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Learning About Absent Outcome in the Presence of Conditioned Excitor and Inhibitor: A Study Using Conditioned Flavor Preference

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We examined whether aversive conditioning of a previously established conditioned inhibitor (A) for sucrose solution (X) affects subsequent consumption and aversive conditioning of X. Experiment 1 established an appetitive conditioned inhibition procedure in which odor A became a conditioned inhibitor for X. In Phase 1 of Experiments 2 and 3, subjects received either inhibitory (Group INH: AB/BX/C) or excitatory conditioning of A (Group EXC: ABX/B/C), or a control treatment (Group CONT: AB/B/CX). In Phase 2, A was paired with an injection of lithium chloride (LiCl) and consumption of X was measured. X was paired with LiCl in Phase 3, and tested in extinction. After a moderate amount of Phase 1 treatment in Experiment 2, animals in Group EXC showed a reduction in consumption of X after A-LiCl pairings, while those in both Groups EXC and INH rapidly acquired an aversion to X during X-LiCl conditioning. However, when extended Phase 1 treatment was given in Experiment 3, animals in Group INH tended to acquire the aversion to X at a slower rate than those in Group CONT. Animals in Group EXC did not show any superiority in acquisition of the X aversion. The results are discussed in terms of mediation processes by event representations.

In a typical Pavlovian conditioning situation, animals acquire associations between the representations of a cue and an outcome, since they receive repeated pairings of them. However, animals also seem to learn such associations without exposure to just the cue-outcome pairings. Holland (1981, 1990) found that rats which first received pairings of a tone (A) with a flavored food (X), and subsequent pairings of A with an illness-inducing agent (injection of lithium chloride: LiCl), showed hesitancy to consume the food in the final test. This finding could not be explained in terms of the operation of a (backward) excitatory X-A link and an A-illness excitatory link in testing, since the suppression of food consumption was not obtained for the rats that underwent the A-LiCl pairings following the backward conditioning procedure, where X had explicitly preceded A (Holland, 1981, Experiment 1). Holland (1981, 1990) then concluded that a representation-mediated acquisition process associated the representation of X with

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that of illness during presenting A upon LiCl (see also Hall, 1996; Ward-Robinson & Hall, 1996).

In a representation-mediated learning experiment, when animals receive pairings of A with LiCl, a representation of X is activated through an A-X excitatory link in spite of being physically absent. In the framework of the SOP model proposed by Wagner (1981), this "primed" representation of X should be activated into A2, the not fully activated state. In later studies, Holland (1983; Hall, 1996) suggested that an excitatory link is established between the representations of a cue in the A2 state and an outcome in the A1 state (but see also Aitken & Dickinson, 2005; Dickinson & Burke, 1996; Larkin, Aitken, & Dickinson, 1998).

Related to this issue are the effects of cue devaluation after establishment of an inhibitory link between the representations of A and X. Espinet, Iraola, Bennett, and Mackintosh (1995) gave their rats alternating exposure to the two bottles of solution with compound flavors, AY and XY (citric acid plus sucrose, and saline plus sucrose), containing one flavor in common (Y; sucrose). While in a group of rats (the experimental group) this treatment was followed by pairing A with LiCl, in the other group (the control group) it was followed by pairing A with saline injection. Testing showed that when X was subsequently paired with LiCl, the animals in the experimental group acquired X aversion more slowly than those in the control group (Experiment 1). In addition, when X was presented in compound with another flavored solution that had been previously paired with LiCl, the experimental animals did not show suppression in consumption of the compound liquid (Experiment 2). That is, X got through the retardation and summation tests of conditioned inhibition. This so-called Espinet effect has been replicated in a conditioned flavor aversion (Artigas, Chamizo, & Peris, 2001, Experiment 1) and in a conditioned suppression in rats (Leonard & Hall, 1999), as well as in a medical diagnosis contingency judgment (Graham, 1999) and a melody-composer conditioning in humans (Artigas et al., 2001, Experiments 2 & 3).

In the procedure of the experiments demonstrating the Espinet effect, alternate exposures to AY and XY should result in the formation of excitatory links between the representations of A and Y and between the representations of X and Y (i.e., within-compound associations) (e.g., Rescorla & Cunningham, 1978). Thus, presenting Y would evoke the representation of X on the AY trials, and the representation of A on the XY trials. This should result in the establishment of a mutually inhibitory link between the representations of A and X (McLaren, Kaye, & Mackintosh, 1989; McLaren & Mackintosh, 2000; *cf.* Wagner, 1981). Based on this assumption, Espinet et al. (1995) proposed a new acquisition rule; if presenting a conditioned excitor produces a positive activation in a representation of its outcome, presenting a conditioned inhibitor should produce a negative activation of the outcome representation. Furthermore, pairing the negative activation in X representation evoked in the presence of conditioned inhibitor A with LiCl should cause a new inhibitory link between the representations of X and illness (see Leonard & Hall, 1999). This acquisition rule could be seen as an extension of the explanation of representation-mediated excitatory learning

proposed by Holland (1981, 1983, 1990; Hall, 1996), where a representation of a cue has a negative, rather than positive, activation.

As an alternative, Bennett, Scahill, Griffiths, and Mackintosh (1999) argued that an inhibitory link from X to A (X → A), rather than from A to X (A → X), was responsible for the Espinet effect. They demonstrated that the rats in Group AY-XY, in which a presentation of AY (lemon-flavored sucrose) always preceded that of XY (lemon-flavored saline) in daily preexposure sessions, passed both retardation and summation tests with X after A-LiCl pairings. However, this Espinet effect was not obtained in animals that received the XY presentation before the AY presentation in daily sessions (Group XY-AY), or in animals given each of these two presentations in different sessions (control group). According to Bennett et al. (1999), in Group AY-XY the inhibitory X → A link should be formed much more strongly than the inhibitory A → X link for the following three reasons. First, during the XY presentation, the representation of X in the A1 state would be paired with that of A in the A2 state activated through a Y → A excitatory link (McLaren et al., 1989; McLaren & Mackintosh, 2000). Second, X presented in compound with Y always followed A presented with Y on each daily session, thus resulting in a backward conditioning of X with A (e.g., Moscovitch & LoLordo, 1968; Plotkin & Oakley, 1975). Third, although the inhibitory A → X link was also expected to be formed during the AY presentation, presenting X after A (in compound with Y) would establish an excitatory trace conditioning of A with X, counteracting the inhibitory A → X link.

Based on their findings, Bennett et al. (1999) argued that the Espinet effect should be explained as a consequence of the chain operation, in testing, of the inhibitory X → A link acquired during the first stage and an excitatory A → illness link. Together, these links result in the negative activation in the representation of illness and an alleviated conditioned aversion to X (see Artigas et al., 2001). Although the Espinet effect does not necessarily imply the new learning rule as proposed by Espinet et al. (1995), the possibility of an acquisition process with the representation of X during the A-LiCl pairing after the formation of an inhibitory A → X link is still open to investigation. There is an interesting report in regard to the issue. Although Bennett et al. (1999) failed to show any statistically significant differences in the test performance between the animals in Group XY-AY and their control animals, the former appeared to consume consistently less of X than the latter in the retardation tests for X (see figures 3 and 4 presented in Bennett et al., 1999). This would suggest that the rats in Group XY-AY would acquire an excitatory, rather than inhibitory, X-illness link during the A-LiCl pairings subsequent to the establishment of the inhibitory A → X link.

In view of the theoretical importance of the issue mentioned so far, the present research examined the effect of pairing of a conditioned inhibitor with LiCl on responding to an appetitive outcome whose absence had been signaled by the conditioned inhibitor. Experimental animals first learned that the presentation of a flavor (A) signaled the absence of a sucrose solution (X); next they received A-LiCl pairings. At test, their consumption of X was compared with the consumptions of animals that had received either an excitatory A-X conditioning

or a training that A and X were noncontingent with respect to each other. In Experiment 1, using a conditioned flavor preference, we demonstrated a conditioned inhibition of A for X through exposure to a compound flavor (AB) and to X flavored with B alone (AB/BX discrimination). Following this, the effect of A-LiCl pairing on the consumption of X was examined in Experiments 2 and 3.

Experiment 1

Using combinations of four distinct flavors (A, B, C, and D), a sucrose solution (X), and tap water, rats were exposed to four types of stimulus (AB, BX, C, and DX). Rescorla (2008, Experiments 2 & 4) found, in food- and water-deprived rats, that four or five pairings of a flavor with a combination of a 20% Polycose and a 4% sucrose were sufficient to establish the flavor as a reliable conditioned excitor for the outcome. In the present experiment, we deprived rats only of water, but administered many more pairings of the stimuli and the sucrose (12 BX and 12 DX) than those used in Rescorla's study (2008). We examined whether A could establish itself as a conditioned inhibitor for X using a summation test, in which tap water flavored with an AD compound and flavored with a CD compound were simultaneously presented to the animals. We expected that the rats would drink more of the CD-flavored water than of the AD-flavored water because C should have no effect on the animals' responding to D, whereas A should inhibit the responding to D.

Method

Subjects

The subjects were 16 male rats of Wistar strain, approximately 90 days of age at the beginning of the experiment with a mean free-feeding weight of 400 g (range: 360-432 g). They were born and reared in the colony room of the Department of Psychology at Nagoya University, Japan. Throughout the experiment, each subject was housed individually in an opaque polycarbonate cage (31 x 36 x 18 cm), with a floor covered with wooden chips and a stainless-steel grid roof. The home cage was placed in the colony room illuminated from 800 to 2000. The temperature and humidity of the colony room were maintained at 22°C and 50%, respectively. The animals were maintained on a water deprivation regime, details of which are described below. They had free access to food in their home cage.

Apparatus and stimuli

We utilized sixteen transparent acrylic cages (measuring 27 x 30 x 20 cm, with the floor covered with wooden chips and a stainless-steel grid roof) as drinking cages, which were placed in a dim-lit (0.5 lx) experimental room outside the animal laboratory. Temperature and humidity were maintained at 22°C and 50%, respectively, along with well ventilation. Clipped on to the roof of each cage was a stainless-steel spout connected, via a plastic tube, to a graduated cylinder filled with fluid. In a single-bottle situation, the spout was presented in the center of the roof, 20 cm apart from the anterior sidewall. In a double-bottle situation, two spouts were presented 20 cm apart from the anterior sidewall, spaced 14 cm apart from each other. Two-percent (v/v) solutions of artificial essences, almond, peppermint, vanilla, and strawberry (Gaban Asaoka, Tokyo, Japan) were used as A, B, C, and D, respectively. When the flavors were presented in a simultaneous compound, each 2 ml of essence was mixed in 96 ml of outcome solution. The outcomes were either a 15% (w/w) sucrose solution (X) or tap water.

Procedure

Drinking training (Days 1 to 6). Water deprivation was started at 1700 on the day before the first experimental day. At 1200 and 1700 on each day, all the rats were first placed in the drinking cage for 10 min, without tap water presentation. Water was then presented for 10 min.

Discrimination training (Days 7 to 30). Table 1 shows the schematized schedule of the training phase. The discrimination consisted of six four-day cycles. On each day of a cycle, the animals were given two sessions (one started at 1200, the other at 1700). There were two cycle types (*a* and *b*), each of which contained the same types of sessions. They were used in the simple alternation order starting with *a*. During each session, the rats were presented with one of four stimuli (AB, B, C, and D), so that each stimulus was presented twice in each cycle. On each session, animals were first placed for 10 min in the drinking cage without stimulus presentation (waiting time). They were then given a stimulus fluid for 10 min. For half the animals, almond was used as B, and peppermint was used as D; the remaining half received the reverse assignment. These flavors were mixed in the sucrose solution, X (BX and DX). In addition, half the animals received strawberry as A and vanilla as C; for the remaining half, vanilla was assigned to A and strawberry to C. AB compound and C were presented in tap water. The assignment of the essences to A and C was orthogonal to that of B and D.

Table 1

Schedule of the discrimination training in Experiment 1

	Type of cycle							
	a				*b*			
	Day of a cycle							
Session	1	2	3	4	1	2	3	4
1200	BX	C	DX	AB	C	BX	AB	DX
1700	AB	DX	C	BX	DX	AB	BX	C

Note: A and C were strawberry and vanilla flavors, counterbalanced, and B and D were almond and peppermint flavors, also counterbalanced, mixed in either sucrose solution (X) or in tap water (no mark).

Summation test (Days 31 and 32). We tested whether A had acquired the ability to inhibit responding to a conditioned excitor, D. During each daily session, all subjects were simultaneously presented with two test fluids: AD- and CD-flavored water. The position of the test stimuli was counterbalanced across the animals. Each test session began at 1200. After the 10-min waiting time in the drinking cage they were presented with the test stimuli for 10 min. At 1700 on each of the two days, the animals were given water for 10 min in their home cages. The fluid consumption was measured to the nearest 0.2 ml throughout the drinking training, discrimination training, and summation test.

Results and Discussion

Reliability of the results was assessed against a Type I error rate of 0.05 in all of the following statistical tests including analyses of variance (ANOVA), analyses of simple main effects, and multiple comparisons with Ryan's procedure (Ryan, 1960).

Discrimination training

Figure 1a displays the consumptions for the four stimuli during the discrimination training. Early in training, consumption of C was higher than that of the other three fluids. As the training proceeded, the consumptions of C and AB decreased while those of BX and DX increased. A two-way ANOVA with stimulus (4: AB, BX, C, and DX) and cycle (6 four-day cycles) as factors revealed significant main effects of stimulus, $MSE = 8.44$, $F(3, 45) = 4.50$, $p < 0.01$, and cycle, $MSE = 1.65$, $F(5, 75) = 45.47$, $p < 0.01$, along with a significant interaction between the two factors, $MSE = 1.34$, $F(15, 225) = 13.48$, $p < 0.001$. The simple main effect of stimulus was significant on Cycles 1, $MSE = 2.52$, ($F(3, 270) = 11.75$, $p < 0.001$), 2 ($F(3, 270) = 3.01$, $p = 0.03$), 4 ($F(3, 270) = 6.31$, $p < 0.001$), 5 ($F(3, 270) = 7.98$, $p < 0.001$), and 6 ($F(3, 270) = 21.58$, $p < 0.001$),. Multiple comparisons found that, during Cycle 1, the C consumption was more than each of the consumptions of the remaining three stimuli, $t(270)$s ≥ 3.93, ps < 0.001. During Cycle 6, the BX and DX consumptions were greater than the AB and C consumptions (smallest $t(270)$ was 4.93, $p < 0.001$). There were no significant differences between BX and DX, or between AB and C, $t(270)$s = 0.75, 0.68 (p = 0.46, 0.50), respectively. These analyses indicate that the rats came to drink more of the sucrose solutions than the solutions not containing sucrose.

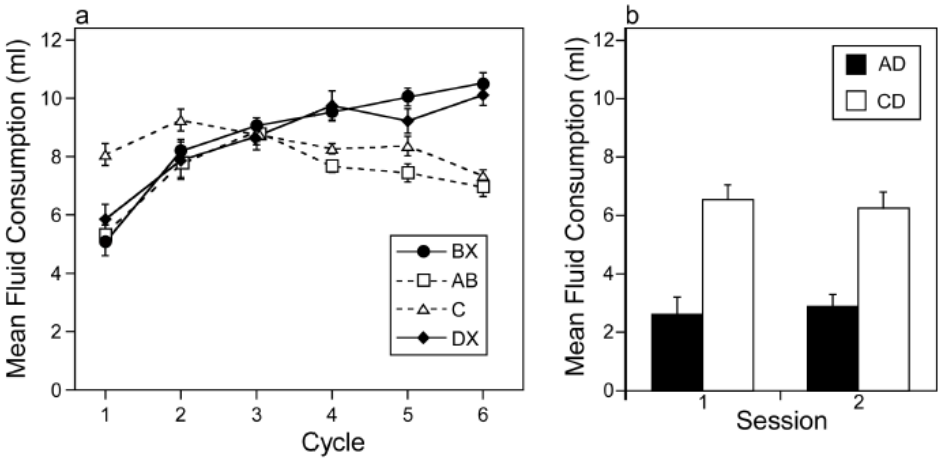

Figure 1. Results of Experiment 1. a) Mean fluid consumption during the 6 four-day cycles of AB/BX/C/DX discrimination training. b) Mean fluid consumption in the summation test.

Summation test

Figure 1b shows the results of our primary interest, those from the summation test during which AD and CD in tap water were simultaneously presented. Consumption of AD was less than that of CD in both test sessions. A

two-way ANOVA with stimulus (2: AD vs. CD) and session (2) as factors confirmed this observation, revealing only a significant main effect of stimulus, $MSE = 8.74$, $F(1, 15) = 24.22$, $p < 0.001$. These results demonstrate that the six four-day cycles of discrimination training was sufficient for A to become a conditioned inhibitor for the sucrose. In subsequent Experiments 2 and 3 we could therefore lay out discrimination with more than six cycles of training.

Experiment 2

This experiment used three groups of rats that underwent different procedures of the eight three-day cycles of discrimination training, in which the animals were presented with intermixed presentations of three combinations of distinct flavors. The first group, Group Inhibitor (INH), received B presented in a sucrose solution (X). Additionally, they received simultaneous compound presentation of A and B in tap water. As was shown in Experiment 1, this training was expected to establish A as a conditioned inhibitor for X. The increase in the amount of conditioned inhibition training by two cycles was expected to produce a more reliable conditioned inhibitor. The second group, Group Excitor (EXC), was presented with B alone in water. They were also presented with simultaneous compound of A and B in X to establish A as a conditioned excitor for X. For the two groups, another flavor, C, was given in water as an irrelevant cue for X (i.e., AB/BX/C for Group INH, and ABX/B/C for Group EXC). For the third group, Group Control (CONT), C was presented in X, while both B and AB-compound were presented in water (AB/B/CX). In this group, A was not related to X. All groups then experienced pairings of their A with an LiCl, and impact of the aversion trials on the subsequent consumption of X was investigated. Finally, acquisition of a conditioned aversion to X by an excitatory X-LiCl conditioning was compared across the three groups (i.e., saving test).

Following the results of earlier representation-mediated learning studies (e.g., Holland, 1981, 1990), we expected that the animals in Group EXC would consume less of X than those in Group CONT after the A-LiCl pairings. Besides, it was expected that they would acquire an aversion to X more rapidly than the control animals in the saving test. However, the most important question of the present experiment concerned the consumption and aversive conditioning of X shown by the animals in Group INH, who experienced pairings of the conditioned inhibitor with LiCl. Because it has been documented that rats will consume a relatively large amount of a flavored solution signaling the omission of nausea (Batson & Best, 1981; Best, Dunn, Batson, Meachum, & Nash, 1985), the valence of the associative link between the representations of X and illness acquired by the animals in Group INH during the A-LiCl pairing (i.e., excitatory vs. inhibitory), if any, should be indicated by their amount of X consumption.

Method

Subjects, apparatus, and stimuli

The subjects were 24 male rats of Wistar strain (Japan SLC, Inc., Hamamatsu, Japan), approximately 80 days of age at the onset of the experiment with a mean free-feeding weight of 340 g (range: 300-370 g). The housing conditions, apparatus, and stimuli were identical to those in Experiment 1. On the sessions of A-LiCl pairing and sucrose-LiCl conditioning, 5 ml/kg of a 0.15M LiCl was administered through an intraperitoneal injection.

Procedure

Discrimination training (Days 7 to 30). After the drinking training, which was similar to that of Experiment 1 (Days 1-6), each animal was assigned to one of the three equal-sized groups: Groups INH, EXC, and CONT (*n*s = 8), matched for the mean amount of water consumption on the last day of the drinking training. The discrimination training consisted of eight three-day cycles. Each day in a cycle had two sessions starting at 1200 and 1700, and in each cycle all the animals experienced two sessions with B alone, simultaneous compound presentation of A and B, and C. There were two cycle types (*a* and *b*, see Table 2), used in simple alternation order starting with *a*. For half the animals in each group, strawberry was used as A; for the remaining half, vanilla was used as A. In addition, for half the animals in each group, almond was used as B, and peppermint was used as C, with the assignments being flipped for the remaining rats. These assignments were orthogonal to each other. The animals in Group INH were given an inhibitory training with A; while the AB compound and C alone were presented in tap water, B was mixed with the sucrose solution (AB/BX/C). An excitatory training with A was applied to the rats in Group EXC; while each of B and C were presented in water, the AB compound was mixed with the sucrose solution (ABX/B/C). The animals in Group CONT were exposed to the A and AB compound in water, but had C in the sucrose solution (AB/B/CX). During each session (and all the subsequent sessions with fluid presentation in the drinking cage), the animals were placed in the cage for 10 min without fluid being available before they were given a stimulus for 10 min.

Table 2
Schedule of the discrimination training in Experiments 2 and 3

	Type of cycle					
	a			*b*		
	Day of a cycle					
Group	1	2	3	1	2	3
INH						
1200	BX	C	AB	C	AB	BX
1700	C	AB	BX	BX	C	AB
EXC						
1200	ABX	C	B	C	B	ABX
1700	C	B	ABX	ABX	C	A
CONT						
1200	CX	A	AB	A	AB	CX
1700	A	AB	CX	CX	A	AB

Note: A was strawberry or vanilla flavor, counterbalanced across animals, and B and C were almond and peppermint flavors, also counterbalanced, mixed in either sucrose solution (X) or in tap water (no mark).

Table 3

Schedule of the A-LiCl pairing and sucrose consumption test in Experiment 2

	Day											
	31	32	33	34	35	36	37	38	39	40	41	42
1200	HC: water	DC: A-LiCl	HC: water	DC: A-LiCl	HC: water	DC: sucrose	DC: A-LiCl	HC: water	DC: sucrose vs. water	HC: water	DC: A-LiCl	HC: water
1700	NT	HC: water	NT	HC: water	HC: water	NT	HC: water	HC: water	HC: water	NT	HC: water	HC: water

Note: HC, home cage; DC, drinking cage; NT, no treatment.

A-LiCl pairing and sucrose consumption test (Days 31 to 42). Following the completion of discrimination training, the animals received pairings of A with LiCl injection, interspersed with sucrose consumption tests (the procedure of the phase is schematized in Table 3). These manipulations were conducted during the sessions starting at 1200. At 1700, the animals were given 10 min access to a bottle of water in their home cages for daily supplement, but not on each day preceding the A-LiCl pairing. This was intended to increase animals' thirst and minimize intersubject differences in A consumption. On Day 31, each animal was allowed access to bottle of water for 10 min in their home cages at 1200. On Days 32 and 34, they were given 5 ml of an A-flavored tap water in the drinking cage. Immediately after the intake, the animals were removed from the drinking cage, and given an injection of the LiCl before being returned to their home cages. On Day 36, they were presented with a 15% sucrose solution not containing any flavors for 10 min (sucrose consumption test with single bottle method). On the next day (Day 37), they received an additional A-LiCl pairing in the same way as performed on Days 32 and 34. Sucrose consumption was tested again on Day 39, using a double-bottle method; the animals were presented with the odorless sucrose solution and tap water simultaneously for 10 min. Position of the two fluids was counterbalanced across animals. On Day 41, an additional A-LiCl pairing was administered again. On the subsequent days of each A-LiCl session (Days 33, 35, 38, and 42) and on Day 40, all the animals were kept in their home cages (for recovery from malaise), and given a 10 min water access at 1200.

Sucrose-LiCl conditioning and extinction test (Days 43 to 49). On Days 43, 45, and 47, the animals were presented with the odorless sucrose solution in the drinking cage. Immediately after the intake they were injected with the LiCl injection. On Day 49, the sucrose consumption was monitored for 10 min in extinction in the drinking cage. Each day following the sucrose-LiCl conditioning (Days 44, 46, and 48) was recovery day. The fluid consumption was measured to the nearest 0.2 ml throughout the experiment.

Results and Discussion

Discrimination training

Figure 2 shows transitions of the mean amounts of fluid consumption shown by the three groups during the discrimination training, in blocks of two cycles. For all the groups, consumption of the flavored sucrose solution increased, while that of the flavored tap water did not change. A three-way ANOVA conducted on the data with group (3), stimulus (3: AB, B, and C), and block (4) as factors, almost confirmed the observations, revealing a significant main effect of block, $MSE = 0.40$, $F(3, 63) = 53.98$, $p < 0.001$, and significant interactions of group x stimulus, $F(4, 42) = 6.61$, $MSE = 8.35$, $p < 0.001$, stimulus x block, $F(6, 126) = 2.18$, $MSE = 0.98$, $p = 0.049$, and group x stimulus x block, $F(12, 126) = 10.25$, $MSE = 0.98$, $p < 0.001$. Each group showed a significant simple simple-main effect of stimulus on the final block, $F(2, 168) = 12.89$ ($p < 0.001$), $F(2, 168) = 11.33$ ($p < 0.001$), $F(2, 168) = 5.56$ ($p < 0.01$), respectively for Groups INH, EXC, and CONT, $MSE = 2.82$. In Groups INH and CONT, the flavored sucrose solutions (BX and CX, respectively) were consumed in greater quantity than their fluids not containing sucrose (AB and C in Group INH, $t(168) = 4.79$, 3.85 ($p < 0.001$), respectively; AB and B in Group CONT, $t(168) = 2.94$, 2.84 ($p < 0.01$).respectively). In both groups, there were no significant differences between the consumptions of the flavored tap waters, $t(168)$s = 0.95 ($p = 0.35$) and 0.33 ($p = 0.92$, respectively for Groups INH and CONT. In Group EXC, consumption of ABX was higher than that of both B and C, $t(168) = 2.86$, 4.73 ($p < 0.01$, 0.001),

respectively. In addition, B intake seemed to be greater than C intake, but this difference did not reach the reliable level, $t(168) = 1.87$, $p = 0.06$.

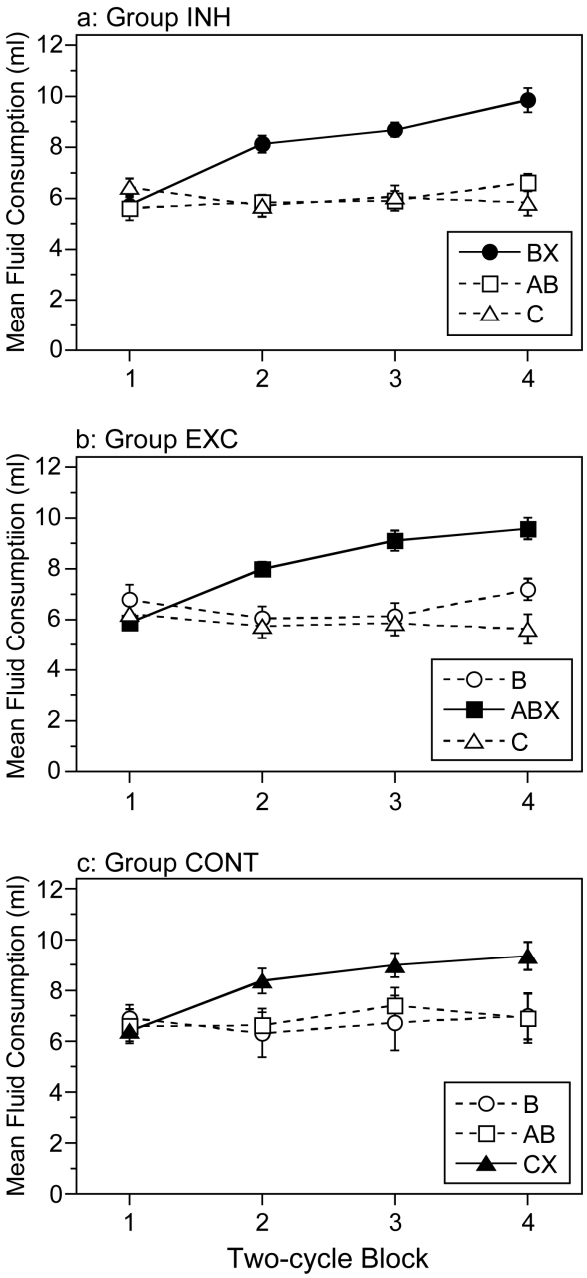

Figure 2. Results of Experiment 2. Mean fluid consumption during the AB/B/C discrimination training shown by Groups INH a), EXC b), and CONT c), in blocks of two cycles.

A-LiCl pairing

The consumption of A for each of the three groups during the A-LiCl pairings is shown in Table 4, with a square-root transformation to normalize the data. On the first session, all the animals drank the defined amount of A-flavored water (5 ml) in less than 10 min. Only one subject in Group EXC and CONT failed to drink 5 ml of the A-flavored water in 10 min on the second session. A two-way ANOVA applied to the data from the third and fourth sessions, group (3) x session (2), showed only a significant main effect of session, $MSE = 0.17$, $F(1, 21) = 35.67$, $p < 0.001$.

Table 4
Experiment 2. Mean (± 1SEs) square-root transformed consumptions of A (ml) in Groups INH, EXC, and CONT during the A devaluation phase

	Session			
Group	1 (Day 32)	2 (Day 34)	3 (Day 37)	4 (Day 41)
INH	2.24 (± 0.00)	2.24 (± 0.00)	1.60 (± 0.18)	0.85 (± 0.20)
EXC	2.24 (± 0.00)	2.21 (± 0.03)	1.42 (± 0.20)	0.42 (± 0.24)
CONT	2.24 (± 0.00)	2.21 (± 0.03)	1.50 (± 0.32)	1.10 (± 0.25)

Sucrose consumption test

Figure 3a displays the results of the single-bottle test. The data were normalized with the square-root transformation. A significant main effect of group was revealed by a one-way ANOVA, $MSE = 0.41$, $F(2, 21) = 4.05$, $p = 0.03$. Subsequent multiple comparisons found that the rats in Group EXC reliably consumed less of the sucrose solution than those in Groups INH and CONT, $t(21) = 2.61, 2.29$ ($p = 0.02, 0.03$), respectively, with no significant difference between the latter two groups, $t(21) = 0.32$, $p = 0.75$. Figure 3b displays the results of the double-bottle test expressed in terms of a "sucrose ratio" denoted as $a/(a + b)$, where a is sucrose consumption, and b is tap water consumption. Each group had a sucrose ratio above 0.5, indicating a preference of sucrose over water. However, we did not find any significant group differences, $MSE = 0.08$, $F(2, 21) = 0.39$, $p = 0.68$.

Sucrose-LiCl conditioning and extinction test

Figure 4a displays the consumption of the sucrose solution during the sucrose-LiCl conditioning. Although group differences were not apparent on the first and second session, the animals in both Groups INH and EXC appeared to drink less of the fluid than those in Group CONT on the third session. A two-way ANOVA with group and session as factors, however, found only a significant main effect of session, $MSE = 0.10$, $F(2, 42) = 67.51$, $p < 0.001$, revealing acquisition of a conditioned aversion to the sucrose solution without reliable group differences. Figure 4b displays the results of the extinction test. Here, consumption of the

sucrose solution in both Groups INH and EXC were small compared to that of Group CONT. This observation was confirmed by a one-way ANOVA, *MSE* = 0.72, $F(2, 21) = 4.31$, $p = 0.03$, showing that the animals in both Groups INH and EXC drank significantly less of the test fluid than those in Group CONT, $t(21) = 2.55, 2.53$ ($p = 0.02$), respectively.

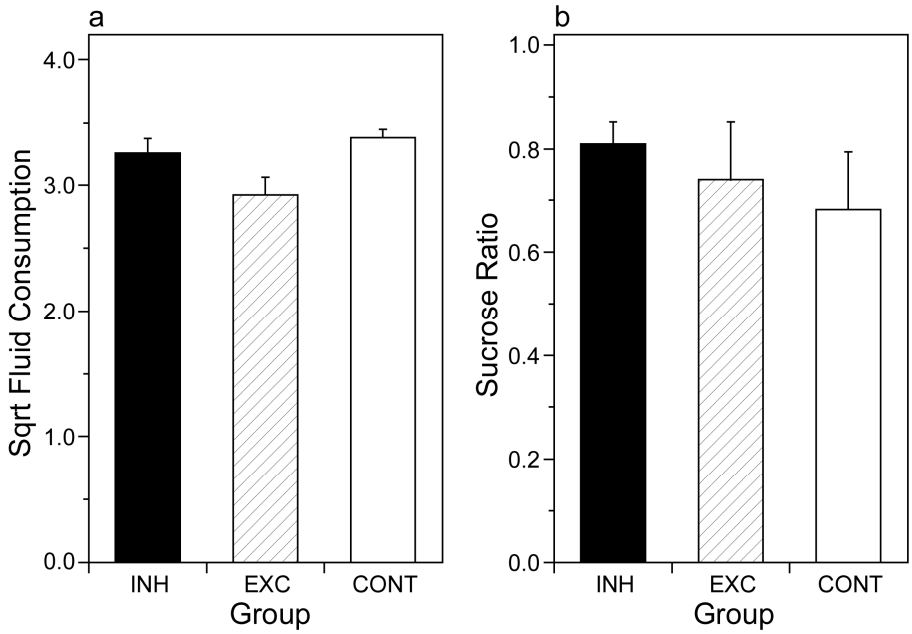

Figure 3. Results of Experiment 2. a) Mean square-root (sqrt) sucrose consumption during the single bottle test. b) Mean "sucrose ratio" denoted as $a/(a + b)$, where a is the consumption of the sucrose solution and b is the consumption of tap water during the double bottle test.

The results of the single-bottle sucrose consumption test and extinction test are consistent with the idea that pairings of a conditioned excitor of sucrose solution with LiCl injection established an aversion to the sucrose solution. The failure to reveal the effect of A-LiCl pairings in the double-bottle test could indicate that the sucrose consumption during the previous single-bottle test extinguished the conditioned aversion in Group EXC. Alternatively, it is also possible that the double-bottle test with target and non-target fluids simultaneously presented was inappropriate for testing a representation-mediated conditioned aversion, which produces, if any, a slight reduction in the palatability of an appetitive outcome. Moreover, we obtained a new finding from the results of the extinction test of X-LiCl conditioning: Pairings of conditioned inhibitor of sucrose solution with LiCl facilitated conditioned aversion to the sucrose solution.

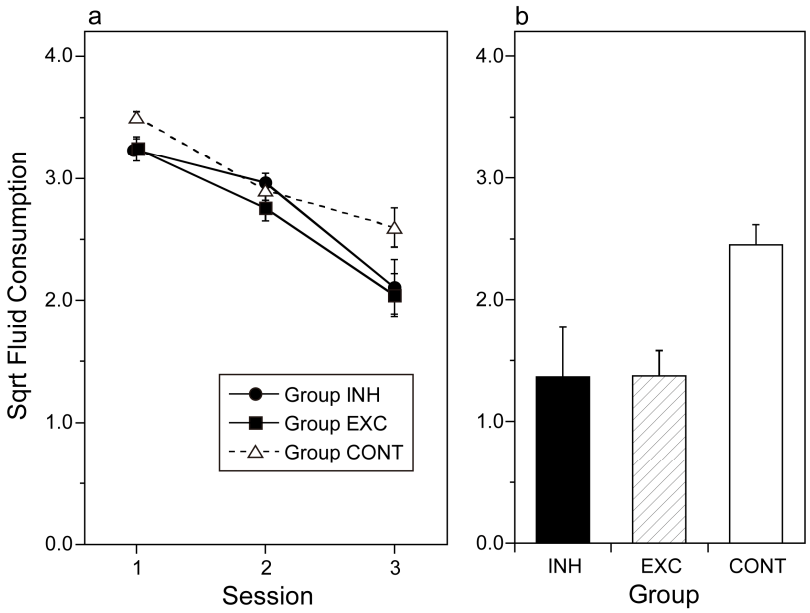

Figure 4. Results of Experiment 2. a) Transition of mean square-root (sqrt) sucrose consumption during the sucrose-LiCl conditioning phase. b) Mean square-root (sqrt) sucrose consumption on the extinction test. Error bars represent standard error.

Experiment 3

In Experiment 2, the animals in Group EXC consumed less of a sucrose solution (X) than those in Group CONT after A-LiCl pairings. Moreover, the animals in Group INH, as well as those in Group EXC, showed facilitation in the acquisition of conditioned aversion to X during X-LiCl conditioning subsequent to the A-LiCl pairings. These results suggest that a representation of X was activated not only in the presence of the conditioned inhibitor but also in the presence of the conditioned excitor, establishing an excitatory link between the representations of X and illness during the A-LiCl pairings.

It might still be possible, however, that the results shown by Group EXC were not dependent on the representation-mediated acquisition processes operating during the A-LiCl pairings, but on performance processes in the test phase. X presented to the animals in testing might retrieve the representation A, via an X-A within-compound excitatory link (e.g., Rescorla & Cunningham, 1978). This could imply that the representation of illness could be activated by virtue of an A-illness excitatory link established during the A-LiCl pairings, with the result of suppression in X consumption. This is the most standard explanation of sensory preconditioning (e.g., Rizley & Rescorla, 1972). Following this, one could expect an increased suppression in X consumption after extending the A-X conditioning, since the excitatory X-A link could be formed more strongly during such extended training. However, it has also been well documented that representation-mediated food aversion is acquired after only a limited amount of training of first-order

excitatory Pavlovian conditioning (A-X pairings), and attenuates with extending A-X conditioning (Holland, 1990, 1998, 2005). From the viewpoint of representation-mediated acquisition, one would therefore expect to observe an attenuated suppression in X-consumption after extended A-X conditioning.

In Experiment 3, we investigated the relationship between the effect of A-LiCl pairing and extended discrimination training. We compared the performance of three groups of animals in a design much like that in Experiment 2. If the facilitated sucrose aversion in Group INH of Experiment 2 was supported by the same processes as Group EXC, one can also expect that after the ten three-day cycles of discrimination training, the animals in Group INH will respond to the sucrose solution in a similar manner as those in Group EXC.

Method

Subjects, apparatus, and stimuli

The subjects were 24 male rats of Wistar strain (Japan SLC, Inc., Hamamatsu, Japan), approximately 65 days of age at the onset of the experiment with a mean free-feeding weight of 262 g (range: 254-274 g). The housing conditions, apparatus, and stimuli were identical to those in Experiment 2.

Procedure

The procedure for drinking training (Days 1 to 6) and discrimination training was basically identical to that of Experiment 2, except for the duration of the discrimination training extended by two three-day cycles. Animals thus received ten three-day cycles of the training (Days 7 to 36).

A-LiCl pairing and sucrose consumption test (Days 37 to 47). All animals received pairings of stimulus A with LiCl injection interspersed with test sessions of sucrose consumption. The major manipulations in this and the subsequent phases were conducted on sessions starting at 1200. At 1700, each animal was given a 10 min water access in the home cage, except on the days preceding A-LiCl pairing. On Days 38, 40, 43, and 45, all the animals were presented with 5 ml of the A-flavored tap water for 10 min in the drinking cage. Immediately after fluid intake, they were removed from the drinking cage and given an injection of LiCl before being returned to their home cages. Days 37, 39, 41, 44, and 46 were recovery days, such that the animals were given only a 10 min access to water in their home cages at 1200. Sucrose consumption was tested with a single-bottle method on Days 42 and 47, in which the animals were presented with odorless sucrose solution for 10 min in the drinking cage.

Sucrose-LiCl conditioning and extinction test (Days 48 to 56). On Days 48, 50, and 52, the animals were exposed to the odorless sucrose solution for 10 min in the drinking cage. They were only allowed to drink a maximum of 5 ml of the fluid in each session in order to avoid group differences in the sucrose experience. Immediately after the completion of fluid intake, they were removed from the drinking cage and injected with the LiCl. Days 49, 51, and 53 were recovery days. Consumption of the odorless sucrose solution was tested without LiCl injection on three successive days (Days 54 to 56). Each animal was presented with the test fluid for 10 min in the drinking cage, and its intake was monitored. The fluid consumption was measured to the nearest 0.2 ml throughout the experiment.

Results and Discussion

Discrimination training

Through the discrimination training, all groups showed an increase in consumption of the flavored sucrose solution. On the final (tenth) cycle, the mean (± 1*SE*) consumptions (ml) of AB, B, and C were 8.0 ± 0.5, 9.7 ± 0.4, and 8.0 ± 0.4, respectively in Group INH. The corresponding scores in Group EXC were 9.6 ± 0.4, 8.1 ± 0.7, and 7.2 ± 0.2, and in Group CONT, 7.2 ± 0.2, 7.6± 0.5, and 9.6 ± 0.4. A two-way ANOVA conducted on the data with group (3) and flavor (3: AB, B, and C) as factors found only a significant interaction between the two factors, MSE = 1.97, $F(4, 42) = 8.42$, $p < 0.001$. This interaction reflects that animals consumed significantly more of the fluid when it was presented with sucrose, MSE = 1.83, $F(2, 63) = 4.95$, 7.00, and 6.79, $p \leq 0.01$, for AB, B, and C, respectively. That is, the animals in Group INH drank significantly more B than those in Groups EXC and CONT, $t(63) = 2.27$, 3.03 ($p < 0.01$) ($p = 0.03$), respectively; the animals in Group EXC drank significantly more AB than those in Groups INH and CONT, $t(63) = 2.49$, 3.66 ($p = 0.02$) ($p < 0.001$), respectively; and the animals in Group CONT drank significantly more C than those in Groups INH and EXC, $t(63) = 2.38$, 3.36 ($p = 0.02$) ($p < 0.001$), respectivly. Significant group differences in consumption were not found between each couple of the flavored tap waters, $t(63) = 0.76$, 1.18, 1.25 ($p = 0.45$, 0.24, 0.22), for AB, B, and C, respectively.

Simple main effects of flavor were also significant within each group, MSE = 1.97, $F(2, 42) = 3.77$, 6.32, and 6.92 ($p = 0.03$) ($p < 0.01$) ($p < 0.01$), for Groups INH, EXC, and CONT, respectively. Multiple comparisons showed that the animals in Group EXC drank AB over C, $t(42) = 3.53$, $p < 0.01$, and that those in Group CONT drank C over both AB and B, $t(42) = 3.49$, 2.86 ($p < 0.01$), respectively, but that any significant differences in consumption among the three flavored fluids in Group INH were not found, $t(42) \leq 2.41$, $p \geq 0.02$ but modified alpha ≥ 0.017).

A-LiCl pairing

Table 5 displays the data from the A-LiCl pairing phase, with the square-root transformation. On the first session (Day 38), all the animals drank 5-ml of the A-flavored water. Thereafter, while the animals in Group EXC showed rapid reduction in consumption of A, those in Group INH acquired the A aversion relatively slowly. A two-way ANOVA with group and session (3; from the second to fourth sessions) as factors confirmed this observation, revealing a significant main effect of both group and session, $MSE = 0.14$, $F(2, 21) = 9.82$, $p < 0.01$; MSE = 0.14, $F(2, 42) = 173.81$, $p < 0.001$, respectively, and a significant interaction between the two factors, $F(4, 42) = 3.09$, $p = 0.03$. This interaction reflects that (a) the animals in Group EXC consumed significantly less of A than those in both Groups INH and CONT during the second session, $MSE = 0.14$, $F(2, 63) = 3.40$, $p = 0.04$; $t(63) = 2.36$, 2.14 ($p = 0.02$, 0.03), respectively; (b) on the third session,

while the rats in Group EXC again consumed reliably less of the fluid than those in both Groups INH and CONT, $F(2, 63) = 12.66$, $p < 0.001$; $t = 5.03$, 2.50 ($p < 0.001$), ($p = 0.02$), respectively, those in Group INH drank significantly more of the fluid than those in Group CONT, $t = 2.53$, $p = 0.02$; and (c) any reliable group differences were not found on the fourth session, $F(2, 63) < 1$. This means that strengths of the conditioned A aversion eventually acquired by the three groups were not different from each other, and group differences in consumption of the sucrose solution in testing henceforth, if any, cannot be interpreted only in terms of group differences in the degree of stimulus generalization from A to the sucrose solution.

Table 5
Experiment 3. Mean (± 1SEs) square-root transformed consumptions of A (ml) in Groups INH, EXC, and CONT during the A devaluation phase

	Session			
Group	1 (Day 38)	2 (Day 40)	3 (Day 43)	4 (Day 45)
INH	2.24 (± 0.00)	2.18 (± 0.04)	1.19 (± 0.17)	0.11 (± 0.07)
EXC	2.24 (± 0.00)	1.74 (± 0.14)	0.26 (± 0.16)	0.06 (± 0.05)
CONT	2.24 (± 0.00)	2.14 (± 0.06)	0.72 (± 0.21)	0.06 (± 0.05)

Sucrose consumption tests

During the first test session, mean (± 1 *SE*) square-root transformed consumptions (ml) of the sucrose solution were 3.21 ± 0.15, 3.00 ± 0.11, and 3.16 ± 0.08, respectively for Groups INH, EXC, and CONT. On the second session, the corresponding scores were 3.00 ± 0.11, 2.85 ± 0.11, and 2.34 ± 0.49, respectively. Although any clear-cut group difference was not obvious in the first session, the animals in both Groups INH and EXC seemed to consume more of the sucrose solution than those in Group CONT in the second session. However, a two-way ANOVA on these scores, group x session, did not confirm the observation and found only a marginally significant main effect of session, $MSE = 1.82$, $F(1, 21) = 4.09$, $p = 0.06$.

Sucrose-LiCl conditioning and extinction test

Displayed in the left part of Figure 5 are the results from sucrose-LiCl conditioning. In the right part are the results from the extinction test. On the first conditioning session, all the animals drank 5-ml of the sucrose solution. Following this, the animals in Group CONT seemed to acquire an aversion to the sucrose solution more rapidly than those in Groups INH and EXC. During the extinction test, the animals in both Groups INH and EXC seemed to have a larger intake of the sucrose solution than the control animals. However, a two-way ANOVA on the sucrose-LiCl conditioning data, group x session (2: the second and third sessions), did not confirm the observation, revealing only a significant main effect of session, $MSE = 0.25$, $F(1, 21) = 6.97$, $p = 0.02$. On the other hand, a two-way ANOVA on

the data from the extinction test, group x session (3), showed a significant main effect of session, $F(2, 42) = 31.13$, $p < 0.001$, and a significant interaction between the two factors, ,$MSE = 0.21$, $F(4, 42) = 3.08$, $p = 0.03$. The significant interaction reflects that the simple main effect of group was close to significance only on the second session, $MSE = 1.31$, $F(2, 63) = 3.02$, $p = 0.06$, in which the animals in Group INH drank reliably more of the sucrose solution than those in Group CONT, $t(63) = 2.42$, $p = 0.02$.

In summary, we obtained two major findings in Experiment 3. First, we confirmed that the extended discrimination training removed the reduction in sucrose (X) consumption subsequent to pairings of its conditioned excitor with LiCl. Second, we also found that the extended discrimination extinguished the facilitation in acquisition of conditioned X aversion by X-LiCl conditioning subsequent to the pairings of its conditioned inhibitor with LiCl. The former finding would suggest that the reduction in consumption of X observed after the A-LiCl pairings (and the facilitation of the conditioned X aversion during the X-LiCl conditioning) shown by the animals in Group EXC of Experiment 2 were dependent on a representation-mediated acquisition of the conditioned X aversion during the A-LiCl pairings, rather than on the performance processes in testing. The latter finding suggests that pairing of the conditioned inhibitor with LiCl after the extended discrimination counteracted the conditioned X aversion acquired during the X-LiCl conditionings. Possible associative processes underlying the finding are discussed in the General Discussion.

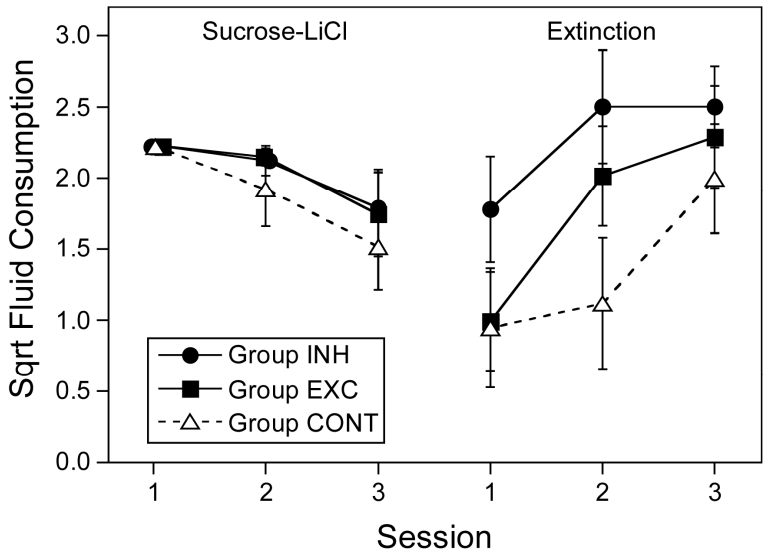

Figure 5. Results of Experiment 3. Transitions of mean square-root (sqrt) sucrose consumption during the sucrose-LiCl conditioning and extinction test.

General Discussion

We examined whether or not pairing of a flavor (A) with an illness-inducing agent (LiCl) subsequent to establishing A as a conditioned inhibitor for a sucrose solution (X) through an AB/BX discrimination training had an influence on animals' responding to X. Experiment 1 showed that A passed the summation test of conditioned inhibition after six cycles of the discrimination, where each cycle contained two presentations each of AB and BX. Slightly longer training was given in Experiments 2 and 3.

In Experiment 2, the rats in Group INH received eight cycles of the discrimination training. They acquired a conditioned aversion to X more readily than the control animals in the saving test subsequent to A-LiCl pairings. The animals in Group EXC, who had received an excitatory training of A for X, consumed less of X than those in both Groups INH and CONT in testing immediately after the A-LiCl pairing. They also showed rapid acquisition of the conditioned X aversion relative to the control animals during the saving test. The results from Group EXC are consistent with earlier studies concerning representation-mediated learning (e.g., Hall, 1996; Holland, 1981, 1990). The animals would acquire a new excitatory link between the representation of X activated in the presence of A, and that of illness, accordingly. Also in Group INH, we can assume that an associatively activated X representation was associated with illness with a new excitatory link during the A-LiCl pairings. That is, irrespective of the valence (excitatory vs. inhibitory) of the previously formed link between the representations of A and X, a similar activation in the X representation would be created in the presence of A. If this was the case, the finding that the X aversion was found in Group EXC immediately after the A-LiCl pairing, but not in Group INH until the saving test, might indicate that the level of activation created in the X representation was higher in the presence of the conditioned excitor than the conditioned inhibitor.

Devaluation of an appetitive outcome by pairing a conditioned inhibitor with LiCl seems to be improbable, if the conditioned inhibitor does not convey precise information about the outcome (e.g., Holland, 1990; Holland, Lasseter, & Agarwal, 2008). Unfortunately, there is little evidence supporting this function of conditioned inhibitor (Bonardi & Hall, 1994). One of few experimental demonstrations was reported by Kruse, Overmier, Konz, and Rokke (1983). Their rats received unpaired presentations of a noise and a food outcome – a training of conditioned inhibition of the noise for the outcome (e.g., Rescorla, 1969; Wagner & Rescorla, 1972). Thereafter, when the noise was superimposed on the test performance of target instrumental behaviors, they found a selective reduction in magnitude and an increase in latency of performance of the target instrumental behavior reinforced with that food (Delamater, LoLordo, & Sosa, 2003). Cotton, Goodall, and Mackintosh (1982) reported a similar finding. They gave rats a discrimination training composed of pairing a tone with a strong electric shock (1.0 mA) and pairing of a compound of the tone and a light with a weak shock (0.4 mA). In subsequent test, although the light signaling a reduction in magnitude of

the outcome alleviated the conditioned suppression to a clicker previously paired with the strong shock (Experiment 1), the light had no effect on responding to a clicker previously paired with the weak shock (Experiment 4; but see also Pearce, Montgomery, & Dickinson, 1981). Without assuming that these conditioned inhibitors were able to convey detailed information about their omitted (or reduced) outcomes, these outcome-specific effects of conditioned inhibition cannot be clearly understood. What therefore seems necessary now is a study concerning the structure of associative representations involved in conditioned inhibition that allows for encoding the properties of outcome event (see Hall, 2002; Konorski, 1967; Pearce & Hall, 1980).

In Experiment 3, the animals in Groups EXC and INH that had received an extended discrimination (10 cycles) showed neither reduction in the X consumption after the A-LiCl pairings nor the facilitated conditioned aversion to X during the subsequent X-LiCl conditioning. Instead, the rats in Group INH tended to consume more of X than the control animals in the saving test. As mentioned above, the results shown by the animals in both Groups EXC and INH are consistent with the findings of earlier studies concerning the effects of extensiveness of a Pavlovian conditioning on subsequent representation-mediated food aversion (Holland, 1990, 1998, 2005). For example, Holland (1998) found that a mediated food aversion in rats by pairings of a CS with LiCl was observed after relatively few CS-food pairings (16 pairings), but not after extended CS-food pairings (40 or more pairings). According to Holland (1990, 1998, 2005), in early stage of first-order Pavlovian conditioning, a representations of CS gains access to a preevaluative processing of its outcome, and given rise to perceptual component normally activated by presentation of the outcome itself. However, as the Pavlovian conditioning continues, that access is replaced by that to a more conceptual and motivational feature of the outcome representation (see also Holland et al., 2008). Within this perspective, as the discrimination training progressed in the present Experiment 3, not only the conditioned excitor but also the inhibitor could have lost access to low-level perceptual processing in the representation of the sucrose solution. Consequently, the mediated sucrose aversions were not found. We should also acknowledge promptly that this conclusion regarding the relationship between the amounts of the discrimination training and the effects of A-devaluation on the new learning with X all relies on cross-experimental comparisons, with which it is usually difficult to deal.

The results from Group INH in Experiment 3 are reminiscent of what Espinet et al. (1995) first demonstrated. They seem to support the idea that an inhibitory X-illness link acquired during the A-LiCl pairings caused the retardation in acquisition of the conditioned X aversion. However, before accepting this representation-mediated formation of the inhibitory link, we should consider whether the operation of an associative chain in testing could give a better explanation for our Espinet effect. The framework of inhibitory sensory preconditioning (Espinet, Gonzalez, & Balleine, 2004) could provide this. When the animals in Group INH received the extended discrimination, they were expected to learn not only A-X but also X-A inhibitory links. Being exposed to X

in testing, the operation of the inhibitory X-A link and an excitatory A-illness link in tandem would inhibit the activation in the representation of illness (Bennett et al., 1999; Espinet, Artigas, & Balleine, 2008). At the same time, in Group INH, the X-illness excitatory link counteracting the process of inhibitory sensory preconditioning would not be well established, since the discrimination training had been extended. A suggestion from the present study is, therefore, that the Espinet effect might be limited in the condition in which its first-order inhibitory conditioning is extensively trained.

In Experiment 3, we also found both a facilitation in Group EXC and retardation in Group INH in acquisition of the conditioned aversion to A. One would still expect that the representation-mediated X-illness excitatory link in Group EXC and X-illness inhibitory link in Group INH acquired during each of their A-LiCl pairings caused the pattern of results (i.e., protection from potentiation, Holland, 2006; representation-mediated potentiation, Holland, 1983). In the above-mentioned discussion, however, the formation of both links was not plausible. Instead, the group differences in rate of acquisition of the A aversion would reflect the difference in general associability of A. According to Mackintosh (1975), while associability of a CS will be high when the CS is the best available predictor of an outcome, its associability will be low when the CS is a poor predictor of the outcome. In Group EXC, A was trained as the best predictor of the occurrence of X. Consequently, A should have maintained high associability during the following A-LiCl pairings. On the contrary, in Group INH, A was trained as a signal for the absence of X, such that its associability should have been kept low during the A-LiCl pairings.

In the present study, we pointed out the amount of primary discrimination training as a possible factor determining whether pairing a conditioned inhibitor with LiCl causes a representation-mediated excitatory learning or an inhibitory sensory preconditioning (the Espinet effect). Of course, our study has some problems. For example, not only the summation test, but also a retardation test, is required for adequate assessment of conditioned inhibition; not the amount of discrimination training, but the other procedural differences between Experiments 2 and 3 could have produced the dramatic difference in the pattern of results. Nevertheless, we believe that it is worth to examine further whether and when a conditioned inhibitor is able to substitute for its outcome in a new excitatory learning about the outcome. Such studies might reveal, within a single experiment, the effect of extensiveness of discrimination training on subsequent devaluation of conditioned inhibitor.

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