness of parametric analysis. An alpha level of p < .05 was adopted.
Results and Discussion

The left side of Figure 1 depicts mean times to complete 5 cumulative seconds of drinking in the presence of the blocked stimulus on Day 11. The main finding was less suppression to the blocked stimulus by Group BB-M than by Group CON1-M, $F(1, 22) = 11.12$, but no difference between Group BB-H and Group CON1-H. A one-way analysis of variance (ANOVA) conducted on the suppression scores for Groups BB-H, CON1-H, and CON2-H revealed a main effect of group, $F(2, 32) = 29.36$. Planned comparisons confirmed that there was no difference in responding between Groups BB-H and CON1-H, $F(1, 32) = 2.71$, but the differences between Groups BB-H and CON2-H and between Groups CON1-H and CON2-H were both significant, $F(1, 32) = 32.53$ and 52.39, respectively. The difference between Groups BB-H and CON2-H indicates that responding in the former group was not unconditioned. These results demonstrate backward blocking with moderate- but not high-intensity CSs.

The right side of Figure 1 depicts mean times to drink in the presence of the blocking stimulus on Day 12. Groups BB-M, BB-H, and CON2-H showed approximately equal and high levels of conditioned suppression. Lower levels of responding to A and A' by Groups CON1-M and CON1-H, respectively, are not surprising because these subjects did not receive any A → B pairings in Phase 2. An ANOVA on the A data for Groups

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</table>

SOC groups matched against SOC groups for number of posttraining B → US pairings

|---------|---------|---------|---------|---------|---------|---------|

SPC groups matched against SOC groups for total number of B → US pairings

|---------|---------|---------|---------|---------|---------|---------|

Note. A and C were a complex tone and white noise, counterbalanced; B and D were a flashing light and buzzer, counterbalanced; X was a click train. All auditory stimuli were of moderate intensity (10 dB[C] above background). The US was a footshock. SOC = second-order conditioning; SPC = sensory preconditioning; → = followed by.

The BB groups were backward blocking groups, whereas the CON groups were their respective controls, which lacked A → B pairings in Phase 3. The critical backward blocking phases are indicated in italicized boldface. See the text for an explanation of the distinction between Groups BB1 and BB2 and between groups CON1 and CON2.
BB-M and CON1-M found a difference in responding between groups, $F(1, 22) = 5.75$. A similar analysis for the three groups trained with high-intensity stimuli also revealed differences, $F(2, 32) = 7.61$. Planned comparisons found differences in responding between Groups CON1-H and BB-H and between Groups CON1-H and CON2-H, $F(1, 32) = 9.65$ and $12.98$, respectively, but not between Groups BB-H and CON2-H, $F < 1$.

In summary, the present findings provide a replication of our previous studies (Miller & Matute, in press), by demonstrating that backward blocking is obtainable in animals provided the blocked stimulus is prevented from becoming biologically significant. More important, the present data demonstrate that if the blocked CS has biological significance (in this instance, by virtue of its high intensity), even the use of an SPC procedure will not suffice to produce backward blocking. Thus, our observation of backward blocking is not a consequence of the SPC procedure per se, but appears to depend on the biological significance of the potentially blocked CS.

**EXPERIMENT 2**

Experiment 1 demonstrated backward blocking in animals when the CSs were of low, but not high, biological significance. Biological significance was operationalized through stimulus intensity. Experiment 2 was designed to elaborate on these findings by operationalizing biological significance in a different way; We examined whether the backward blocking that is obtainable with an SPC procedure could be attenuated if, prior to training, the outcome (B) was given biological significance through B → US pairings. Specifically, we used a second-order conditioning (SOC) procedure. In conventional SOC, a CS (B) is paired with the US in Phase 1. Then in Phase 2, A is paired with B. As a result of these two phases of training, A acquires biological significance and produces conditioned responding at test. Experiment 2 investigated the consequences of making the outcome in a backward blocking procedure biologically significant through conditioning prior to blocking phases (see Table 2). Some subjects received SOC, that is, B → US training prior to the backward blocking treatment (i.e., AX → B and A → B pairings), whereas others received SPC, that is, the B → US training only after the backward blocking treatment, as in Experiment 1.

The critical manipulation in this study was whether the surrogate for the US (B) was made biologically significant before or after backward blocking training (Phases 2 and 3). Groups SOC-BB and SOC-CON constituted backward blocking and
blocking control groups, respectively, and both groups received SOC experience in Phases 1 and 2. The other four groups were SPC groups that were exposed during Phase 1 to the same number of USs as the SOC groups, but these USs were paired with an irrelevant stimulus (D). All subjects received identical Phase 2 treatment, AX → B, which constituted the first phase of a backward blocking procedure. In Phase 3, the three blocking groups (BB) received A → B presentations, which served as the second phase of the backward blocking procedure, whereas the three control groups (CON) did not. Phase 4 was intended to equate Groups SPC-BB2 and SPC-CON2 with Groups SOC-BB and SOC-CON in total number of B → US pairings over Phases 1 and 4. Finally, all groups of animals were presented with B → US pairings in Phase 5. This was to (a) ensure that B was strongly excitatory at test for all groups (B would otherwise not have been paired with the US since Phase 1 for Groups SOCBB and SOC-CON) and (b) provide a motivational basis for responding with the same retention interval prior to testing (3 days) for all groups.

To summarize, for the SOC groups, the outcome B was made biologically significant prior to backward blocking training, whereas for the SPC groups, the outcome B was made biologically significant following backward blocking training. The CON groups served as controls in which backward blocking was not expected because A alone was never paired with the outcome B (i.e., in Phase 3, they received C → B pairings rather than the A → B pairings of the BB groups). If only cues of high biological significance are immune to cue competition, then backward blocking would not be expected in Group SOCBB, but backward blocking would be expected in Groups SPCBBI and SPC-BB2.

Method

Subjects and apparatus

The subjects were 36 male (355 g to 430 g) and 36 female (250 g to 320 g) experimentally naive Sprague-Dawley rats. Water deprivation was identical to Experiment 1, and subjects were randomly assigned to one of six groups (n = 12), counterbalanced for sex. The apparatus was the same as in Experiment 1 except for the addition of a buzzer stimulus. CSs B and D were the buzzer and flashing light, counterbalanced. All other CS assignments were the same as in Experiment 1. All auditory CSs were presented at moderate intensities (10 dB[C] above background).
**Procedure**

All training sessions were 60 min in duration. Acclimation on Day 1 was the same as in Experiment 1. During Phase 1 training (Day 2), the SOC groups received four presentations of B followed immediately by the US (i.e., $B \rightarrow US$). The SPC groups received identical treatment, but with D paired with the US. In Phase 2 (Day 3), all subjects were exposed to four compound pairings of A and X followed at termination by B. In Phase 3 (Days 4-8), the blocking groups (BB) were exposed to four presentations of A followed immediately by the outcome B. The control groups (CON) received equivalent training, but with C substituted for A. During Phase 4 (Day 9), Groups SOC-BB, SOC-CON, SPC-BB1, and SPC-CON1 received four presentations...
of D followed immediately by the US; Groups SPC-BB2 and SPC-CON2 received identical treatment except that B was paired with the US. Finally, in Phase 5 (Day 10), all groups received four presentations of B followed by the US. Stimulus presentations occurred 10, 20, 37, and 50 min into each session. Reacclimation (Days 11 and 12) and testing with X and A (Days 13 and 14) were the same as in Experiment 1.

Two subjects from Group SPC-C0N2 did not drink during the first 60 s in the experimental chambers on the first test day (Day 13) and were therefore excluded from all analyses.

**Results and Discussion**

Backward blocking was prevented in Group SOC-BB, for which the to-be-blocked stimulus (X) was made biologically significant (as a result of Phases 1 and 2) prior to the backward blocking training (Phase 3). In fact, equal levels of responding were seen in Group SOC-BB and its control group (SOC-CON). Additionally, less conditioned responding was seen in Groups SPC-BB1 and SPC-BB2 than in their control groups (SPC-CON1 and SPC-C0N2, respectively), which received training in Phases 2 and 3 with neutral stimuli. This latter finding once again demonstrates backward blocking in animals with cues of low (but not high) biological significance.

The left side of Figure 2 depicts mean times to complete 5 cumulative seconds of drinking in the presence of X on Day 13. Reduced levels of responding to X in Groups SPC-BB1 and SPC-BB2 relative to their control groups, and equivalent suppression in Group SOC-BB and its control group, were confirmed by statistical analyses. A 3 x 2 ANOVA was performed with Phases 1 and 4 treatment (SOC vs. SPC1 vs. SPC2) as one factor and Phase 3 treatment (BB vs. CON) as the other factor. This ANOVA revealed a significant interaction of Phases 1 and 4 treatment with Phase 3 treatment, $F(2, 64) = 6.59$, a main effect of Phase 3 treatment, $F(1, 64) = 25.89$, but no main effect of Phases 1 and 4 treatment, $F(2, 64) = 3.03$. Bonferroni comparisons confirmed that the observed differences in responding between Groups SPC-BB1 and SPC-CON1 and between SPCBB2 and SPC-C0N2 were significant, $F_s(1, 64) = 22.31$ and 16.14, respectively, and that there was no difference in responding between Groups SOC-BB and SOC-CON, $F < 1$. Finally, comparisons between Groups SOC-BB and SPC-BB1 and between Groups SOC-BB and SPC-BB2 revealed that these differences were significant, $F_s(1, 64) = 11.61$ and 14.91, respectively.

The right side of Figure 2 depicts the response means for Stimulus A. A 3 x 2 ANOVA, with the same factors used in analyzing the X data, was performed on the A data. The
ANOVA revealed no main effect of either Phases 1 and 4 treatment, $F(2, 64) = 1.12$, or Phase 3 treatment, $F(1, 64) = 1.13$, and no interaction of these factors, $F < 1$.

These results provide further evidence that backward blocking is obtainable in animals. This claim is supported by the observed low levels of responding to $X$ by Groups SPC-BB1 and SPC-BB2 relative to their control groups (which lacked the essential Phase 3 treatment). Additionally, the backward blocking effect appears to depend critically on the biological significance of the competing cues during backward blocking training.

**GENERAL DISCUSSION**

Experiments 1 and 2 investigated backward blocking in animals using procedures in which the biological significance of the competing cues was varied during blocking training. Both experiments demonstrated that backward blocking can be obtained with animals (see Miller et al., 1990, and Schweitzer & Green, 1982, for prior failures), a finding previously restricted to studies of human causal judgment (e.g., Chapman, 1991; Shanks, 1985; Van Hamme, 1994; Williams et al., 1994). Experiment 1 illustrated that cues of high, in contrast to low, biological significance (operationalized as high physical intensity) are relatively immune to cue competition. Experiment 2 led to the same conclusion using a different operationalization of biological significance; specifically, biological significance was manipulated through pairings, during blocking training, with another cue that itself was or was not biologically significant. With this procedure, backward blocking was observed only in groups for which the cues were of low biological significance during backward blocking training. Experiment 1 also demonstrated that the backward blocking we obtained previously (Miller & Matute, in press) was not due to our use of SPC per se.

These results, in combination with our previous ones (Miller & Matute, in press), demonstrate the importance of biological significance in modulating cue competition. In demonstrations of backward blocking using human subjects, the blocked cue is ordinarily of low biological significance. For example, the US surrogate in many of those studies is an allergic reaction or a novel illness experienced by a fictitious patient. Although subjects readily learn about the described relationships, the stimuli are clearly not as biologically significant to the subjects as would be stimuli paired with food, water, or electric shock, which are the commonly used USs in cue competition studies with animals. The present studies, as well as our previous backward blocking studies, suggest that the previous failures to observe backward blocking in animals were due to the high biological
significance of the events used, rather than to a species difference in information processing or fundamentally different processes underlying conditioning and causal judgment. Additional support for the role of biological significance in studies of cue competition comes from our finding (Miller & Matute, in press. Experiment 3) that forward blocking as well as backward blocking is attenuated if the target cue is of high biological significance (see Hall, Mackintosh, Goodall, & Dal Martello, 1977, and Mackintosh, 1976, for additional evidence).

Why cues of low biological significance are subject to cue competition whereas those of high biological significance are protected is not entirely clear. One hypothesis, based on an evolutionary perspective, is that biologically significant cues may be privileged in information processing. As such, they are at least partially protected from the effects of cue competition, which itself is a defense against interference due to information overload. In previous studies of backward blocking, the target stimulus was of high biological significance during training because it was paired with the US in Phase 1. Thus, the effort in Phase 2 was to reduce the biological significance already acquired by the to-be-blocked stimulus by pairing the blocking stimulus alone with the US. However, in conventional forward blocking, only the blocking stimulus is given high biological significance during Phase 1 training. In Phase 2, the effort is to prevent the blocked stimulus from acquiring biological significance. It may be easier to prevent a stimulus from acquiring biological significance (e.g., forward blocking) than it is to degrade biological significance after it has been acquired (e.g., backward blocking). In contrast, when there is a predictive component to the putative association without any affective component (i.e., no biological significance, as in human causal learning or SPC), the predictive value of stimuli can be blocked either prospectively (forward blocking) or retrospectively (backward blocking). The notion that biologically significant cues are relatively immune from the effects of cue competition is fully consistent with the observed results of our studies, as well as past failures to observe backward blocking in animals.
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