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The easy-to-hard effect in a voluntary exposure to toxin paradigm with rats☆

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ABSTRACT

In Experiment 1, one group of rats (Group Easy) received initial discrimination training consisting of alternate presentations of two flavor stimuli easily discriminable (presentations of a compound consisting of 0.15% saccharin and 0.15 M lithium chloride, LiCl, and presentations of the saccharin alone). In a subsequent phase, these rats learned a hard version of the discrimination (in which the concentration of the saccharin solution was increased to 1.2%) faster than another group of rats (Group Hard) that received continuous training with the hard discrimination throughout all of the experiment. Experiment 2 led us to discard a possible interpretation of these results in terms of differences in the rates with which the neophobic reaction to the saccharin was habituated in the two groups. This study constitutes the first demonstration of an easy-hard effect in a free-intake toxin paradigm.

Initial training with an easy version of a discrimination facilitates subsequent learning of a harder task involving stimuli that vary along the same dimension. This *easy-to-hard* effect has been demonstrated in a wide variety of species and procedures (e.g., Lawrence, 1952; Liu, Mercado, Church, & Orduña, 2008; Scahill & Mackintosh, 2004; Suret & McLaren, 2003; Walker, Lee, & Bitterman, 1990). For example, Scahill and Mackintosh (2004; Experiment 1) trained rats to learn a discrimination between two flavor compounds: saline + lemon and saccharin + lemon. Consuming from one of these compounds was safe, but consumption of the other was followed by an injection of Lithium Chloride (LiCl) that caused gastrointestinal malaise. In the *easy-trained* condition, the discrimination was easy, since the concentration of the distinctive features of the two compounds was relatively high (0.9% saline and 0.05% saccharin). In the *hard-trained condition*, however, the discrimination was more difficult, since the concentration of the distinctive features was lower (0.05% saline, 0.01% saccharin). Following this pre-training phase, the rats from the two conditions were required to learn the hard discrimination. In this second phase, the discriminative performance (i.e., avoiding the compound followed by the LiCl injection, and maintaining consumption of the safe compound) was found to be better in the *easy* than in the *hard-trained* condition, although the animals in this latter condition were trained on the hard discrimination from the outset. In this demonstration of the easy-to-hard effect, Scahill and Mackintosh used a "forced exposure" to toxin paradigm (cf., Good, Kavaliers, & Ossenkopp, 2013). In this type of paradigm the animal receives a fixed amount of toxin (depending on its body weight) regardless of the amount of flavor consumed previously. This feature of the procedure does not match the natural conditions usually encountered by the organism in which the amount of toxin (and the magnitude of the induced illness) directly depends

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Table 1
Experimental designs.

Stage 1	Stage 2
Experiment 1	
Group EASY	
3 × (LiCl + sac/sac)	6 × (LiCl + SAC/SAC)
Group HARD	
3 × (LiCl + SAC/SAC)	
Experiment 2	
Group LOW	
3 × (NaCl + sac/sac)	6 × (LiCl + SAC/SAC)
Group HIGH	
3 × (NaCl + SAC/SAC)	

Note: All substances were ingested. Number of trials of a given type are indicated. LiCl: 0.15 M lithium chloride solution; NaCl: 0.15 M sodium chloride solution. SAC = Saccharin solution at 1.2%; sac = Saccharin solution at 0.15%. Substances separated by a forward slash (/) were presented on alternate days.

on how much of the toxic food the animal consumes. However, a "voluntary exposure" to toxin paradigm can be readily employed under laboratory conditions by allowing the animals to orally ingest the food or solution containing the LiCl. This oral route of administration has been shown to produce a robust conditioned aversion to the salty taste of the LiCl (e.g., Ladowsky & Ossenkopp, 1986; Loy & Hall, 2002). In addition, a group of studies using oral administration of LiCl have also provided demonstrations of Pavovian discriminations (e.g., Kiefer, 1978; Nakajima & Nagaishi, 2005). For example, Arriola, Vázquez, Alonso, & Rodríguez (2014; Experiment 2) demonstrated that training consisting of alternate presentations of a LiCl + saccharin compound and the saccharin alone resulted in rats avoiding the compound containing LiCl and gradually increasing their consumption of the saccharin alone. Critically, it was found that this discriminative response depended on the concentration of the saccharin (0.15% vs. 0.3%), with the differential response being lower as the concentration increased. In other words, it was found that enhancing the concentration of the common feature of the two flavors (i.e., the saccharin) made the discrimination more difficult. This suggests that this sort of "voluntary exposure" to toxin paradigm also has the potential to provide a demonstration of the easy to hard effect. The aim of the present study, therefore, was to attempt to obtain such a demonstration.

Experiment 1

This experiment consisted of two stages (see Table 1). All rats received identical discrimination training in Stage 2, in which presentations of a LiCl + 1.2% saccharin compound were alternated with presentations of the 1.2% saccharin alone. Given that the intensity (and/or salience) of the common feature of the two stimuli to be discriminated was relatively high (i.e., the saccharin was highly concentrated at 1.2%) we anticipated that learning to discriminate between these two stimuli would be relatively difficult. The two groups of rats differed in the discrimination training that they received in Stage 1. Group EASY received an easy version of the discrimination employed in Stage 2. Specifically, animals in this group received presentations of a LiCl + 0.15% saccharin compound alternated with presentations of the 0.15% saccharin alone. Given the weaker concentration of the common feature of the two stimuli to be discriminated (i.e., the saccharin), we anticipated that learning this discrimination would be relatively easy. Group HARD received in Stage 1 the same discrimination training received in Stage 2. The relevant question was whether or not the present procedure in which animals are voluntarily exposed to the toxin (i.e., the LiCl) will provide a demonstration of the easy-to-hard effect of the sort found by Scahill & Mackintosh (2004).

Method

Subjects, stimuli and apparatus

The subjects were 16 experimentally naïve male Wistar rats with an ad lib. mean weight of 367 g (range: 324–408 g). Animals were singly housed with continuous access to food in a room with a constant temperature (23 °C), humidity (50%) and a 12:12-h light: dark cycle, with light on at 08:00. Access to water was restricted as detailed below.

The solutions used as experimental stimuli were administered in the home cages at room temperature in 50-ml plastic centrifuge tubes, fitted with a metal spout. The following flavored solutions were used: two solutions of saccharin, at 0.15% (w/v) and 1.2%, and two compounds, one consisting of .15 M LiCl and 0.15% saccharin, and the other consisting of .15 M LiCl and 1.2% saccharin. Consumption was measured by weighing the tubes before and after trials, to the nearest 0.1 g.

Procedure

The water deprivation regime was initiated by removing the standard water bottles overnight. On each of the next four days access to water was restricted to two daily sessions of 30 min, beginning at 14:00 (afternoon session) and 19:00 (evening

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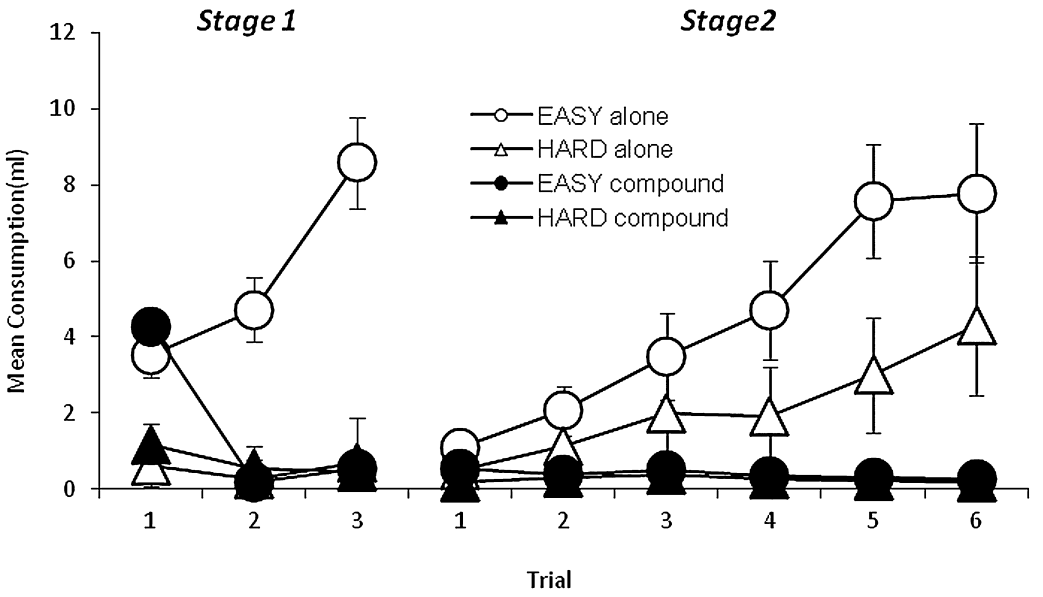

Fig. 1. Experiment 1. Group mean consumption of the LiCl + saccharin compound (black symbols) and the saccharin alone (white symbols) during discrimination training in Stages 1 and 2. For Group EASY (circles), the concentration of the saccharin solution was .15% in Stage 1 and 1.2% in Stage 2. For Group HARD (triangles), the concentration of the saccharin solution was 1.2% in both stages. The compound always consisted of saccharin in its corresponding concentration mixed with a .15 M solution of LiCl. Vertical bars represent the standard errors of the means.

session). Presentation of fluids continued to be given at these times daily throughout the experiment. The experimental sessions were conducted in the afternoon session. In the evening session all animals received access to water. At the end of the deprivation stage, rats were randomly assigned to one of the two equal-sized ($n = 8$) groups (EASY and HARD).

Stage 1

Over the next six days, all subjects received three 10-minpresentations of the LiCl + saccharin compound and three 10-min presentations of the saccharin alone. The two types of trials were strictly alternated and counterbalanced between subjects. Half of the animals in each group received the presentations of the compound on the odd days, and the presentations of the saccharin alone on the even days. The other half of animals in each group received the compound on the even days and the saccharin alone on the odd days. For Group EASY, the concentration of the saccharin solution was 0.15% (w/v), and for Group HARD it was 1.2% (w/v).

Stage 2

In this stage, all the animals received identical discrimination training as that received by Group HARD in Stage 1, with the exception that in this case the training lasted for 12 days rather than six.

Results and discussion

Stage 1

Fig. 1 (left) depicts group mean consumption of the LiCl + saccharin compound and the saccharin alone in Stage 1. Group EASY initially showed more general consumption than Group HARD. This difference may be indicating a bigger neophobic response to the most intense solution of saccharin. As the discrimination training progressed, these animals considerably increased the consumption of the saccharin alone and decreased consumption of the compound (which contained the toxin) – that is, they exhibited discriminative performance. Group HARD, however, exhibited the same low consumption of both the compound and the saccharin alone throughout all of Stage 1. This pattern of results is consistent with the notion that the discrimination was easier when the concentration of the saccharin (i.e., the common element between the two stimuli to be discriminated) was lower in Group EASY. An analysis of variance (ANOVA) with Group (EASY vs. HARD), Stimulus (Compound vs. Alone), and Trial as factors confirmed these impressions. There were significant main effects of Group, $F(1,14) = 46.27$, Stimulus, $F(1,14) = 9.89$, and Trial, $F(2,28) = 4.44$ (here and elsewhere a criterion of statistical significance of $p < .05$ was adopted). The Group × Trial interaction, $F(2,28) = 2.85$, was not significant ($p = 0.075$). However, The Group × Stimulus interaction, $F(1,14) = 12.12$, the Stimulus × Trial interaction, $F(2,28) = 25.34$, and the Group × Stimulus × Trial interaction, $F(2,28) = 17.91$, were significant. Subsequent analyses performed in order to clarify the source of this three-way interaction revealed that for Group EASY, the effect of stimulus was significant on trials 2,

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$t(7) = 3.84$, and 3, $t(7) = 4.76$, but not on trial 1, $t(7) = 0.59$. For Group HARD, however, the effect of Stimulus was significant on trial 1, $t(7) = -2.58$, but not on trial 2, $t(7) = 0.86$, and trial 3, $t(7) = 1.61$. In addition, groups differed in their consumption of the compound on trial 1, $t(14) = 4.22$, but not on trial 2, $t(14) = 1.17$, and trial 3, $ts(14) = 0.57$. However, groups differed in their consumption of saccharin alone on all the three trials, $t(14) > 3.51$.

Stage 2

Fig. 1 (right) depicts group mean consumption of the LiCl + saccharin compound and the saccharin alone in Stage 2. For both groups, the consumption of the compound (which contained the toxin) remained very low throughout all the trials. However, the consumption of the saccharin alone gradually increased across trials. It is evident that the rate of this increase was higher for Group EASY than for Group HARD. An ANOVA with Group, Stimulus, and Trial as factors confirmed all these impressions. The main effect of Group was not significant, $F(1,14) = 2.84$. The Group × Stimulus interaction, $F(1,14) = 2.16$, and the Group × Trial interaction, $F(5,70) = 1.96$, were not significant either ($ps > .16$). However, the main effects of Stimulus, $F(1,14) = 16.01$, and Trial, $F(5,70) = 13.48$, were significant. The Stimulus × Trial interaction, $F(5,70) = 17.15$, and the triple interaction Group × Stimulus × Trial, $F(5,70) = 2.60$, were also significant. Subsequent analyses performed in order to clarify the source of the three-way interaction showed that the Group × Stimulus interaction was only significant on trial 5, $F(1,14) = 4.66$. Groups did not differ in their consumption of the compound in any trial, $ts(14) < 1.45$, $ps > 0.16$, but differed in their consumption of saccharin alone on trial 5, $t(14) = 2.16$. On the remaining trials, group differences in the consumption of saccharin alone were not significant, $ts(14) < 1.52$, $ps > .14$. In addition, for Group EASY, the effect of stimulus was significant on trials 4, 5, and 6, $ts(7) > 2.44$, $ps < 0.04$, and fell close to significance on trials 1, 2, and 3, $ts(7) > 1.96$, $ps < 0.09$. For Group HARD, however, the effect of Stimulus was significant on trials 2–6, $ts(7) > 2.52$, $ps < 0.04$, but not on trial 1, $t(14) < 1$.

Group EASY showed a greater differential response than Group HARD in Stage 2. This suggests that pretraining in the easy version of the discrimination facilitated the subsequent learning of the hard version, relative to training on the same hard discrimination. Our results thus seem to reflect an easy-to-hard effect. However, there are possible alternative interpretations based on the fact that, in Stage 1, subjects in Group HARD drank a lower amount of saccharin alone than those in Group EASY. On the one hand, this difference in consumption suggests that, at the end of Stage 1, the habituation of the neophobic response to the saccharin (i.e., the habituation of a tendency to reject its consumption) was less in Group HARD than in Group EASY. So, the lower consumption of saccharin (either alone or in compound) shown by Group HARD in Stage 2 might reflect less habituation of the neophobia rather than a reduced ability to discriminate the stimuli. Another alternative interpretation of our results relies on the phenomenon of perceptual learning. The relatively high consumption of the saccharin alone shown by animals in Group EASY in Stage 1 could have allowed them to establish a good representation of that stimulus. Despite the fact that the concentration of saccharin was increased from Stage 1 to Stage 2 for this group, the good representation of the features shared by the less and more concentrated saccharin could have helped to solve the discrimination in Stage 2. The low level of consumption shown by Group HARD in Stage 1, however, may not have been great enough to produce a clear benefit in the establishment of the stimulus representation. Experiment 2 was designed to test these possible interpretations.

Experiment 2

If the critical factor producing the differences between Groups in Stage 2 was the amount of saccharin consumed in Stage 1, then the presence of the unconditioned stimulus (US, i.e., the LiCl) should not be necessary to obtain the effect. Thus, in Experiment 2 we used a similar design to that employed in Experiment 1 but substituted an equimolar solution of sodium chloride (NaCl) for LiCl in the Stage 1 compound. We anticipated that, in Stage 1, neophobia would be more marked to the higher than the lower concentration of saccharin. This should bring about more consumption of the less concentrated saccharin (either alone or in compound with NaCl). If these differences in consumption are enough to produce the differences that we observed in Stage 2 of Experiment 1 (i.e., the bigger differential response in Group EASY than Group HARD), then we should observe a parallel effect in the present experiment.

Method

Subjects, stimuli and apparatus

The subjects were 16 experimentally naïve male Wistar rats with an ad lib. mean weight of 358 g (range: 324–402 g). As in Experiment 1, a saccharin solution was employed in different concentrations (0.15% and 1.2%), but in this experiment it was mixed in compound with a 0.15 M NaCl solution in Stage 1, and with 0.15 *M* LiCl in Stage 2.

Procedure

At the end of the deprivation schedule, rats were randomly assigned to one of the two equal-sized ($n = 8$) groups (LOW and HIGH). In Stage 1, subjects received exposure to the saccharin alone and the NaCl + saccharin compound in the same way as described in Experiment 1. For Group LOW, the concentration of the saccharin solution was 0.15% (w/v), and for Group HIGH it was 1.2% (w/v). During Stage 2, Groups LOW and HIGH received identical treatment to that received by Groups

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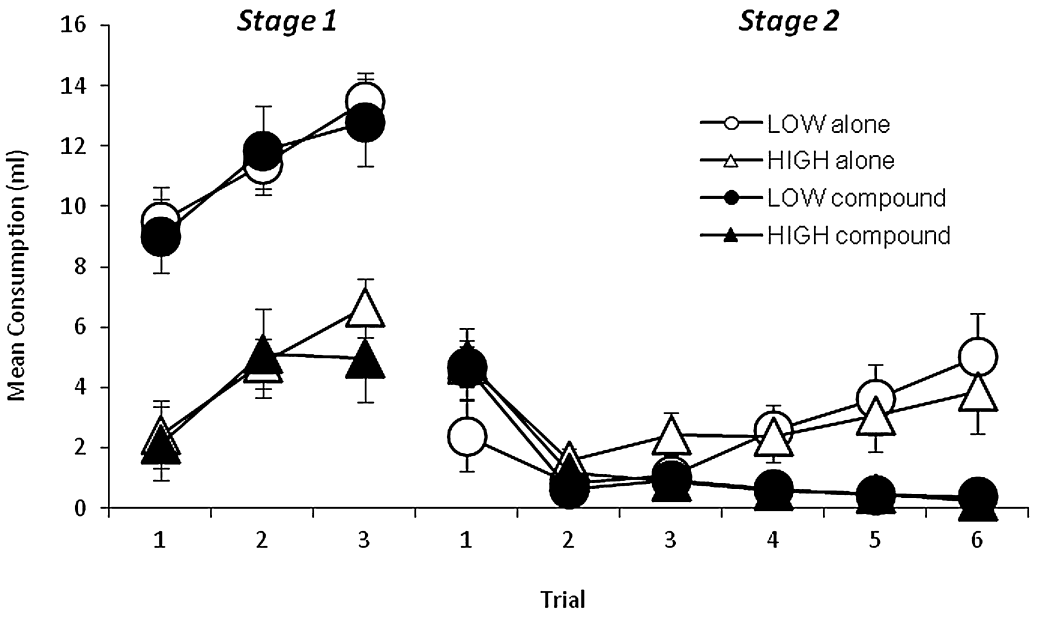

Fig. 2. Experiment 2. Group mean consumption of the compound (black symbols) and the saccharin alone (white symbols) during discrimination training in Stages 1 and 2. For Group LOW (circles), the concentration of the saccharin solution was .15% in Stage 1 and 1.2% in Stage 2. For Group HIGH (triangles), the concentration of the saccharin solution was 1.2% in both stages. During Stage 1, the compound consisted of saccharin in its corresponding concentration mixed with a .15 M solution of NaCl. During Stage 2, the compound consisted of saccharin in its corresponding concentration mixed with a .15 M solution of LiCl. Vertical bars represent the standard errors of the means.

EASY and HARD, respectively, in Stage 2 of Experiment 1. The procedure was the same as that described for the previous experiment.

Results and discussion

Stage 1

Fig. 2 (left) depicts the mean consumption of NaCl + saccharin and saccharin throughout Stage 1. It is evident that initial consumption in Group LOW was higher than that of Group HIGH. For both groups, consumption gradually increased across trials, and the differences between the two groups remained constant throughout this phase. This pattern of results confirms that the more concentrated saccharin produced a bigger neophobic response (i.e., less consumption), and that this was habituated with the repeated presentations of the substance (i.e., the consumption increased across trials). An ANOVA with Group, Stimulus and Trial as the factors confirmed all these impressions. It revealed main effects of Group, $F(1,14) = 31.93$, and Trial, $F(2,28) = 24.05$. Neither the main effect of Stimulus nor any of the interactions were significant, $Fs < 1.44$, $ps > 0.25$.

Stage 2

Fig. 2 (right) depicts group mean consumption of the LiCl + saccharin compound and the saccharin alone in Stage 2. For both groups, the consumption of the compound (which contained the toxin) started slightly higher than that of the saccharin alone, decreased from the second trial and then remained very low throughout all the subsequent trials. The consumption of the saccharin alone slightly increased across trials to a similar extent in both Groups. An ANOVA with Group, Stimulus, and Trial as factors confirmed all these impressions. Neither the main effect of Group nor any interaction involving this factor was significant, $Fs < 1.69$, $ps > 0.15$. The main effects of Stimulus, $F(1,14) = 8.51$, and Trial, $F(5,70) = 16.56$, and the interaction between these two variables, Stimulus × Trial, $F(5,70) = 13.23$, were significant. Subsequent analyses performed to reveal the source of this interaction showed that the stimulus effect was significant on trials 4–6, $ts(15) > 3.44$, $ps < 0.04$, but not significant on trials 1–3, $ts(15) < 1.6$, $ps > 0.13$. In contrast, the consumption of both the saccharin alone, $F(5,70) = 5.69$, and the compound, $F(5,70) = 64.93$, varied among trials. Pairwise comparisons using t-tests showed that consumption of saccharin alone first decreased from the first to the second and third trial, and then increased trial by trial. Consumption of the compound, however, was shown to decrease across trials.

The present experiment confirms that the saccharin at the present concentrations produces different levels of neophobia, there being more neophobia to the 1.2% than to the 0.15% saccharin solution. More importantly, this experiment shows that these differences are not enough to produce differences in the magnitude of the differential response to the saccharin and the

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LiCl + saccharin compound in Stage 2. It therefore seems that the most plausible interpretation of our results of Experiment 1 is in terms of an easy-to-hard effect.

General discussion

To the best of our knowledge, the results obtained in Experiment 1 constitute the first demonstration of an easy-to-hard effect in a free-intake toxin paradigm. The most accepted explanation for this effect is in attentional terms (Mackintosh, 1975; but see Logan, 1966; Sanjuán, Nelson, & Alonso, 2013). According to this explanation, attention to the dimension that is critical for solving the discrimination in Stage 2 is established more firmly by the easy than by the hard pre-training. In our experiments, the critical dimension in the two stages is the presence, or the absence, of the salty taste of the LiCl. During Stage 1, animals in the Easy condition had a better opportunity than those in the Hard condition to learn to pay attention to this dimension (since presumably the less concentrated saccharin overshadowed the salty taste to a less extent than the more concentrated saccharin). According to this attentional account (e.g., Mackintosh, 1975), the presence of a US during the pre-training (which is what determines the presence of a relevant dimension) is a necessary condition for the effect to appear. Thus, taken together, our results from Experiments 1 and 2 add to previous studies (e.g., Scahill & Mackintosh, 2004; Suret & McLaren, 2003) in supporting this account, showing that the easy-to-hard effect is not obtained after unreinforced preexposure to the stimuli (although see, Sanjuán et al., 2013).

From a procedural point of view, our results add to previous evidence suggesting that well-established associative phenomena, such as Pavlovian discrimination (e.g., Arriola et al., 2014), latent inhibition, sensory preconditioning, and overshadowing (e.g., Loy & Hall, 2002) can be obtained in procedures in which orally administered LiCl is used as a US. This type of procedure presents a series of advantages over the more usual procedures in which the LiCl is administered by an injection. Firstly, it has a positive impact on the welfare of animals used as subjects, since it eliminates the pain that they suffer from the intraperitoneal injection while also reducing the total amount of LiCl that is administered to the animal. As the conditioning procedure progresses, the animal tends to drink less and less LiCl and is thus exposed to a lower amount of toxin. In the "forced exposed" to toxin procedures (e.g., Sanjuán et al., 2013; Scahill & Mackintosh, 2004), the animals receive larger amounts of the LiCl, since they receive a fixed amount of the toxin depending on their body weight rather than on the amount of flavored solution consumed on that trial. As the present procedure allows for the programming of a greater number of reinforced trials, it facilitates the study of learning phenomena that usually require extended training, as is the case in Pavlovian discrimination. Finally, it can be argued that presenting the LiCl orally, in compound with the target taste, mirrors more closely the conditions under which animals are likely to establish taste aversions in their natural environment. This approach thus has the potential for providing a more useful tool for translational studies such as developing ways in which animals can be taught to avoid certain foodstuffs in the wild.

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