Effects of extended context discrimination training and context extinction on transfer of context dependency of conditioned flavor aversion

Behavioural Processes 103 (2014) 218-227

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Authors: Yoshio Iguchi[a*], Kazuya Fukumoto[b], Kosuke Sawa[c], Kiyoshi Ishii[d*]

Affiliations: [a]*Department of Psychiatry & Neurobiology, School of Medicine, Kanazawa University, Japan*

[b]*Futuristic Environmental Simulation Center, Research Institute of Environmental Medicine, Nagoya University, Japan*

[c]*Department of Psychology, School of Human Sciences, Senshu University, Japan*

[d]*Department of Psychology, Graduate School of Environmental Studies, Nagoya University, Japan*

Running Head: TRANSFER OF CONTEXT DEPENDENCY

*Corresponding authors. E-mail address: yoshio.iguchi@nagoya-u.jp (Y. Iguchi); kishii@cure.ocn.ne.jp (K. Ishii)

Abstract

We trained rats in a context discrimination paradigm by pairing a sucrose solution with lithium chloride in one context (conditioning context) and simple exposure to the same fluid in a second (neutral) context to establish a context-dependent aversion to the conditioned fluid. We then investigated whether transfer of the context dependency to a test fluid (a sodium chloride solution) was affected by two post-discrimination training treatments, an extended context discrimination training, and non-reinforced exposure to the conditioning context (context extinction). We found that the context-dependent flavor aversion that had been specific to sucrose transferred to the test fluid after the extensive training (Experiment 1). Context extinction eliminated the transfer effect that had been observed immediately after the context discrimination training (Experiment 2). In addition, an aversion acquired by sucrose through a simple conditioning of sucrose-LiCl pairings did not generalize to the test fluid (Experiment 3). These results emphasize the importance of a Pavlovian excitatory association between the conditioning context and nausea as a primary source of transfer of the context dependency, rather than a generalization of aversion acquired by the conditioned fluid to the test fluid.

Highlights

1. A context-dependent aversion to a sucrose solution was established in rats by using a context discrimination training to investigate the characteristics of transfer of the context dependency.
2. The context dependency of the flavor aversion, having been specific to sucrose, transferred to a test fluid (NaCl) after an extended discrimination training.
3. The transfer effect, having been observed immediately after the context discrimination training, was eliminated by post-training non-reinforced exposures to the conditioning context (context extinction).
4. These results suggest a Pavlovian excitatory association between the conditioning context and nausea as a key factor of transfer of the context dependency of flavor aversion.

1. Introduction

In Pavlovian conditioning paradigms, most acquisition and expression of conditioned responses come under the influence of the experimental context in which these responses have been conditioned (e.g., Bouton & King, 1983; Bouton & Swartzentruber, 1986; Hall & Honey, 1990). In studies employing a flavored, ingestible stimulus (such as food or a solution) as well as signaling where such stimulus is presented (Shishimi & Nakajima, 2007) or potentiating consumption of the stimulus (Petrovich, Ross, Gallagher, & Holland, 2007), a conditioning context affects a preference for or aversion to the stimulus. For example, Archer, Sjoden, and Nilsson (1985) reported that an aversion to a saccharin solution, conditioned in a context by pairings of saccharin with an injection of lithium chloride (LiCl), did not appear in a distinct, test context (see also Bonardi, Honey, & Hall, 1990; Leon, Callejas-Aguilera, & Rosas, 2012). More recently, context discrimination training has been employed to investigate systematically the role of training contexts in which aversion is acquired to flavor stimulus. In context discrimination training, animals are given repeated pairings of a conditioned fluid with an LiCl injection in a conditioning context and simple exposures to the conditioned fluid in another (neutral) context. After establishment of the context discrimination, animals consume less of the conditioned fluid in the conditioning context than in the neutral context (e.g., Boakes, Westbrook, Elliott, & Swinbourne, 1997; Ishii, Iguchi, & Sawa, 2006; Lopez & Cantora, 2003; Loy, Alvarez, Rey, & Lopez, 1993; Murphy & Skinner, 2005; Nakajima, Kobayashi, & Imada, 1995; Puente, Cannon, Best, & Carrell, 1988; Skinner, Martin, Pridgar, & van der Kooy, 1994).

Currently, there are two explanations for the context dependency of flavor aversion learning. First, the conditioning context-nausea association account argues that during discrimination training, not only a conditioned fluid but also a conditioning context is associated with nausea via an excitatory link. According to this account, when the conditioned fluid is presented in the conditioning context at testing (after discrimination training), an aversion to the conditioned fluid is observed because of the combination of the associative strengths acquired by the conditioned fluid and conditioning context (Loy et al., 1993). Employing a blocking design, Lopez and Cantora (2003) demonstrated the associative strength acquired by a conditioning context. They first established a context-dependent sucrose aversion in rats through context discrimination training; animals then received a flavor aversion conditioning with a sodium chloride (NaCl) solution. Half of the animals (the blocking group) received this second conditioning in the original conditioning context, whereas the remaining animals (the control group) received the conditioning in the original neutral context. They found that the animals in the blocking group acquired a weaker NaCl aversion than those in the control group, suggesting that the conditioning context acquired a substantial associative strength with nausea during the discrimination training, and this association blocked acquisition of the conditioned aversion to NaCl (see also Kwok & Boakes, 2012; Symonds & Hall, 1997; Symonds, Hall, Lopez, Ramos, & Rodriguez, 1998; Willner, 1978).

The second explanation for the context dependency of a flavor aversion is that a conditioning context is not established as a conditioned excitor; rather, it acquires the function of occasion setting. According to the occasion setter account, a conditioning context positively modulates an association between a conditioned fluid and nausea by reducing the threshold for a representational activation of nausea, or by associating hierarchically with the conditioned fluid-nausea association (Boakes et al., 1997; Murphy & Skinner, 2005). Loy and Lopez (1999) demonstrated the validity of this explanation by establishing a biconditional context discrimination in rats. Animals received both repeated pairings of a vinegar solution with LiCl and simple exposures to a coffee solution in a context (Context A). After demonstrating a differentiated consumption between the two solutions in Context A, the role of two solutions was reversed in a second context (Context B); that is, animals received both coffee-LiCl pairings and simple exposures to vinegar in Context B. After the successive discrimination training, Loy and Lopez (1999) found specific suppressions in consumption of vinegar in Context A, and in consumption of coffee in Context B (for similar findings in conditioned flavor preference studies, see Dwyer & Quirk, 2008; Gonzalez, Garcia-Burgos, & Hall, 2012). In the biconditional discrimination, each of the contexts in itself cannot signal reinforcement or non-reinforcement of the flavor stimuli; it is therefore difficult to explain the established context-dependent behavior in terms of simple excitatory associations acquired by the training contexts (cf. Brandon & Wagner, 1998; Pearce, 2002).

To test the distinct predictions made by the two accounts, the effect of non-reinforced exposures to a conditioning context after establishing a context-dependent flavor aversion and transfer of the context dependency have been evaluated. For example, some studies demonstrated that a context dependency of a flavor aversion disappeared (Loy et al., 2003; Skinner et al., 1994) or attenuated (Nakajima et al., 1995) following exposures to the conditioning context without reinforcement but with drinking water that differs from the conditioned fluid. According to the conditioning context-nausea account, this “context extinction” is expected to reduce an excitatory associative strength between the conditioning context and nausea (or produce a new inhibitory link antagonistic to the excitatory association). Because the context-dependent aversion is partly supported by the excitatory association acquired by the conditioning context, the contextual control of aversion should decrease when the association is weakened. In contrast, the occasion setter account predicts that a context-dependent aversion should be intact even after context extinction. This is because it has been widely recognized that post-conditioning non-reinforced exposures to a stimulus do not attenuate its established role of occasion setting (e.g., Holland, 1989, 1992; Rescorla, 1986; Swartzentruber, 1995).

Interestingly, Murphy and Skinner (2005) succeeded in both the disruption of a context-dependent aversion by a context extinction with a water presentation and showing failure of the context extinction effect by a context extinction without the water presentation (see also Nakajima et al., 1995; Skinner et al., 1994). The authors argued that the role of a conditioning context as an occasion setter could be diminished only by the context extinction in the presence of an appropriate target of the occasion setter, in this case, drinking response, and concluded that their results were in favor of the occasion setter account. The validity of this explanation should be further tested in future studies. However, it is important to note that the associative property of conditioning context acquired during context discrimination training remains elusive because of the multiple effects of context extinction.

The second effect on which the two accounts have made distinct predictions is transfer of a context dependency of aversion to a second, untrained test fluid, which is examined in the present study. The occasion setter account cannot successfully predict transfer to test fluid, i.e., that trained animals would consume less of a test fluid in the conditioning context than in the neutral context. This is because, according to the account, a modulation function acquired by the conditioning context is usually specific to the conditioned fluid (e.g., Bonardi, 1989; Holland, 1983). In contrast, the context-nausea association account assumes that the associative strength acquired by the conditioning context is a key factor of context-dependent aversion; this account thus allows for successful prediction of transfer based on summation of the associative strengths acquired by the conditioning context and the strength of associations generalized from the conditioned fluid to the test fluid. However, the results of previous studies are mixed because they have reported both successful transfer (Boakes et al., 1997; Ishii et al., 2006; Loy et al., 1993) and failed transfer (Puente et al., 1988).

However, in the first place, whether the successful transfer is evident cannot by itself elucidate the associative property of a conditioning context (cf. Lopez & Cantora, 2003; Symonds & Hall, 1997; Symonds et al., 1998). Indeed, either hypothesis can explain both success and failure of transfer by post hoc assumptions regarding the degree of generalization from conditioned fluid to test fluid. The conditioning context-nausea association account typically predicts a success of transfer rather than a failure. However, if the stimulus generalization is weak, an available associative strength should not reach the threshold for suppression of consumption when the test fluid is presented in the conditioning context, resulting in a failure of transfer. In contrast, the occasion setter account usually predicts a failure of transfer rather than a success. However, if the stimulus generalization between the conditioned and test fluids is strong, the conditioning context should exert its modulation ability on the test fluid, resulting in a successful transfer (Bonardi & Ward-Robinson, 2001).

At present, as is the case with context extinction, only limited conclusions can be drawn directly from success and failure of transfer in clarifying the acquired function of a conditioning context. This difficulty might be attributable in part to lack of knowledge about the factors influencing success and failure of transfer. Therefore, in the present study, we sought to reveal the basic characteristics of transfer by examining the effects of extensive discrimination training (Experiment 1) and context extinction (Experiment 2): According to the context-nausea association account, the two treatments were expected to affect success and failure of transfer, as explained in detail below. However, a stimulus generalization between a conditioned fluid and a test fluid would confound the transfer effect. In our experiments investigating the effects of post-context discrimination treatments, we employed the fluids between which the stimulus generalization would be unexpected: They are a sucrose solution as conditioned fluid and an NaCl solution as test fluid. Although such generalization has not been found in our laboratory, some authors have pointed out the difficulty in excluding this stimulus generalization effects completely from interpreting data (Lopez & Cantora, 2003; Symonds & Hall, 1997; Symonds et al., 1998). Consequently, we conducted an additional experiment (Experiment 3) to test whether an aversion to the conditioned fluid may have generalized to the test fluid in either Experiment 1 or 2.

2. Experiment 1

Ishii et al. (2006) noted, as an important determinant of success and failure of transfer of the context dependency, the difference between conditioned fluid and a fluid presented in animals' home cage as daily fluid supply in the course of discrimination training phase. In their study, rats were given a context discrimination training with tap water as conditioned fluid (i.e., tap water-LiCl pairings in a conditioning context and simple exposures to tap water in a neutral context). During the training, one group of animals received the same tap water in their home cage, whereas another group of animals received a more distinct fluid, an NaCl solution, in the home cage. Results indicated that although a context-dependent aversion to tap water was established for both groups, transfer of the context dependency to a test fluid was shown only for the second group (that received NaCl in the home cage).

In the present experiment, we sought to replicate, in part, the findings of Ishii et al. (2006) by employing a sucrose solution as conditioned fluid and an NaCl solution as test fluid: A group of rats (Group DN) received three cycles of discrimination training, and each cycle included one sucrose-LiCl pairing in the conditioning context and two simple exposures to sucrose in the neutral context. In addition, the animals were presented with the sucrose solution in their home cage during the context discrimination training phase. We anticipated that a context-dependent aversion being specific to sucrose would be established through the training, that is, the established context dependency of aversion would not transfer to NaCl.

The second aim of Experiment 1 was to test whether the predicted loss of transfer would recover following extended context discrimination training (Group DE) because the conditioning context-nausea association account predicts the restoration of transfer by the extended training. As mentioned above, this account argues that a context-dependent flavor aversion is expressed as a result of combination of the associative strengths acquired by the conditioned fluid and conditioning context (Loy et al., 1993). From this viewpoint, a context-dependent aversion being specific to the conditioned fluid is a consequence of the fact that neither the conditioned fluid nor the conditioning context has acquired a substantial associative strength with nausea (Ishii et al., 2006). In this case, only if both of them are presented together, the sum of associative strength acquired to each element can exceed the threshold to reveal the apparent aversion. On the other hand, when discrimination training is extended beyond the point at which fluid-specific context dependency develops, the strength of the association between the conditioning context and nausea may increase sufficiently to reveal successful transfer of this dependency to the test fluid. The design of Experiment 1 is shown in Table 1.

---Insert Table 1 about here--

2.1. Methods

2.1.1. Subjects

Sixteen male Wistar rats, approximately 70 days of age, with a mean free-feeding weight of 260 g (range, 232–280 g) at the start of the experiment, were used. The animals were born and reared in the colony room of the Department of Psychology, Nagoya University. Throughout the experiment, they were housed individually in opaque polycarbonate cages (home cage, 31 × 36 × 18 cm). The floor of each cage was covered with wood chips, and the ceiling was made of stainless-steel grids. The colony room containing the home cages was illuminated daily from 08:00 to 20:00. The temperature and humidity of the room were maintained at 22°C and 50%, respectively. Animals had free access to food in their home cages but were maintained on a water deprivation regime, the details of which are described below. All procedures were approved by the Institutional Animal Use and Care Committee at Nagoya University and were conducted in accordance with the guidelines of the Japanese Society for Animal Psychology.

2.1.2. Fluids and contexts

The conditioned and test fluids were a 3% (wt/vol) sucrose solution and a 0.6% (wt/vol) NaCl solution, respectively. The unconditioned stimulus was an intraperitoneal injection with 10 ml/kg of a 0.15 M LiCl. In the present experiment, we defined two distinct contexts, labeled A and B. Context A consisted of transparent acrylic cages (27 × 43 × 20 cm, with a stainless-steel grid roof) placed in an experimental room outside our laboratory; the room was dimly illuminated (approximately 0.5 lx), and a background white noise (approximately 75 dB) was present in it. The floor of each cage was covered with wood chips, and a stainless-steel spout, connected to a graduated cylinder, was inserted into the center of the ceiling. Context B was a set of opaque polycarbonate cages (31 × 36 × 18 cm), with plain wooden board ceilings, placed in a relatively well-lit experimental room (approximately 55 lx). The floor of each cage was covered with commercial paper litter, and a spout, identical to that used in Context A, was inserted into the center of one wall. In both Contexts A and B, the temperature and humidity were maintained at 22°C and 50%, respectively.

2.1.3. Procedure

Animals were randomly assigned to either the discrimination extended (DE) group or the discrimination non-extended (DN) group. To test all subjects at the same time and on the same day (after the discrimination training), Group DE began the training procedure eight days before Group DN.

2.1.3.1. Acclimation.

Subjects were on a schedule that restricted their access to water for four days; on each day, they could consume tap water in two 10-min sessions starting at 12:00 and 17:00 in their home cage. On the following six days, they were trained to drink water in the training contexts. On the first, third, and fifth days of this phase, animals were placed in Context A at 12:00. After waiting for 10 min, they were then presented with water for 10 min. At 17:00 on these days, they were placed in Context B and, as in Context A, waited for 10 min and were then presented with water for 10 min. On the second, fourth, and sixth days, animals were placed in Context B at 12:00 and in Context A at 17:00, and were given water in the same manner.

2.1.3.2. Context discrimination training.

During the following 12 days, animals received three, four-day cycles of context discrimination training with the sucrose solution. An outline of the training procedure is shown in Table 2. There was a conditioning session on the first day of each cycle: At 12:00 on the day, each animal was placed in the conditioning context (half the animals in Context A and the remaining animals in Context B). After waiting for 10 min, they were given the sucrose solution for 10 min. When the spout was removed, they were immediately injected with LiCl before being returned to their home cage. At 12:00 on the second day of each cycle, they were presented with the sucrose solution for 10 min in the home cage. On the third and fourth days of each cycle, they were presented with two non-conditioning sessions: During these sessions, each animal was placed in the neutral context (Context B for the animals conditioned in Context A; Context A for those conditioned in Context B) at 12:00. After a 10-min waiting period, the conditioned fluid was presented for 10 min. No LiCl injection was given after these sessions. The animals in Group DE received two additional cycles of the training, whereas those in Group DN did not receive the extended training. Throughout the context discrimination training phase, at 17:00 on each day, all animals were presented with the sucrose solution for 10 min in their home cage.

---Insert Table 2 about here--

2.1.3.3. Transfer test

For two days following the context discrimination training phase, consumption of the NaCl solution was measured in both the conditioning and neutral contexts. In each group, half the animals were tested in the conditioning context first, followed by testing in the neutral context on the following day. The order of testing was reversed for the remaining animals. In each test session that started at 12:00, after waiting for 10 min in the training context, the animals were given the test fluid for 10 min. At 17:00 on these days, they were given tap water for 10 min in the home cage.

2.1.4. Data analysis

Fluid consumption was measured to the nearest 0.2 ml throughout the experiment. The reliability of results was assessed against a Type I error rate of .05 in the statistical tests. We conducted analyses of variance (ANOVAs), analyses of simple main effects with pooled error terms, and post-hoc multiple comparisons using Ryan’s procedure (Ryan, 1960).

2.2. Results

2.2.1. Context discrimination training

Since the context type, A or B, did not affect the observed level of fluid consumption for both groups, this context factor was collapsed for the following analyses. As shown in Figure 1, in the first three cycles, the animals in both groups (DN and DE) showed a similar context discrimination performance. A 2 (Group) × 3 (Cycle) × 3 (Session within cycle; one conditioning session and two non-conditioning sessions) ANOVA revealed significant main effects of Cycle and Session, Fs(2,28) = 45.75, 42.83, respectively, and a significant Cycle × Session interaction, $F(4, 56) = 46.08$. None of the Group effects (main effect or interactions) reached the level of significance (all Fs < 1).

To more closely examine the significant Cycle × Session interaction, we conducted separate analyses for each cycle using the pooled error term ($MSE = 3.08$). During the first cycle ($F[2, 84] = 106.79$), the sucrose consumption was greater in the conditioning session (C-1) than in either of the non-conditioning sessions, E-1 or E-2, ts(84) = 14.61, 7.56, respectively. Consumption in E-1 was less than in E-2, $t(84) = 7.05$. During the second cycle ($F[2, 84] = 14.04$), consumption in C-2 was greater than that in E-3, $t(84) = 4.23$, but did not differ from that in E-4, $t(84) = 0.65$. There was also greater consumption in E-4 than in E-3, $t(84) = 4.88$. During the third cycle ($F[2, 28] = 12.90$), consumption in C-3 was less than that in E-6, $t(84) = 4.98$, but did not differ from that in E-5, $t(84) = 1.61$. Consumption in E-5 was less than in E-6, $t(84) = 3.37$.

During the extended discrimination training (i.e., the fourth and fifth cycles of Group DE), the animals continued to show evidence of the context-dependent sucrose aversion and a decrease in consumption in the conditioning context. A 5 (Cycle) × 3 (Session) ANOVA on the data from Group DE revealed significant main effects of Cycle, $F(4, 28) = 20.06$, and Session,

$F(2, 14) = 9.87$, along with a significant Cycle × Session interaction, $F(8, 56) = 34.84$. To further examine the significant interaction, we conducted separate analyses for each session (one conditioning and two non-conditioning) using the pooled error term ($MSE = 3.12$). A simple main effect of Cycle reached significance for the conditioning session, $F(4, 84) = 82.28$. Consumption in both C-4 and C-5, which did not differ from each other, $t(84) = 0.65$, was less than that in C-1, C-2, and C-3, $ts(84) > 3.99$. There was also a significant simple main effect of Cycle for the first non-conditioning session, $F(4, 84) = 2.96$, such that consumption in E-9 was greater than that in E-1, $t(84) = 3.31$. For the second non-conditioning session, no simple main effect of Cycle reached significance, $F(4, 84) = 0.94$.

We then conducted separate analyses for the fourth and fifth cycles again using the pooled error term ($MSE = 4.26$). During the fourth cycle, consumption in C-4 was less than that in both E-7 and E-8, $ts(84) = 4.56$, 7.22, respectively, and consumption in E-7 was less than that in E-8, $t(84) = 42.67$. During the fifth cycle, consumption in C-5 was less than that in both E-9 and E-10, $ts(84) = 6.86$, 7.80, respectively, which did not differ from each other, $t(84) = 0.95$.

---Insert Fig. 1 about here--

2.2.2. Transfer test

Figure 2 shows the results of testing with the NaCl solution. The animals in Group DN appeared to consume similar amounts of the test fluid in both contexts, indicating the absence of transfer of the context-dependent flavor aversion. However, the animals in Group DE appeared to drink less of the test fluid in the conditioning context than in the neutral context: The context dependency of the sucrose aversion seemed to successfully transfer to the test fluid after the extended context discrimination training. This observation was confirmed by a 2 (Group) × 2 (Context) ANOVA: There were significant main effects of Group, $Fs(1, 14) = 9.95$, and Context, $Fs(1, 14) = 58.26$, along with a significant interaction between these factors, $F(1, 14) = 30.78$. The simple main effect of Context was significant for Group DE, $F(1, 14) = 86.87$, but not for Group DN, $F(1, 14) = 2.17$. Between-groups comparisons led to a similar result. In the conditioning context, the animals in Group DE consumed significantly less NaCl than those in Group DN, $F(1, 28) = 29.90$. However, there was no significant group difference in the neutral context, $F(1, 28) < 1$.

---Insert Fig. 2 about here---

2.3. Discussion

In the context discrimination training of Experiment 1, we employed the sucrose solution both as conditioned fluid and as daily fluid supply in the home cage. By the end of the third cycle of the training, the animals drank less of the conditioned fluid in the conditioning context than in the neutral context (Figure 1), indicating establishment of a context-dependent aversion. However, the animals in Group DN (that received the transfer test immediately after the three cycles of discrimination training) did not show a differential NaCl consumption between the conditioning and neutral contexts (Figure 2). Ishii et al. (2006) reported that a context dependency of a tap water aversion failed to transfer to a test fluid when the animals were exposed to the same conditioned fluid in the home cage during the discrimination training. The present results were congruent with the pattern of results found by Ishii et al. (2006). As mentioned above, the occasion setter account usually predicts a failure of transfer such that this finding was also consistent with the idea that the conditioning context had acquired an occasion-setting function.

Moreover, the animals in Group DE that received the discrimination training that was extended to five cycles showed an extra suppression of the conditioned fluid consumption in the conditioning context (Figure 1), suggesting that a stronger contextual control was learned through extended training. Interestingly, the animals in Group DE showed a conditioning context-specific suppression of NaCl in the transfer test (Figure 2): They exhibited a restoration of the transfer effect. The occasion setter account seems to have difficulty in explaining the process in which the extended training restored the transfer effect without putting the case that the acquired aversion to the conditioned fluid had generalized to the test fluid during the extended training.

According to Ishii et al. (2006), non-reinforced exposures to the conditioned fluid outside the training contexts during discrimination training would result in (1) a reduction in the associative strength of the excitatory link between the conditioned fluid and nausea and (2) a retardation in the formation of the excitatory link between the conditioning context and nausea. The latter consequence was anticipated because of a reduction in potentiation by the conditioned fluid due to the process of (1) (e.g., Best, Brown, & Sowell, 1984; Mitchell & Heyes, 1996).

Following Ishii et al. (2006), a possible explanation as to why extended training produced recovery of transfer to the test fluid is as follows: In Group DN, the associative strengths acquired by each of the conditioned fluid and conditioning context would not be so substantial. Accordingly, a reduction in consumption was not observed unless the conditioned fluid was presented in the conditioning context (Figure 1), where the two associative strengths would be combined. However, the extended discrimination training would increase the strength of the conditioning context-nausea association by the potentiation effect. Consequently, the associative strength acquired by the conditioning context alone should be sufficient to suppress consumption when the test fluid was presented in the conditioning context (Figure 2), even if little generalization would be expected between the conditioned and test fluids.

3. Experiment 2

Previous studies have examined the effects of context extinction on the once-established context-dependent flavor aversion to a conditioned fluid (Loy et al., 1993; Murphy & Skinner, 2005; Nakajima et al., 1995; Skinner et al., 1994). However, few studies have entertained whether context extinction has impacts on *transfer* of the context dependency. To the best of our knowledge, one exception is a study by Boakes et al. (1997): In the experiment employing a sucrose solution as the conditioned fluid, the authors examined the effects of the nonreinforcement sessions, in which tap water was presented alone, inserted sporadically into the discrimination training. They demonstrated a successful transfer for the animals who had not received such context extinction by showing a context-dependent aversion to both the conditioned fluid and test fluid (an NaCl solution). In contrast, for the animals that had experienced the context extinction sessions, although the context-dependent sucrose aversion was retained, its transfer to NaCl was found to be eliminated.

In Experiment 2, we employed a three-cycle context discrimination training, during which animals were presented with, in their home cage, a fluid (tap water) that was distinct from the conditioned fluid (sucrose). First, we anticipated a reversed pattern of results of Experiment 1: An established context-dependent sucrose aversion was expected to readily transfer to NaCl without any post-discrimination training treatments. Then, we examined whether the context-dependent sucrose aversion and its predicted transfer to NaCl were affected by context extinction. The design of Experiment 2 is shown in Table 1.

Several parameters employed in the present experiment differed from those of Boakes et al. (1997). For example, we did not incorporate their methods of timing of context extinction and of water presentation in a context extinction session. In the present experiment, the context extinction sessions were conducted after completion of the context discrimination training, which is the method typically employed in previous studies investigating the effects of context extinction on the context-dependent aversion to conditioned fluid. In addition, during the context extinction phase, the conditioning context was presented in the absence of fluids or drinking responses. Based on the report by Murphy and Skinner (2005), we expected that the context-dependent sucrose aversion, once established, would be quite immune to this type of context extinction (See Section 1 “Introduction”).

Next, we examined the effects of context extinction on transfer of the context dependency. It was anticipated that the predicted successful transfer would disappear after context extinction. This is because the conditioning context-nausea association account predicts that the associative strength between the conditioning context and nausea, a key factor of the context-dependent sucrose aversion and its transfer to NaCl suggested in Experiment 1, should be reduced or extinguished by the context extinction.

3.1. Methods

3.1.1. Subjects, fluids, and contexts

Sixteen male Wistar rats, approximately 70 days of age and with a mean free-feeding weight of 312 g (range, 292–336 g) at the beginning of the experiment, were used. The animals were maintained as in Experiment 1. The conditioned fluid, test fluid, and unconditioned stimulus were identical to those used in Experiment 1. The two contexts, A and B, were also the same as in Experiment 1.

3.1.2. Procedure

3.1.2.1. Acclimation and context discrimination training.

Acclimation training was conducted in the same manner as in Experiment 1. Animals were trained to drink water steadily in both the conditioning and neutral contexts. They then received three 4-day cycles of context discrimination training with the sucrose solution. The context discrimination training procedure was also identical to Experiment 1 with the exception that tap water was given to animals in their home cage instead of sucrose. The outline of procedure for the context discrimination training is shown in Table 2.

3.1.2.2. Context extinction.

After completion of the context discrimination training, animals were randomly assigned to either the context extinction (CE) group or the context non-extinction (CN) group. The animals in Group CE received five daily exposure sessions to the conditioning context. On these days, each animal was placed in its conditioning context for 30 min starting at 12:00, without any stimulus presentations. The animals in Group CN were kept in their home cage during the period. Immediately after the context extinction treatment, the animals in Group CE were returned to their home cage. Then, all animals were given tap water for 10 min.

3.1.2.3. Testing.

Consumptions of the novel NaCl and conditioned sucrose solutions were monitored in both the conditioning and neutral contexts. All animals received 10-min presentations of NaCl (starting at 12:00) on the first two days, and sucrose on the following two days. Half the animals in each group were tested in the conditioning context in the first session of each fluid presentation and in the neutral context in the second session. The order of the context testing was reversed for the remaining animals. In each test session, there was an initial 10-min waiting period followed by the 10-min presentation of the test fluid. Throughout the context extinction and testing, animals were given tap water for 10 min every day at 17:00 in their home cage.

3.2. Results

3.2.1. Context discrimination training

The context type (A or B) did not affect the observed level of fluid consumption for each group; therefore, this factor was collapsed for the following analyses. As shown in Figure 3, the animals in both groups steadily acquired a context-dependent sucrose aversion, without any clear group differences. A 2 (Group) × 3 (Cycle) × 3 (Session in cycle) ANOVA revealed significant main effects of Cycle and Session, $Fs(2, 28) = 7.84$, 23.54, respectively, and a significant Cycle × Session interaction, $F(4, 56) = 55.04$. Neither the main effect of Group nor interactions with the Group factor reached statistical significance ($Fs < 1.89$).

To unpack the significant interaction, we conducted separate analyses for each cycle using the pooled error term ($MSE = 4.95$). During the first cycle ($F[2, 84] = 54.94$), the sucrose consumption was greater in the conditioning session (C-1) than in either of the subsequent non-conditioning sessions, E-1 and E-2, $ts(84) = 10.00$, 2.28, respectively, and consumption was less in E-1 than in E-2, $t(84) = 7.73$. During the second cycle ($F[2, 84] = 9.55$), consumption in C-2 was greater than that in E-3, $t(84) = 2.48$, but did not differ from that in E-4, $t(84) = 1.87$. There was also greater consumption in E-4 than in E-3, $t(84) = 4.36$. During the third cycle ($F[2, 84] = 62.38$), consumption in C-3 was less than that in both E-5 and E-6, $ts(84) = 9.43$, 9.90, respectively, which did not differ from each other, $t(84) = 0.48$. The change in consumption across cycles indicated that a context-dependent aversion to the sucrose solution was established in both groups by the end of the third cycle.

---Insert Fig. 3 about here--

3.2.2. Testing

Figure 4A shows the results of the transfer test with NaCl. The animals in Group CN appeared to consume less of the test fluid in the conditioning context than in the neutral context: The context dependency of the sucrose aversion seemed to successfully transfer to the test fluid in this group. In contrast, the animals in Group CE appeared to consume similar amounts of the test fluid in the two contexts, indicating a failure of transfer. This observation was confirmed by a 2 (Group) × 2 (Context) ANOVA. There was a significant main effect of Context, *F*s(1, 14) = 55.85, along with a significant interaction between these factors, *F*s(1, 14) = 41.16. The simple main effect of Context was significant for Group CN, *F*(1, 14) = 96.45, but not for Group CE, *F*(1, 14) = 0.56. Between-groups comparisons also showed that in the conditioning context, NaCl consumption was less in Group CN than in Group CE, *F*(1, 28) = 30.24, whereas in the neutral context, it was greater for Group CN than for Group CE, *F*(1, 28) = 4.76.

Fig. 4B shows the results of the sucrose test. The animals in both groups seemed to drink less of sucrose in the conditioning context than in the neutral context, indicating the absence of any disruptive effects of context extinction on the context dependency of the sucrose aversion. In support of this observation, a 2 (Group) × 2 (Context) ANOVA revealed only a significant main effect of Context, *F*(1, 14) = 69.80.

---Insert Fig. 4 about here---

3.3. Discussion

In Experiment 2, the animals were presented with tap water in their home cage during the three-cycle context discrimination training. As a result, the established context dependency of the sucrose aversion was found to readily transfer to the NaCl solution (Figure 4A), in line with the pattern of results found by Ishii et al. (2006). This finding contrasts with that obtained in Experiment 1, where although the subjects were given the conditioned fluid in their home cages, they showed little aversion to the test fluid even in the conditioned context (Figure 2). This contrast seems to support the hypothesis mentioned above: Briefly, when the animals were not exposed to the conditioned fluid outside the training contexts, the conditioned fluid was likely to acquire substantial associative strengths by the end of the discrimination training and thus would potentiate the associative strength between the conditioning context and nausea. Consequently, the associative strength of the conditioning context alone would be sufficient to suppress consumption not only when the conditioned fluid was presented in the conditioning context (Figure 3 & Figure 4B) but also when the test fluid was presented in the conditioning context (Figure 4A).

In the present experiment, context extinction after the discrimination training did not affect the context-dependent sucrose aversion (Figure 4B, Group CE). Because our context extinction did not include any presentations of fluids or drinking responses in the conditioning context, the pattern of results was consistent with the finding by Murphy and Skinner (2005)—the context extinction in the absence of fluid presentations did not disrupt an established context-dependent flavor aversion (see also Nakajima et al., 1995 and Boakes et al., 1997). It should be noted that this aspect of the present results appeared consistent with the occasion setter account. However, we also found a failure of transfer after context extinction (Figure 4A, Group CE) (cf. Boakes et al., 1997). From the perspective of the occasion setter account, it would be difficult to explain unequivocally the process in which the transfer effect disappeared over the course of the context extinction treatment, even if the acquired aversion to the conditioned fluid would generalize to the test fluid.

The context-nausea association account, on the other hand, can predict that the strength of the conditioning context-nausea association would be diminished for the animals in Group CE. Consequently, a possible explanation is that the Group CE animals' fluid consumption was successfully suppressed only when the conditioned fluid, which had been expected to acquire substantial associative strengths by the end of the discrimination training, was presented in the conditioning context (Figure 4B), and the two associative strengths would be combined. However, the failure of suppression in consumption was obvious when the test fluid that had no associative strength with nausea was presented in the conditioning context (Figure 4A), and the available associative strength should not reach the threshold for suppression of consumption.

In Experiment 2, we also found that the NaCl consumption in the neutral context was greater in Group CN than in Group CE (Figure 4A). We do not have data that directly address the source of the group difference. However, because the animals in Group CN consumed less NaCl than those in Group CE in the conditioning context, the stronger aversion to the conditioning context might have caused the animals in Group CN to perceive the neutral context as "safer."

4. Experiment 3

The aim of the experiment was to test whether the conditioned aversion to sucrose might have generalized to the test fluid (NaCl) in Experiments 1 and 2 and thus have influenced their results. Preliminary experiments conducted in our laboratory have shown that rats (Wistar) have less difficulty in discriminating the NaCl solution from the sucrose solution; that is, the generalization between the two fluids was minimal and fell below measurable limits. Nevertheless, we sought to demonstrate the absence of such generalization by using a procedure similar to that used in Experiments 1 and 2. To test the generalization under the condition being free from all the possible confounding factors, we chose a home-cage test, whereby some procedures such as acclimation or drinking training in the test context could be excluded. As the animals in Group DE in Experiment 2 received five cycles of context discrimination training, in the present experiment, we evaluated the generalization after five conditioning trials.

4.1. Method

4.1.1. Subjects, fluids, and contexts

Sixteen male Wistar rats, approximately 70 days of age and with a mean free-feeding weight of 312 g (range, 292–336 g) at the beginning of the experiment, were used. The animals were maintained as in Experiment 1. The conditioned fluid, test fluid, and unconditioned stimulus were identical to those used in Experiment 1. The two contexts, A and B, were also the same as in the previous experiments.

4.1.2. Procedure

4.1.2.1. Acclimation.

For the first four days, the animals were maintained on a schedule that restricted their water access as in Experiment 1. On the following two days, they were trained to drink water in either Context A or B. At 12:00 on each day, half of the animals were placed in Context A as the conditioning context, while the remaining animals were placed in Context B as their conditioning context. After an initial 10-min waiting period, animals were presented with water for 10 min and were then placed back in their home cage.

4.1.2.2. Conditioning.

The animals were randomly assigned to either the experimental (E) group or the control (C) group; the first conditioning session then took place on the following day. Each animal was placed in its conditioning context at 12:00. After a 10-min waiting period, they were presented with sucrose for 10 min. Upon removal of the spout, the animals in Group E were injected with LiCl before being returned to their home cage. Those in Group C were injected with saline (0.9% NaCl solution) instead of LiCl. For the following three days (recovery days), the subjects received no explicit experimental treatments, but they had access to water for 10 min, at 12:00, in their home cage. Four more conditioning sessions took place on the fifth, ninth, thirteenth, and seventeenth days of the conditioning phase, with a three-day recovery interval between the conditioning days.

4.1.2.3. Stimulus generalization test.

At 12:00 on the following day of the conditioning phase, subjects were presented with NaCl in their home cage for 10 min. The test fluid was presented with a spout identical to that employed during conditioning. On the following day, consumption of NaCl was monitored in the conditioning context. Throughout acclimation, conditioning, and testing, the animals were given 10-min access to tap water in their home cage at 17:00 each day.

4.2. Results and discussion

4.2.1. Conditioning

As shown in Figure 5A, the rats in Group E quickly acquired an aversion to the sucrose solution during the five conditioning sessions. With the exception of the first session, the animals in Group E appeared to consume less sucrose than those in Group C. The animals in Group C did not show any decrease in consumption during the phase. A 2 (Group) × 5 (Session) ANOVA showed significant main effects of Group, $F(1, 14) = 344.98$, and Session, $F(4, 56) = 20.58$, along with the significant Group × Session interaction, $F(4, 56) = 33.82$. The simple main effects of Group were significant from the second to the last conditioning sessions, Fs(1, 70) = 139.39, 189.22, 183.12, 187.17, respectively, but not for the first session, $F(1, 70) = 2.37$. A significant simple main effect of Session was observed for Group E, $F(4, 56) = 53.25$, but not for Group C, $F(4, 56) = 1.15$.

4.2.2. Stimulus generalization test

Figure 5B shows the results of the test sessions. While there seemed to be no group difference in the NaCl consumption in the home cage, the rats in Group E appeared to consume less test fluid than those in Group C in the conditioning context. A 2 (Group) × 2 (Session) ANOVA revealed a significant main effect of Group, $F(1, 14) = 20.70$, and a significant interaction between Group and Session, $F(1, 14) = 20.70$. The significant interaction indicated that although no group difference was found in the home cage consumption, $F(1, 28) = 0.25$, the animals in Group E consumed less test fluid than those in Group C in the conditioning context, $F(1, 28) = 41.15$. Within-group comparisons provided similar results. Although the animals in Group E consumed significantly less NaCl in the conditioning context than in the home cage, $F(1, 14) = 20.09$, those in Group C consumed similar quantities of the test fluid in the two contexts, $F(1, 14) = 3.81$.

---Insert Fig. 5 about here---

We observed, in Experiment 3, the absence of a significant group difference in consumption of the test fluid in the home cage. That is, the acquired sucrose aversion did not generalize to NaCl after five sucrose-LiCl pairings. Moreover, the significant group difference in the test fluid consumption in the conditioning context suggested that the conditioning context, as well as the conditioned fluid, would become associated with nausea.

5. General discussion

In the present study, we established a context-dependent sucrose aversion in rats through a context discrimination training. Then, the effects of two post-context discrimination training treatments on transfer of the context dependency to a test fluid, NaCl solution, were entertained. Experiment 1 examined the effects of an extensive discrimination training, and Experiment 2 examined those of context extinction, or non-reinforced exposures to the conditioning context after discrimination training. In addition, Experiment 3 confirmed that the conditioned aversion acquired to the sucrose solution did not generalize to the NaCl solution after five non-discriminative pairings of sucrose with LiCl. This finding would reduce the complexity in explanation for the transfer effects observed in Experiments 1 and 2: Under such condition, basically, one cannot access the occasion setter account in predicting a successful transfer.

The animals in Group DN of Experiment 1 received three cycles of discrimination training, as did all animals in Experiment 2. Each cycle included a pairing of the conditioned fluid with LiCl in the conditioning context and two simple exposures to the conditioned fluid in the neutral context. Subsequently, a context dependency of sucrose aversion did not transfer to NaCl in Experiment 1 (Figure 2, Group DN), in which the same sucrose was given to the animals as the daily supply of fluid in their home cage during the discrimination training phase. However, a successful transfer was observed in Experiment 2 (Fig 4A, Group CN), in which tap water was given to the animals as the daily fluid supply in their home cage. Employing tap water as conditioned fluid, Ishii et al. (2006) found that there was a failure of transfer to another fluid (a saccharin solution) in the animals presented with the same water in their home cage during the discrimination training, whereas a successful transfer to the test fluid occurred in the animals presented with a different fluid (NaCl) in the home cage. Thus, although one should be cautious when comparing results across experiments, the present pattern of results replicated the findings of Ishii et al. (2006) by using a sucrose solution as conditioned fluid, suggesting that success and failure of transfer of a context dependency of flavor aversion depend on whether the conditioned fluid had been presented (without reinforcement) outside both the conditioning and neutral contexts.

In Experiment 1, we gave the rats in Group DE an extensive context discrimination training, three cycles of the discrimination training and two additional cycles, and then tested whether the context dependency of the conditioned sucrose aversion transferred to NaCl. After the extended discrimination training, the context dependency was observed to transfer to the test fluid (Figure 2, Group DE); these findings then can be understood within the framework of the conditioning context-nausea association account as described in the discussion section of Experiment 1 (Section *2.3*). In contrast, the occasion setter account does not seem to provide a clear explanation regarding why the successful transfer was observed only after the extended discrimination training.

In Experiment 2, we examined whether the context dependency and its transfer were affected by context extinction. After the context extinction sessions, the context-dependent sucrose aversion was found to be perfectly preserved (Figure 4B, Group CE). This type of finding has been presented as a support for the occasion setter account (Boakes e al., 1997; Murphy & Skinner, 2005) and, at the same time, as evidence against the context-nausea association account. This is because the context-nausea association account predicts a reduction in associative strength between the conditioning context and nausea through the context extinction treatment, and then, a loss (or attenuation) of contextual control over aversion to the conditioned fluid. However, as described in the discussion section of Experiment 2 (Section *3.3*), this aspect of the results of Experiment 2 can also be understood within the framework of the conditioning context-nausea association account.

Interestingly, in Experiment 2, we found that the successful transfer (Figure 4A, Group CN) disappeared after the context extinction (Figure 4A, Group CE). This finding does not appear consistent with the occasion setter account, because this viewpoint argues that presenting the conditioning context alone does not allow for alterations in its ability to modulate conditioned responses (e.g., Holland, 1989; 1992; Rescorla, 1986; Swartzentruber, 1995). Regarding this point, we mentioned in the discussion section of Experiment 2 (Section *3.3*) that the conditioning context-nausea association account can provide a clear explanation of the findings.

We suggest that the conditioning context-nausea association account is sufficient to explain the present findings. Nevertheless, this does not exclude the possibility that the training contexts would have acquired the function of occasion setting. In reviewing the literature concerning previous theoretical conflict between the two accounts, some authors have concluded that the two associative roles of a conditioning context, a conditioned excitor and occasion setter, should not be considered as mutually exclusive (e.g., Balaz, Capra, Hartl, & Miller, 1981; Gonzalez, Garcia-Burgos, & Hall, 2012). Indeed, it has been reported that a discrete cue can acquire the function of a conditioned excitor and occasion setter, simultaneously, and their relative contributions in controlling learned behavior are modulated according to a temporal parameter (Urcelay & Miller, 2010). This is of importance because it might be implied that some parameters employed in our context discrimination training favored the conditioning context with a conditioned excitor to nausea, and at the same time, did not provide a suitable condition for the training contexts to acquire the function of occasion setting. In future studies exploring determinants for the relative contribution of the two mechanisms, monitoring a context-dependent aversion to a conditioned fluid alone might not be expected to provide the answers to the questions. Rather, studying the factors affecting the success and failure of transfer to a test fluid, such as extended discrimination training and context extinction, should provide understanding about the processes underlying context-dependent learned behaviors.

In addition, a brand-new theoretical axis might be needed to explain the associative processes underlying context-dependent flavor aversion. This is suggested by our present findings that cannot be adequately explained by either of the current theories: In Experiment 2, the context-dependent aversion to the conditioned fluid was highly immune, but its transfer to the test fluid was vulnerable, to context extinction. The results are reminiscent of Murphy and Skinner’s (2005) findings that although context extinction without water presentation did not affect a context-dependent aversion to their conditioned fluid, it did disrupt an avoidance of the conditioning context, which had been evident prior to context extinction. This similarity in the pattern of results seems to imply a common process underlying transfer of an established context-dependent aversion and avoidance of a conditioning context. In this connection, according to Parker (2003), a flavor aversion that is reflected in orofacial expressions of disgust and a flavor avoidance that is reflected in a reduction in consumption are simultaneously acquired to a flavor stimulus that has been paired with nausea. This analysis suggests the possibility that a successful transfer of a context dependency of flavor aversion, i.e., suppression in a test fluid consumption in the conditioning context, might reflect avoidant inhibition of the fluid consumption when the animals are exposed to the conditioning context, rather than aversion to the test fluid. Future studies should test this hypothesis by comparing orofacial expressions of rats in response to test fluid in both the conditioning and neural contexts after establishment of a context-dependent flavor aversion.

Acknowledgements

Support for this research was provided by Japanese Ministry of Education, Culture, Sports, and Technology, Grant-in-Aids for Scientific Research (KAKENHI) #15530469.

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Table 1

Designs of experiments

Group	Discrimination training	Post-discrimination treatment	Test 1 (transfer test)	Test 2 (Sucrose test)
Experiment 1				
DN	CC: Suc → LiCl NC: Suc HC: Suc	--	CC: NaCl NC: NaCl	--
DE	CC: Suc → LiCl NC: Suc HC: Suc	CC: Suc → LiCl NC: Suc (Extended discrimination training) HC: Suc	CC: NaCl NC: NaCl	--
Experiment 2				
CN	CC: Suc → LiCl NC: Suc HC: Water	HC: Water	CC: NaCl NC: NaCl	CC: Suc NC: Suc
CE	CC: Suc → LiCl NC: Suc HC: Water	CC: (Context extinction) HC: Water	CC: NaCl NC: NaCl	CC: Suc NC: Suc

Note. Suc = sucrose (conditioned fluid); NaCl = test fluid; CC = conditioning context; NC = neutral context; HC = home cage; → LiCl = paired presentation with lithium chloride; -- = no experimental treatment.

Table 2

Summary of the context discrimination training procedure

Session	Day 1	Day 2	Day 3	Day 4
Experiment 1				
12:00-	CC: Suc → LiCl	HC: Suc	NC: Suc	NC: Suc
17:00-	HC: Suc	HC: Suc	HC: Suc	HC: Suc
Experiment 2				
12:00-	CC: Suc → LiCl	HC: Water	NC: Suc	NC: Suc
17:00-	HC: Water	HC: Water	HC: Water	HC: Water

Note. Suc = sucrose as conditioned fluid; → LiCl = paired presentation with lithium chloride; CC = conditioning context; NC = neutral context; HC = home cage.

Figure legends

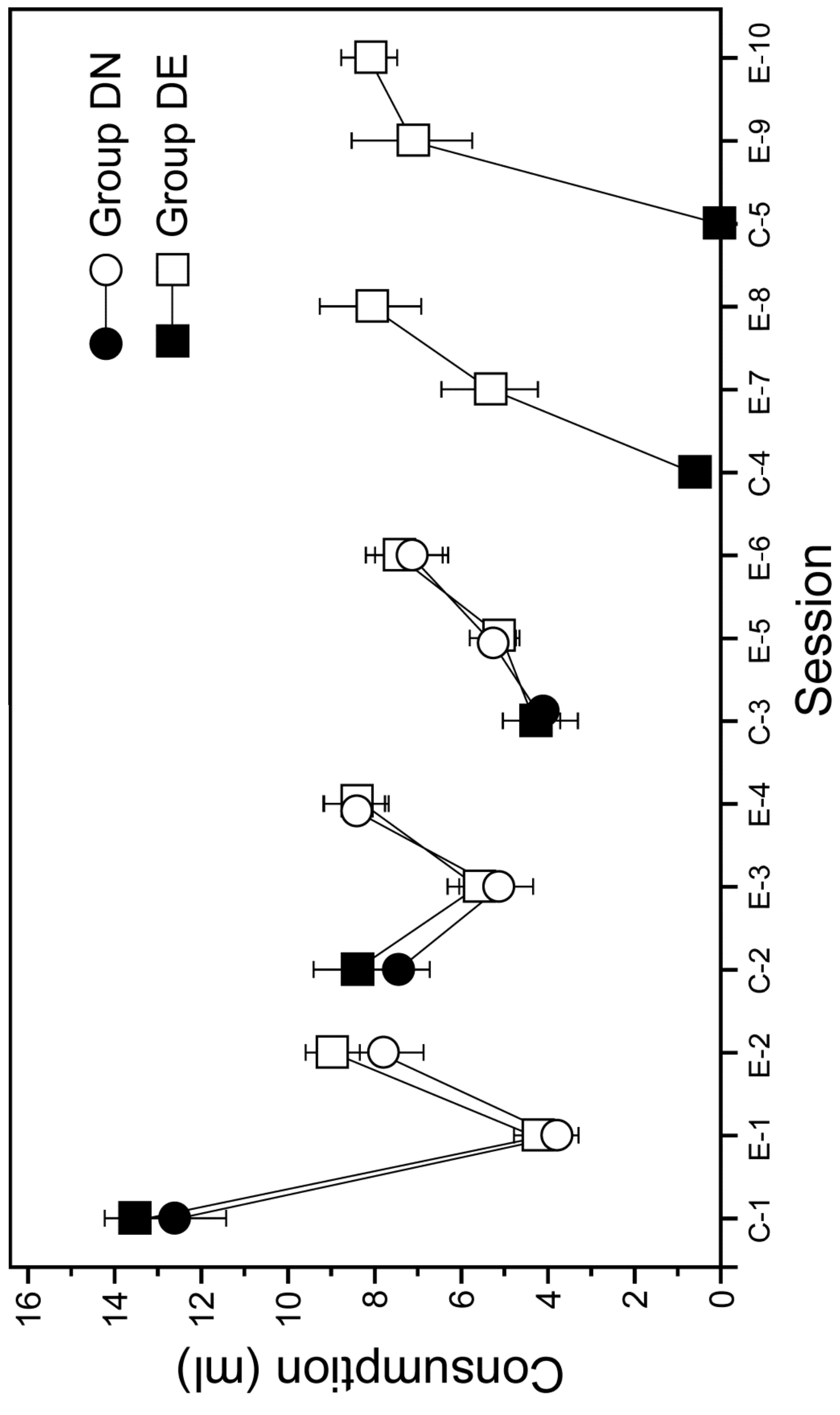
Fig. 1. Results of Experiment 1. Mean consumption of the sucrose solution for three (Group DN) or five (Group DE) cycles of the context discrimination training. “C” and “E” in the x-axis labels denote the conditioning and non-conditioning (extinction) sessions included in each cycle, respectively. Error bars represent standard errors of the mean.

Fig. 2. Results of Experiment 1. Mean consumption of the NaCl solution in the transfer test. Error bars represent standard errors of the mean.

Fig. 3. Results of Experiment 2. Mean consumption of the sucrose solution for three cycles of the context discrimination training. “C” and “E” in the x-axis labels denote the conditioning and non-conditioning (extinction) sessions included in each cycle, respectively. Error bars represent standard errors of the mean.

Fig. 4. Results of Experiment 2. *A*: Mean consumption of the NaCl solution in the transfer test. *B*: Mean consumption of the sucrose solution in the conditioned fluid test. Error bars represent standard errors of the mean.

Fig. 5. Results of Experiment 3. *A*: Mean consumption of the sucrose solution for five cycles of conditioning. *B*: Mean consumption of the NaCl solution in the transfer test. Error bars represent standard errors of the mean.


Group DN
Group DE
Consumption (ml)
16
14
12
10
8
6
4
2
0
C-1
E-1
E-2
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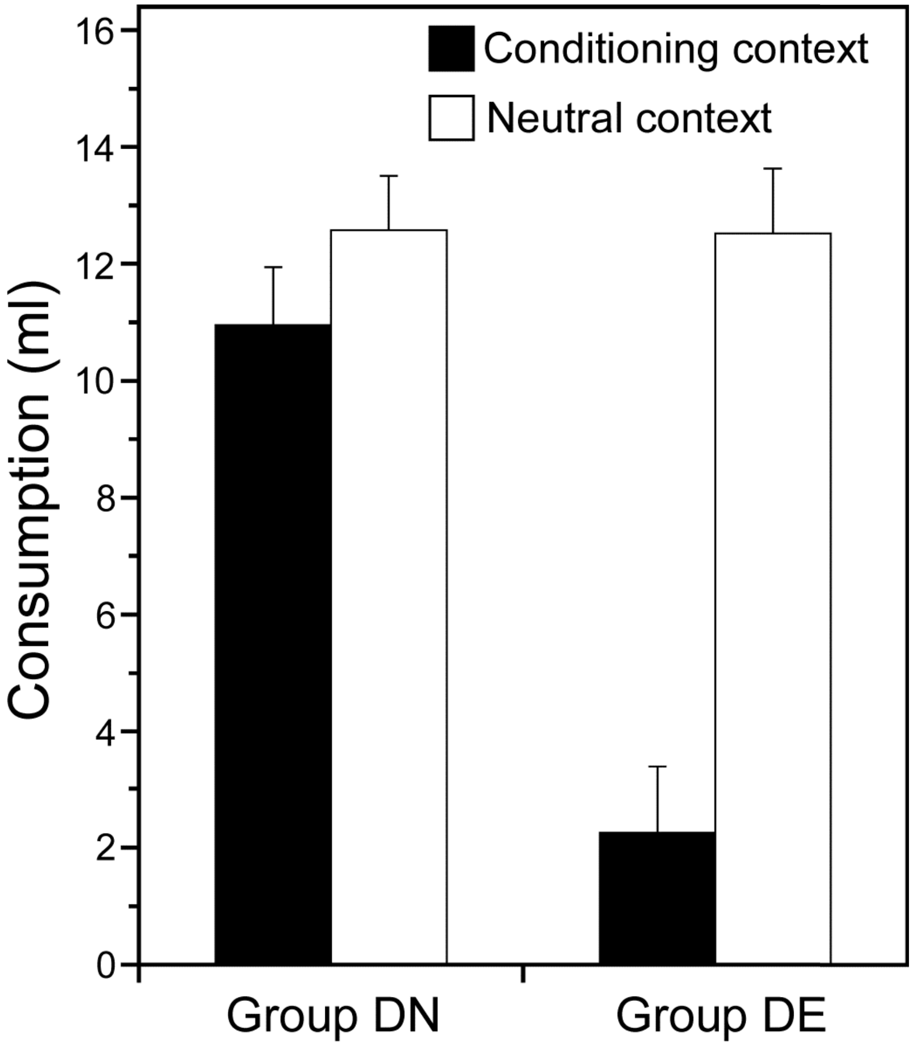
E-9
E-10
Session


Conditioning context
Neutral context
Consumption (ml)
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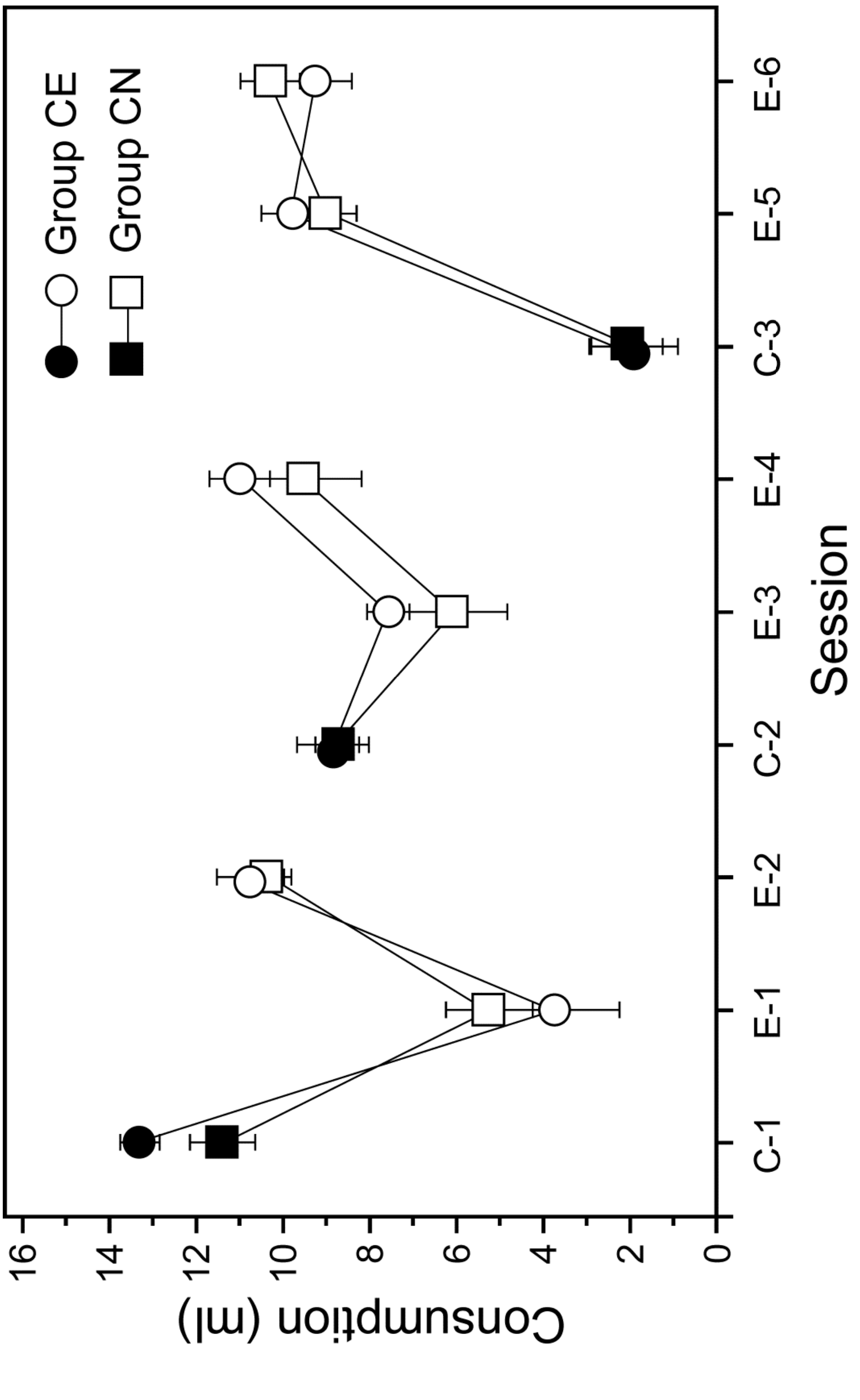
16
Group DN
Group DE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Group CN
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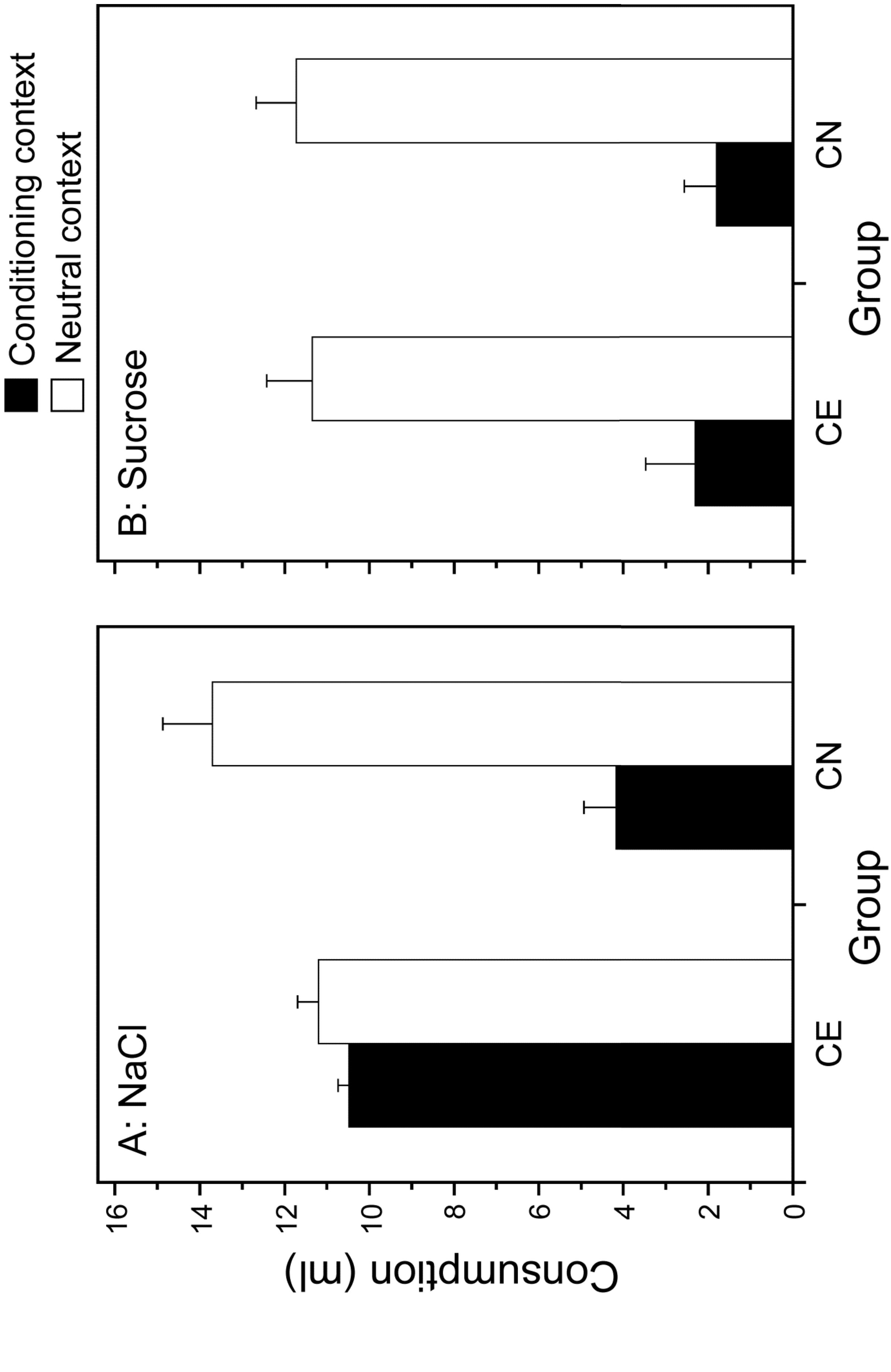
Conditioning context
Neutral context
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B: Sucrose
Consumption (ml)
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8
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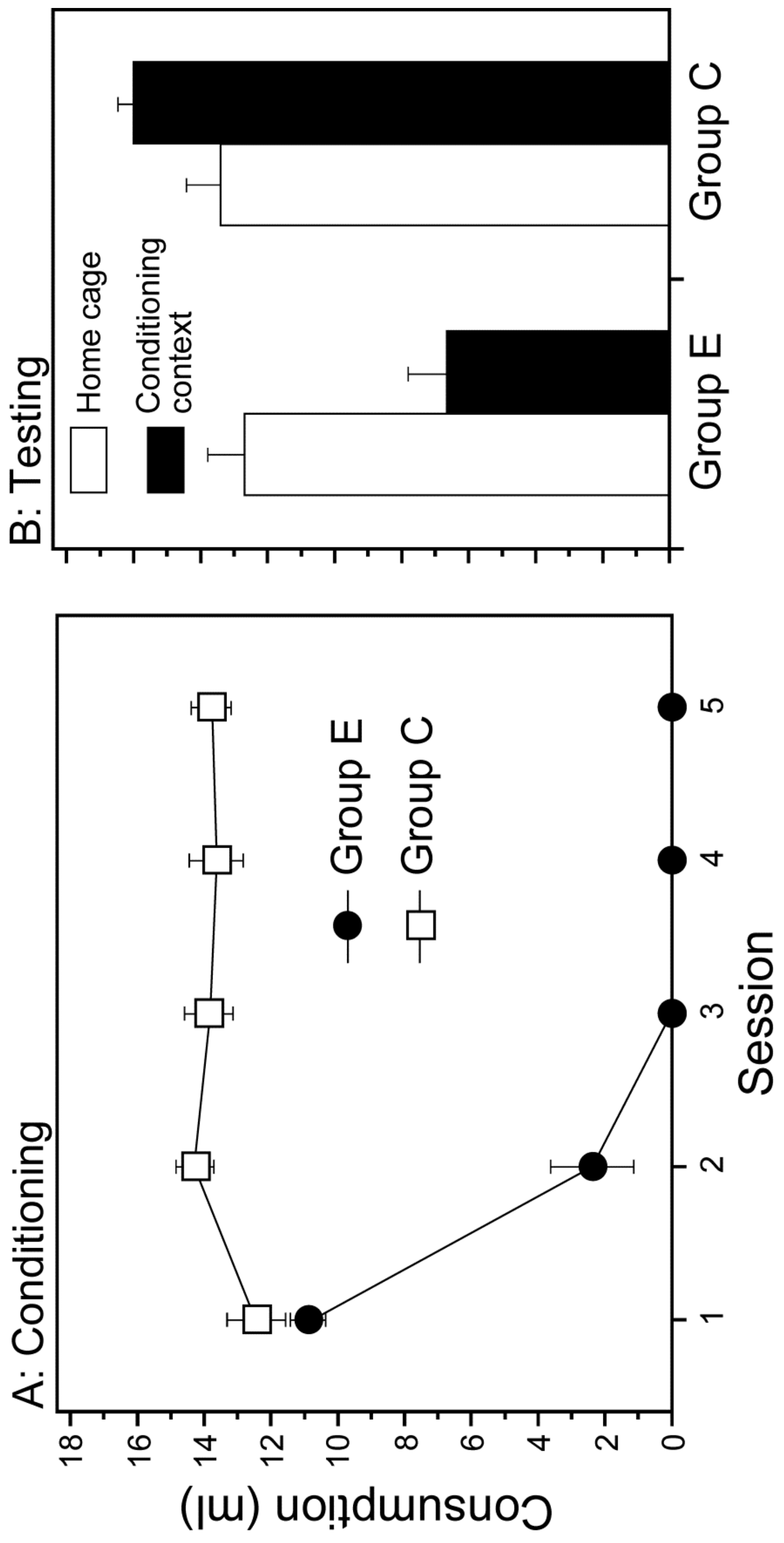
12
14
16
CE
CN
Group


A: Conditioning
Consumption (ml)
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16
18
1
2
3
4
5
Session
Group E
Group C
B: Testing
Home cage
Conditioning
context
Group E
Group C