

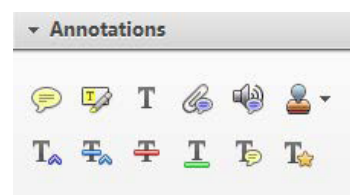
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Perceptual Learning After Rapidly Alternating Exposure to Taste Compounds: Assessment With Different Indices of Generalization

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Exposure to two similar stimuli (AX and BX; e.g., two tastes) reduces the extent to which a conditioned response later established to BX generalizes to AX. This example of perceptual learning is more evident when AX and BX are exposed in an alternating manner (AX, BX, AX, BX, . . .) than when AX and BX occurs in separate blocks (e.g., AX, AX, . . . BX, BX, . . .). We examined in male rats ($N = 126$) the impact of rapid alternation to AX and BX on generalization of a taste aversion from BX to AX. Experiment 1 showed that such alternating presentations (with 5-min intervals between AX and BX) reduced generalization relative to blocked exposure; but only as assessed by consumption levels and not by lick cluster size (an index of hedonic reactions). Experiment 1 also showed that the nature of exposure did not affect how A influenced performance to a novel conditioned taste, Y. Experiment 2 replicated the pattern of results involving the different influences of rapidly alternating and blocked exposure on generalization from BX to AX, and showed that this effect was only evident when rats received access to water during the 5-min intervals between AX and BX. These results reinforce parallels between perceptual learning effects in rats and humans, both at empirical and theoretical levels.

Keywords: associative learning, flavor aversion, licking microstructure, stimulus generalization

Perceptual learning can be defined as a long-lasting change in the ability to discriminate two stimuli as a function of experience or practice with those stimuli (e.g., Gibson, 1969). One real-world case where perceptual learning has been implicated is in becoming a wine connoisseur (James, 1890; see Hughson & Boakes, 2009). Indeed, the recommended process for developing such expertise is closely linked to the interests of those who study perceptual learning in the laboratory: When sampling a succession of wines—presumably engaging the processes underpinning perceptual learning and discrimination—it is recommended that a piece of bread is washed down with water to clear the palate of the remnants of one wine before the sampling the next. As James (1890, p. 496) wrote in the context of discrimination: “One cannot judge accurately of the differences between two similar wines, whilst the second is still

in one’s mouth. . . . we must get the dying phases of both sensations of the pair we are comparing.” More recent theoretical analyses of perceptual learning (e.g., Hall, 2009; McLaren & Mackintosh, 2000; see also, McLaren et al., 1989) have embodied the fact that manipulations that determine how stimuli are sampled affects perceptual learning in nonhuman animals (e.g., Blair & Hall, 2003; Honey et al., 1994; Honey & Bateson, 1996; Mackintosh et al., 1991; Symonds & Hall, 1995) and humans (e.g., Dwyer et al., 2004; Mundy et al., 2006, 2007).

In a simple perceptual learning procedure, rats might first receive exposure to two similar taste compounds (AX and BX; e.g., sucrose + quinine and saline + quinine). To assess the impact of this exposure on the discriminability of AX and BX, one of the flavors (BX) is then paired with an injection of lithium chloride (LiCl) and the extent to which the resulting aversion generalizes to AX is measured. Rats given exposure to AX and BX show less generalization from BX to AX (i.e., by consuming more of AX) than those rats who encounter the flavors for the first-time during conditioning with BX and the test with AX (Mackintosh et al., 1994; see also, Honey & Hall, 1989). This outcome is explicable in many ways, including the possibility that exposure to AX and BX might disrupt the development of an aversion to X (a latent inhibition effect; Lubow & Moore, 1959) and reduce generalization to AX (see McLaren et al., 1989; Rescorla, 1976). However, this explanation is undermined by the fact that the way in which AX and BX are presented and sampled by the rat is important: Perceptual learning is more marked when the presentations of AX and BX occur in an alternating fashion (AX, BX, AX, BX, . . .) than when they occur in blocks (AX, AX, . . . BX, BX, . . .). That is, despite the fact that X (and A and B) have been presented on the same

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number of occasions during the two exposure schedules, generalization from BX to AX is less marked after alternating than blocked exposure (Blair & Hall, 2003; Symonds & Hall, 1995).

The scheduling effect described in the previous paragraph is a general one. As already indicated, it has been demonstrated flavor-aversion learning in both rats (e.g., Symonds & Hall, 1995) and humans (e.g., Dwyer et al., 2004); but it also occurs in filial imprinting in chicks (Honey et al., 1994; Honey & Bateson, 1996), and the processing of faces (Mundy et al., 2006, 2007) and more abstract checkerboards (e.g., Lavis & Mitchell, 2006; Mundy et al., 2009) in humans. However, even the procedures used in studies of perceptual learning using tastes as stimuli in rats and humans are quite different. For example, the presentation of AX and BX in rats is usually separated by many hours or days (e.g., Blair & Hall, 2006; Symonds & Hall, 1995), whereas in humans they are presented within seconds or minutes of one other (e.g., Dwyer et al., 2004; Mundy et al., 2006). This fact, together with other considerations, has encouraged the view that the perceptual learning effects observed using analogous procedures in nonhuman animals and humans might in fact be based on the operation of different mechanisms (Hall, 2009; Mitchell & Hall, 2014). For example, while it is distinctly implausible to argue that a process of (direct) comparison of AX and BX resulted in perceptual learning in rats (Gibson, 1969), it seems more plausible to adopt this form of explanation in the case of humans, where the stimuli are much closer together in time. In short, if it transpired that the benefits of alternating presentations of AX and BX in rats required that the stimuli were presented many hours or days apart, then it would be difficult to maintain that the mechanism was the same as in humans, where timescales are orders of magnitude shorter. However, there has been relatively little published research in rats that has investigated rapid alternation to stimuli that are primarily discriminated on the basis of their taste.

Recent research has suggested that rapid alternating and blocked exposure to compounds (AX and BX), principally discriminated by their odors (i.e., A and B; caramel and hazelnut), has different consequences: Alternating exposure increases the capacity of A to interfere with the expression of an aversion to Y relative to blocked exposure (Recio et al., 2018). One interpretation of this effect (and perceptual learning in general) is that alternating exposure to AX and BX results in the salience of A (and B) being higher than after blocked exposure; and that this difference salience affects the ability of A to disrupt the expression of the aversion acquired by Y (e.g., Hall, 2009). This interpretation also applies to the more conventional test procedure in which generalization to AX is tested after conditioning with BX (e.g., Symonds & Hall, 1995). However, Recio et al. (2018) also showed that the effect of rapid alternation (on generalization from Y to AY) was reduced when a distractor (D) was placed between successive presentations of AX and BX during the exposure stage. The distractor had no effect when placed between successive presentations of AX and AX in group Blocked. This fact is consistent with the idea that concurrent processing of AX and BX contributes to the results (see Dwyer et al., 2011; Mundy et al., 2007), but it is less clear why a distractor should have interfered with changes in the salience of A when it was placed between successive presentations of AX and BX. Moreover, as we shall now show, the effect of the distractor need not have been on a process of perceptual learning per se (cf. Dwyer et al., 2011).

There is an alternative explanation for the results reported by Recio et al. (2018), which derives from the use of odors and the specific test procedure employed. This explanation relies on the possibility that when AX and BX are rapidly alternated, the strong odor components (A and B) will not have fully dissipated over the 5-min intervals between AX and BX. This potential for the odors to linger might have allowed the representations of A and B to become directly linked, or otherwise combined. Under these conditions, at least a part of the ability of the presence of A to impact the consumption of Y might have been mediated by its ability to retrieve B in the intermixed group, but not the blocked group: The associatively activated representation of B (B*) might have contributed to the external inhibition (Pavlov, 1927) produced when A was combined with Y after alternating exposure (A + B* + Y) but not blocked exposure (A + Y). In fact, the impact of associatively activated representations on performance has been formally implemented in a recent application of model of Pavlovian learning and performance (Heidi; Honey et al., 2020) to higher-order conditioning (Honey & Dwyer, 2021, 2022). The supplementary finding reported by Recio et al. (2018)—that placing a distractor between successive presentations of the compounds AX and BX (group Alternating) or AX and AX (and BX and BX; group Blocked) reduced the difference between the groups—might have reflected a disruption to the formation of a (direct) association between A and B in group Alternating, rather than to a process of perceptual learning (see cf. Holland, 1980; Honey & Dwyer, 2021, 2022; Urcelay & Miller, 2009).

Given the paucity of evidence concerning the effects of rapid alternating presentations of two tastes in rats, and the ambiguity concerning the interpretation of the evidence involving odors, the aims of Experiments 1 and 2 were threefold. First, to examine whether rapidly alternating exposure to taste compounds (AX and BX) results in a reduction in generalization between them. Second, to assess whether such a reduction is evident in different measures of generalized conditioned aversions. Theoretical analyses of perceptual learning (e.g., Hall, 2009; McLaren et al., 1989; McLaren & Mackintosh, 2003) are constrained (without additional assumptions) to predict that the reduction in generalization (the index of perceptual learning) will be evident independently of how the aversion is measured. It is known that pairing a flavor (e.g., BX) with LiCl results in a reduction in consumption and a reduction in the number of licks per drinking bout (a measure of hedonic reactions called lick-cluster size; for a review, see Dwyer, 2012). The standard measure of generalization used to examine perceptual learning is consumption of AX. Here, for the first time, we examined both consumption and conducted an analysis of licking microstructure to assess perceptual learning (cf. Dwyer et al., 2012). Finally, we sought to investigate the origins of the perceptual learning effect generated by rapid alternation of AX and BX through manipulating the details of the test stage (Experiment 1) and exposure stage (Experiment 2).

Experiment 1

Table 1 summarizes the design of Experiment 1. Two groups first received alternating exposure to two taste compounds (AX and BX; e.g., sucrose + quinine and saline + quinine) on each of 4 days, while the other two groups received a block of presentations of AX (e.g., sucrose + quinine) on 2 days and a block of

Table 1
Design of Experiment 1

Group	Exposure	Conditioning	Test
Alternating-AX	AX-W-BX BX-W-AX	BX-LiCl	AX
Blocked-AX	AX-W-AX BX-W-BX	BX-LiCl	AX
Alternating-AY	AX-W-BX BX-W-AX	Y-LiCl	AY
Blocked-AY	AX-W-AX BX-W-BX	Y-LiCl	AY

Note. Rats received exposure to sequences of taste compounds (AX and BX), which were presented in an alternating (e.g., AX then BX) or blocked fashion (e.g., AX then AX). During the 5-min intervals between successive 10-min compound presentations, rats received access to water (W). After the exposure stage, half of the rats in each exposure condition received pairings of BX with lithium chloride (LiCl) and were tested with AX (groups Alternating-AX and Blocked-AX); and the remainder received conditioning with Y and testing with AY (groups Alternating-AY and Blocked-AY). Conditioning and test trials were 30 min.

presentations of BX (e.g., saline + quinine) on 2 days. Both groups received water in the 5-min interval between successive presentations on a given day. This procedure mimics that used in studies of perceptual learning in humans, where participants take a sip of water between presentations of the tastes (e.g., AX and BX; see Dwyer et al., 2004; Mundy et al., 2006). After the exposure stage, half of the rats from each condition received conditioning trials with BX and were tested with AX (Alternating-AX and Blocked-AX), and the remainder received conditioning trials with Y and were tested with AY (Alternating-AY and Blocked-AY). The comparison between groups Alternating-AX and Blocked-AX provides an assessment of whether perceptual learning can be observed after rapid alternating exposure. The comparison between groups Alternating-AY and Blocked-AY is the same as that used by Recio et al. (2018) and enables an assessment of whether an effect observed with odors (where there was the potential for a direct association between A and B) is also observed with tastes (where this possibility had been reduced). More generally, this comparison provides the opportunity to assess whether any perceptual learning effect (evident in groups Alternating-AX and Blocked-AX) reflects an increase in the salience of A (Hall, 2009). If this explanation for perceptual learning effects applies to the current procedures, then generalization should be less evident in group Alternating-AY than in group Blocked-AY.

Method

Subjects

Sixty naïve male Lister Hooded rats were used (supplied by Envigo, Blackthorn, United Kingdom). The rats were housed in pairs in standard cages and maintained on 12-hr/12-hr light/dark cycle (lights on at 7 a.m.). Their mean ad libitum weight was 374 g (range = 290–449 g) when the water-deprivation regimen began, and they had continuous access food when they were in their home cages. Research was conducted in accordance with the Home Office regulations under the Animal (Scientific Procedures) Act 1986. There were 15 rats in each group because 4 rats from the original cohort of 64 were taken for use in a separate

electrophysiology study. This sample size has proven adequate in the past to detect perceptual learning effects using a consumption measure and similar procedures and design (e.g., groups sizes were 8 in Recio et al., 2019, and either 8 or 16 in Symonds & Hall, 1995).

Apparatus

Rats received exposure, conditioning and test in 16 custom-made drinking chambers (supplied by Med Associated Inc., St Albans, VT; 32 × 15 × 12 cm, L × W × H). The chambers had white acrylic walls, and wire mesh floors and ceilings. Access to fluids was via stainless steel drinking spouts, attached to 50 ml tubes, which could be inserted through the left-hand or right-hand side of the mesh lid of the chamber. Here, the tubes were inserted in the left-hand side. A contact-sensitive lickometer registered the time of each lick to the closest .01 s, and the licks were recorded by a computer using MED-PC software (Med Associates Inc.). Consumption was measured by weighing the tubes before and after each fluid presentation. The stimuli were solutions of 2% sucrose and .9% salt (that served as A and B), and solutions of 2% lemon juice and 0.000015 M quinine (that served as X and Y; all wt/wt). These solutions were combined to create the two compounds (AX, BX, and AY) in a way that maintained their concentrations.

Procedure

The water deprivation schedule began with rats receiving access to water for 30 min starting at 10:00 a.m. and 4:00 p.m. on each of the first 2 days. On the subsequent 4 days rats received exposure to AX and BX at 10:00 a.m. and 30-min access to water at 4:00 p.m. Solutions of sucrose and salt served as A and B, and solutions of lemon juice and quinine served as X and Y. The identities of the stimuli that served these roles were otherwise fully counterbalanced. Rats received successive periods of 10 min, 5 min, and 10 min in which they received access to 10 ml, 8 ml, and 10 ml of the designated solutions. For groups Alternating-AX and Alternating-AY, the designated solutions were respectively: AX, Water, BX, and BX, Water, AX, counterbalanced across subgroups, with the sequence alternating across days (e.g., AX, Water, BX, on Days 1 and 3 of the exposure stage, and BX, Water, AX, on Days 2 and 4). For groups Blocked-AX and Blocked-AY, the solutions were AX, W, AX, and BX, W, BX; with the order being counterbalanced across subgroups: AX, Water, AX, on Days 1 and 2, and BX, Water, BX, on Days 3 and 4, for one subgroup; and BX, Water, BX, on Days 1 and 2, and AX, Water, AX, on Days 3 and 4, for the second subgroup.

Rats received conditioning trials on Days 5 and 7 and recovery days on Days 6 and 8. On conditioning trials, rats in groups Alternating-AX and Blocked-AX received 30-min access to 15 ml of BX followed by an injection of .15 ml LiCl at 10 ml/kg body-weight. Rats in groups Alternating-AY and Blocked-AY received an identical conditioning treatment to their namesakes with the exception that access to Y was paired with LiCl. On the recovery days, rats received access to water for 30 min at 11:00 a.m. At 11:00 a.m. on Day 9 rats in groups Alternating-AX and Blocked-AX received access to AX for 30 min, whereas those in groups Alternating-AY and Blocked-AY received access to AY. After this test, rats received water for 30 min in the afternoon, and we

also assessed performance to AB. However, the results of this test were not informative and will not be reported here.

Data Analysis

During the exposure stage, rats consumed the small quantities of AX and BX within the 10-min periods, which meant that a reliable analysis of lick microstructure was not possible. Therefore, the analysis that follows focusses on consumption and lick-cluster sizes during 30-min conditioning trials with BX or Y and the 30-min test with AX or AY. The analysis of lick microstructure during conditioning and testing followed reported protocols (e.g., Dwyer, 2012; Patitucci et al., 2016). A cluster was defined as a set of licks, each separated by an interlick-interval of no more than .5 s, as most pauses greater than that are also greater than 1 s (e.g., Davis & Smith, 1992; Spector et al., 1998). General linear model null hypothesis testing analyses were conducted, assuming a rejection level of $p < .05$ for mixed factorial analysis of variance. Partial eta squared, and Cohen’s d tests were used to measure effect sizes.

Transparency and Openness

This study was not preregistered. All data from this study are available by emailing the corresponding authors.

Results

During the exposure phase, rats in groups Alternating-AX, Blocked-AX, Alternating-AY, and Blocked-AY consumed 4.77, 4.75, 4.37, and 4.01 g, respectively, of the AX solution and 4.67, 4.79, 4.37, and 4.19 g, respectively, of the BX solution. Analysis of variance (ANOVA) revealed no effect of exposure schedule (Alternating or Blocked), conditioned stimulus (BX vs. Y), or solution (AX vs. BX), and there were no significant interactions between these factors (all $F_s < 1$).

Table 2 shows consumption and lick clusters sizes during the BX and Y conditioning trials. Inspection of the table shows that consumption of BX (for group Alternating-AX and Blocked-AX) and Y (for groups Alternating-AY and Blocked-AY) declined between the two conditioning trials; and that consumption scores were generally higher for the familiar compound (BX) than for the novel stimulus (Y). There was also a reduction in lick cluster sizes in the four groups between the two trials, with lick cluster size being higher for BX than Y. An ANOVA conducted on the consumption scores, with exposure condition (Alternating or Blocked), conditioned stimulus

(BX or Y), and trials (1 or 2) as factors, revealed an effect of conditioned stimulus, $F(1, 56) = 205.31, p < .001, \eta_p^2 = .786, MSE = 4.07$, an effect of trial, $F(1, 56) = 205.31, p < .001, \eta_p^2 = .786, MSE = 4.07$, and an interaction between the three factors, $F(1, 56) = 4.24, p = .044, \eta_p^2 = .070, MSE = 7.36$, there was no significant effect of exposure condition or other two-way interactions (largest $F(1, 56) = 1.65, p = .204, \eta_p^2 = .029, MSE = 4.07$ for the Exposure Condition \times Conditioned Stimulus interaction). Inspection of the descriptive statistics in Table 2 suggests that the significant three-way interaction stems from the fact that, for the groups conditioned with BX there was a tendency for the blocked exposure group to show a smaller decrease in consumption across conditioning than the alternating exposure group, while for the groups conditioned with Y, this was reversed. Despite these impressions, separate ANOVAs performed on each conditioned stimulus only showed main effect of trial for BX, $F(1, 28) = 14.20, p < .001, \eta_p^2 = .336, MSE = 10.42$, and for Y, $F(1, 28) = 33.22, p < .001, \eta_p^2 = .543, MSE = 4.30$, the effect of Exposure Condition or Trial \times Exposure Condition interaction were nonsignificant (largest $F(1, 28) = 2.76, p = .108, \eta_p^2 = .090, MSE = 3.26$ for main effect of exposure condition in the groups conditioned with Y).

An equivalent ANOVA conducted on the lick cluster sizes revealed an effect of conditioned stimulus, $F(1, 56) = 43.15, p < .001, \eta_p^2 = .435, MSE = 97.54$, an effect of trial, $F(1, 56) = 60.85, p < .001, \eta_p^2 = .521, MSE = 37.87$, and an interaction between the three factors $F(1, 56) = 6.55, p = .013, \eta_p^2 = .105, MSE = 37.87$, again there was no significant effect of exposure condition or other two-way interactions (largest $F(1, 56) = 2.97, p = .090, \eta_p^2 = .050, MSE = 97.54$ for the Exposure Condition \times Conditioned Stimulus interaction). Inspection of the descriptive statistics in Table 2 suggests that the significant three-way interaction stems from the fact that for the groups conditioned with BX there was a tendency for the blocked exposure group to show a smaller decrease in lick cluster size across conditioning than the alternating exposure group, while for the groups conditioned with Y this pattern was reversed. A separate ANOVA conducted on the groups conditioned with BX revealed only a significant main effect of trial, $F(1, 28) = 15.47, p < .001, \eta_p^2 = .356, MSE = 50.55$, and no significant effect of Exposure Condition or Trial \times Exposure Condition interaction (largest $F(1, 28) = 2.00, p = .168, \eta_p^2 = .067, MSE = 50.55$ for the Trial \times Exposure Condition interaction), while the analysis performed on groups conditioned with Y revealed a main effect of trial, $F(1, 28) = 63.29, p < .001, \eta_p^2 = .693, MSE = 25.19$, and a Trial \times Exposure Condition interaction $F(1, 28) = 5.92, p = .022, \eta_p^2 = .175, MSE = 25.19$, but no

Table 2
M (+SEM) Consumption and Lick Cluster Size on the Conditioning Trials in Experiment 2

Group	Trial 1		Trial 2	
	Consumption	Lick cluster size	Consumption	Lick cluster size
Alternating-AX	10.84 (0.14)	32.79 (2.41)	6.34 (0.64)	22.97 (2.12)
Blocked-AX	9.31 (0.98)	27.17 (2.33)	7.53 (0.81)	22.55 (2.95)
Alternating-AY	4.04 (0.44)	16.51 (1.33)	1.63 (0.61)	9.35 (1.57)
Blocked-AY	5.49 (0.53)	22.86 (2.54)	1.73 (0.4)	9.39 (1.00)

Note. Consumption is measured in milliliters and lick cluster size in licks per bout. For groups Alternating-AX and Blocked-AX the two conditioning trials were with BX, while for groups Alternating-AY and Blocked-AY they were with Y. The group names denote whether AX and BX were presented in an alternating or blocked fashion, and whether BX was conditioned and AX was presented at test, or Y was conditioned and AY was presented at test.

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significant main effect of exposure condition $F(1, 28) = 2.46, p = .128, \eta_p^2 = .081, MSE = 62.47$.

F1 Figure 1 depicts consumption and lick-cluster sizes for the test trial with AX and AY. Inspection of the left-hand panel shows that rats in group Alternating-AX consumed more AX than those in Blocked-AX. There was, however, no difference in consumption to AY between groups Alternating-AY and Blocked-AY; with consumption of AY being lower than AX. Inspection of the right-hand panel reveals that the lick-cluster sizes paralleled those for consumption, with these sizes being larger in group Alternating-AX than in group Blocked-AX (and larger in group Blocked-AY than Alternating-AY). As we shall see, however, the sole statistically significant effect involving click cluster size was the nature of the test stimulus (AX vs. AY)

ANOVA conducted on the consumption scores revealed an effect of test stimulus (AX or AY), $F(1, 56) = 23.86, p < .001, \eta_p^2 = .299, MSE = 26.51$, an interaction between exposure condition and test stimulus, $F(1, 56) = 4.78, p = .033, \eta_p^2 = .079, MSE = 26.51$, but no effect of exposure condition (Alternating or Blocked), $F(1, 56) = .42, p = .520, \eta_p^2 = .007, MSE = 26.51$. A *t* test conducted on the AX consumption scores revealed that the difference between groups Alternating-AX and Blocked-AX did not reach conventional levels of standard levels of significance on a two-tailed test, $t(28) = 1.99, p = .056, d = -.73$. There was no significant difference between the AY consumption scores in groups Alternating-AY and Blocked-AY, $t(28) = 1.09, p = .283, d = .4$.

A parallel analysis of the lick-cluster scores revealed only a main effect of the test compound (AX vs. AY), $F(1, 56) = 12.36, p < .001, \eta_p^2 = .181, MSE = 148.83$, with no effect of exposure condition (Alternating or Blocked), $F(1, 56) < .01, p = .970, \eta_p^2 < .001, MSE = 148.83$, and no interaction between exposure condition and test compound, $F(1, 56) = 3.42, p = .070, \eta_p^2 = .058, MSE = 148.83$.

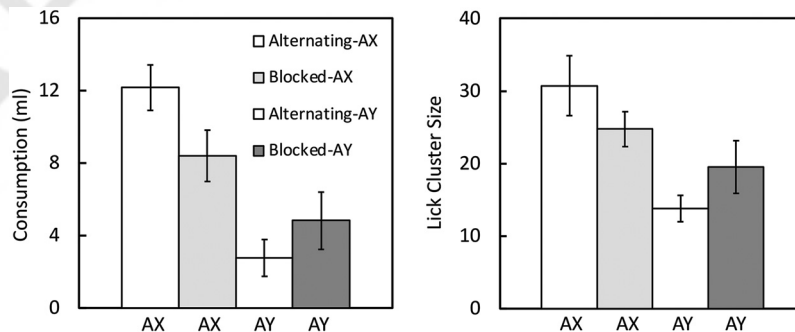
Discussion

Experiment 1 demonstrated that manipulating how compound tastes (AX and BX) are exposed (rapidly alternating or blocked) interacts with later assessments of generalization of an aversion: When the assessment involved conditioning an aversion to BX

and testing AX alternating exposure tended to reduce generalization to AX relative to blocked exposure; however, when it involved conditioning an aversion to Y and testing AY the patterns of results was if anything in the opposite direction. This pattern of results provides no support for the suggestion that the perceptual learning effect reflected the salience of A being higher after alternating than blocked exposure. While there were effects of the nature of the conditioned flavor (BX or Y) and trial on both consumption and lick cluster size, the effect of exposure condition on generalization to AX and AY was evident when consumption, but not lick cluster size, was the measure of generalization. The basis for this apparent dissociation will be given further consideration in the General Discussion, after the results of Experiment 2 have been presented. These results allow an assessment of its reliability, which is especially important given the fact that the general pattern of results appeared to be similar across the two measures of generalization.

The contrast between the results of Experiment 1, using tastes, and those reported by Recio et al. (2018), using odors, is marked. The procedures used in groups Alternating-AY and Blocked-AY closely parallel those from their study, and yet the results were quite different: In our case, alternating exposure to AX and BX resulted in no greater tendency for A to disrupt the aversion to Y than did blocked exposure, and in their procedure it did. We have argued that the effect observed with odors might well have reflected greater external inhibition; but resulting from the capacity of A to evoke a memory of B during the test rather than from the effective salience of A being higher after alternating than blocked exposure. The possibility that the odor of A might remain until odor B is presented (and allow an association to form between them) seems a plausible one. It also seemed plausible to argue that this possibility is reduced by providing access to water between presentations of AX and BX. Experiment 2 examined the latter suggestion directly, while providing an opportunity to confirm the reliability of the pattern of results evident in groups Alternating-AX and Blocked-AX; as in Experiment 1 the difference between these two groups would only be evident using a one-tailed test.

Figure 1
The Test Results From Experiment 1 Involving Presentations of AX or AY



Note. Mean (\pm SEM) consumption (left-hand panel) and mean lick cluster size (right-hand panel) during test trials with AX and AY. Groups had previously received either alternating or blocked exposure to AX and BX, and then groups Alternating-AX and Blocked-AX received conditioning trials with BX while those in groups Alternating-AY and Blocked-AY received conditioning trials with Y.

Experiment 2

T3 **Table 3** summarizes the design of Experiment 2. Groups Alternating-W and Blocked-W received an equivalent treatment to groups Alternating-AX and Blocked-AX in Experiment 1; including the fact that they received access to water in the 5-min intervals between the presentations of the taste compounds within a day (e.g., between AX and BX in group Alternating-W, and between AX and AX in group Blocked-W). Two further groups also received alternating or blocked exposure to AX and BX: Alternating-N and Blocked-N. However, for these groups there was no access to water during the 5-min intervals between the taste compounds, but instead this access occurred immediately following the second taste compound within a day. In this procedure, any tendency for A to become linked to B during alternating exposure should increase generalization from BX to AX through a process of sensory preconditioning (e.g., Dwyer et al., 2012; Rescorla & Cunningham, 1978). Indeed, Recio et al. (2019) described just such an effect when odors were used as A and B, and rats received a limited amount of intermixed exposure to AX and BX (see also, Alonso & Hall, 1999). However, to the extent that rapid alternation to our tastes results in perceptual learning then it should be evident in a reduction in generalization from BX to AX. Moreover, this effect might be expected to be influenced by whether or not the taste can linger between successive presentations of AX and BX in group Alternating-N but not group Alternating-W; either because it affords greater opportunity for stimulus comparison and increases perceptual learning (Gibson, 1969; cf. James, 1890) or it enables A and B to become linked which would counteract perceptual learning (e.g., Dwyer et al., 2012; Rescorla & Cunningham, 1978; see also, Honey & Bateson, 1996).

Method

Subjects and Apparatus

Sixty-four naïve male Lister Hooded rats were used (supplied by Envigo). The rats were housed and maintained in the same way as Experiment 1. Their mean ad libitum weight was 296 g (range = 260–325 g) when the water-deprivation regimen began. The

Table 3
Design of Experiment 2

Group	Exposure	Conditioning	Test
Alternating-W	AX–W–BX–N	BX–LiCl	AX
	BX–W–AX–N		
Blocked-W	AX–W–AX–N	BX–LiCl	AX
	BX–W–BX–N		
Alternating-N	AX–N–BX–W	BX–LiCl	AX
	BX–N–AX–W		
Blocked-N	AX–N–AX–W	BX–LiCl	AX
	BX–N–BX–W		

Note. Rats received exposure to sequences of taste compounds (AX and BX), which were presented in an alternating (e.g., AX then BX) or blocked fashion (e.g., AX then AX). During the 5-min intervals between successive 10-min compound presentations, rats either received access to water (W; groups Alternating-W and Blocked-W) or no water (N; groups Alternating-N and Blocked-N). All rats then received conditioning trials in which BX was paired with lithium chloride (LiCl) and test trials with AX. Conditioning and test trials were 30 min.

apparatus was the same as that used in Experiment 1. The stimuli were solutions of 2% sucrose and .9% salt (that served as A and B counterbalanced), and 0.000015 M quinine (that served as X). These tastes were combined to create the two compounds (AX and BX) in a way that maintained their concentrations.

Procedure

The rats were divided into four groups ($n_s = 16$: Alternating-W, Blocked-W, Alternating-N, and Blocked-N). The 2-day water deprivation schedule was the same as in Experiment 1. On the subsequent 4 days rats received exposure to AX and BX at 10:00 a.m. and 30-min access to water at 4:00 p.m. Rats in groups Alternating-W and Blocked-W received the same treatment as groups Alternating-AX and Blocked-AX in Experiment 1. The Alternating-N and Blocked-N groups receive the same training as their W-subscripted namesakes, with the exception that they did not receive water in the 5-min intervals between the flavor compound presentations on a given day, but rather in the 5-min period that immediately followed the second compound presentation on each day.

Rats received conditioning trials on Days 5 and 7 and recovery days on Days 6 and 8. On conditioning trials, rats received 30-min access to 15 ml of BX immediately followed by an injection of .15 ml LiCl at 10 ml/kg bodyweight. On the recovery days, rats received access to water for 30 min at 11:00 a.m. At 11:00 a.m. on the next 6 days (Days 9–16), rats received access to AX for 30 min, and in the afternoon they received 30-min access to water. The analysis that follows again focusses on consumption and lick-cluster sizes during conditioning with BX and the tests with AX. The analysis of lick microstructure during conditioning and testing followed reported protocols (e.g., Dwyer, 2012; Patitucci et al., 2016).

Results

During the exposure phase, rats in groups Alternating-W, Blocked-W, Alternating-N, and Blocked-N consumed 4.52, 4.34, 5.30, and 5.57 g, respectively, of the AX solution and 4.64, 4.39, 4.90, and 5.53 g, respectively, of the BX solution. ANOVA revealed an effect of water placement (W vs. N), $F(1, 60) = 18.11$, $p < .001$, $\eta_p^2 = .232$, $MSE = 23.3$, presumably because of the effect of water consumption before the second solution presented each day in the Alternating-W and Blocked-W groups. As expected, there was no significant effect of exposure schedule (Alternating or Blocked) or no effect of solution (AX vs. BX), nor any significant interactions (largest $F(1, 60) = 2.75$, $p = .102$, $\eta_p^2 = .044$, $MSE = 3.54$, for the Exposure Condition \times Water Placement interaction).

The levels of consumption and lick clusters sizes during the BX conditioning trials are shown in Table 4. Inspection of the table shows that the consumption of BX decreased between the two conditioning trials in the four groups, with some evidence that the reduction was somewhat greater in the groups given water between presentations than the groups that did not. There was also a reduction in lick cluster size between the two trials, with an indication that lick cluster size was smallest on the second trial in group Alternating-W. An ANOVA conducted on the consumption scores with exposure condition (Alternating or Blocked), water placement (W or N), and conditioning trial (1 or 2) as factors

Table 4*M (+SEM) Consumption and Lick Cluster Sizes on the BX Conditioning Trials in Experiment 2*

Group	Trial 1		Trial 2	
	Consumption	Lick cluster size	Consumption	Lick cluster size
Alternating-W	10.83 (0.25)	34.62 (2.93)	6.92 (0.75)	21.16 (1.80)
Blocked-W	10.92 (0.30)	29.60 (1.76)	7.23 (0.97)	28.81 (3.17)
Alternating-N	10.01 (0.68)	34.30 (2.48)	8.36 (0.72)	27.92 (2.63)
Blocked-N	11.08 (0.24)	39.73 (3.73)	8.58 (0.70)	31.51 (3.61)

Note. Consumption is measured in grams and lick cluster size in licks per bout. All groups received two conditioning trials with BX. The group names denote whether AX and BX were presented in an alternating or blocked fashion, and whether water was placed in the 5-min intervals between successive presentations (W) or not (N).

revealed a main effect of conditioning trial, $F(1, 60) = 35.43, p < .001, \eta_p^2 = .371, MSE = 7.79$, but no other significant main effects or interactions (largest $F(1, 60) = 3.05, p = .086, \eta_p^2 = .048, MSE = 7.79$, for the Conditioning Trial \times Water Placement interaction). A parallel analysis of the lick cluster size revealed main effects of conditioning trial, $F(1, 60) = 14.94, p < .001, \eta_p^2 = .199, MSE = 111.41$, and water placement, $F(1, 60) = 5.00, p = .029, \eta_p^2 = .077, MSE = 148.68$, but no other significant main effects or interactions (largest $F(1, 60) = 3.77, p = .057, \eta_p^2 = .059, MSE = 111.41$, for the Conditioning Trial \times Water Placement \times Exposure Condition interaction).

F2 Figure 2 shows the results of principal interest from Experiment 2. This figure shows the consumption scores (left-hand panel) and lick-cluster sizes (right-hand panel) for AX across three, two-test blocks. Inspection of the left-hand panel shows that rats in group Alternating-W consumed more than those in Blocked-W, and it also suggests that—if anything—the opposite difference is evident in groups Alternating-N and Blocked-N. In contrast, inspection of the right-hand panel reveals that there no marked or consistent differences in lick-cluster sizes between the groups.

ANOVA conducted on the consumption scores revealed main effect of test block (1–3), $F(2, 120) = 22.14, p < .001, \eta_p^2 = .27, MSE = 2.82$, and critically, an interaction between exposure condition and water placement, $F(1, 60) = 4.80, p = .032, \eta_p^2 = .074, MSE = 12.66$; but no significant effects of exposure condition (Alternating or Blocked), $F(1, 60) = .33, p = .565, \eta_p^2 = .006, MSE = 12.66$, water placement (W or N), $F(1, 60) = 2.85, p = .097, \eta_p^2 = .045, MSE = 12.66$, or other interactions (Test Block \times Water Placement, $F(2, 120) = .16, p = .849, \eta_p^2 = .003, MSE = 2.82$; Test Block \times Exposure Condition, $F(2, 120) = .04, p = .959, \eta_p^2 < .001, MSE = 2.82$; Test Block \times Water Placement \times Exposure Condition, $F(2, 120) = .80, p = .450, \eta_p^2 = .0013, MSE = 2.82$). Separate ANOVAs were conducted with the W and N groups to follow up the exposure condition and water placement interaction. For the W groups, the ANOVA revealed a main effect of exposure condition $F(1, 30) = 4.33, p = .046, \eta_p^2 = .126, MSE = 11.21$, confirming greater consumption in Alternating-W than Blocked-W. The main effect of test block was also significant, $F(2, 60) = 9.29, p < .001, \eta_p^2 = .236, MSE = 3.50$, but the Block \times Exposure Condition interaction was not $F(2, 60) = .19, p = .825, \eta_p^2 = .006, MSE = 3.50$). For the N groups, the ANOVA revealed a main effect of test block, $F(2, 60) = 14.21, p < .001, \eta_p^2 = .236, MSE = 2.14$, but no main effect exposure condition, $F(1, 30) = 1.17, p = .289, \eta_p^2 = .037, MSE = 14.10$, or Block \times Exposure

Condition interaction, $F(2, 60) = .80, p = .454, \eta_p^2 = .026, MSE = 2.14$.

A parallel ANOVA conducted on the lick-cluster-size scores (summarized in the right-hand panel of Figure 2) revealed an interaction between water placement and test block, $F(2, 120) = 3.46, p = .035, \eta_p^2 = .055, MSE = 51.92$, but no effects of exposure condition (Alternating or Blocked), $F(1, 60) = .76, p = .398, \eta_p^2 = .012, MSE = 593.51$, water placement (W or N), $F(1, 60) = .10, p = .748, \eta_p^2 = .002, MSE = 593.51$, or test block (1–3), $F(2, 120) = .238, p = .789, \eta_p^2 = .004, MSE = 51.92$, and other interactions were nonsignificant (Test Block \times Exposure Condition, $F(2, 120) = 1.76, p = .176, \eta_p^2 = .029, MSE = 51.92$; Water Placement \times Exposure Condition, $F(1, 60) = .09, p = .770, \eta_p^2 = .001, MSE = 593.51$; Test Block \times Water Placement \times Exposure Condition, $F(2, 120) = 1.34, p = .266, \eta_p^2 = .0022, MSE = 51.92$).

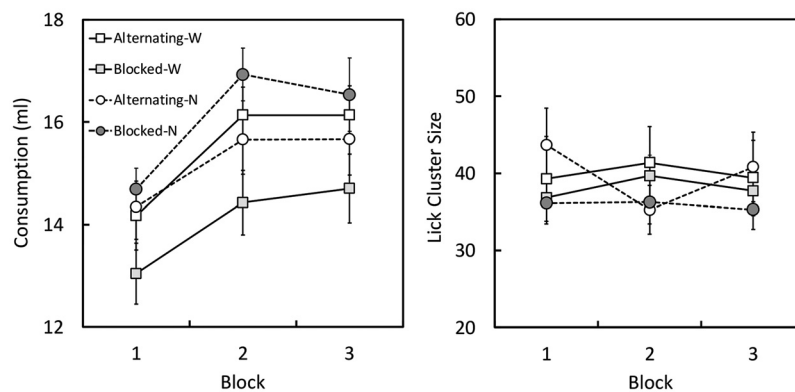
Discussion

Experiment 2 demonstrated that rapidly alternating exposure to AX and BX resulted in a reduction in generalization from BX to AX relative to blocked exposure. This effect was only evident when access to water was provided between successive presentations of AX and BX (e.g., during alternating exposure) and AX and AX (e.g., during blocked exposure). The finding that this effect was not evident when there was no access to water between presentations of AX and BX is consistent with the suggestion that the lingering taste of the first compound allows it to become associated with the second compound; that would tend to increase generalization from BX to AX through the tendency of A (and X) to activate B during the test (e.g., Dwyer et al., 2012; Rescorla & Cunningham, 1978). The perceptual learning effect involving rapidly alternating tastes reinforces that observed in Experiment 1 (cf. Recio et al., 2018); and the observation that this effect is evident in one measure of generalization (consumption) but not another (lick cluster size; cf. Dwyer et al., 2012) also reinforces the same pattern of results observed in Experiment 1.

General Discussion

The study of perceptual learning in rats has made extensive use of flavor-aversion procedures. These procedures assess how exposure to complex flavors (AX and BX; sucrose + quinine and saline + quinine) affects later generalization of a conditioned aversion between them. A reduction in generalization is taken to be evidence perceptual learning (e.g., Honey & Hall, 1989;

Figure 2
The Test Results From Experiment 2 Involving Presentations of AX



Note. Mean (\pm SEM) consumption (left-hand panel) and mean lick cluster size (right-hand panel) during test trials with AX. Rats had received either alternating or blocked exposure to AX and BX followed by conditioning with BX. During the exposure stage, rats in groups Alternating-W and Blocked-W received access to water in the 5-min intervals between successive exposures; whereas those in groups Alternating-N and Blocked-N did not receive water access during these intervals.

Mackintosh et al., 1991; Symonds & Hall, 1995). Studies with humans that have adopted analogous flavor-aversion procedures (e.g., using the same flavors) have yielded similar findings (Dwyer et al., 2004; Mundy et al., 2006; see also Mundy et al., 2007). However, the studies with humans have involved a much-compressed timescale, with presentations of AX and BX occurring within seconds and minutes of one another, rather than the hours and days that is typical in studies with rats. This might mean that the parallels between the effects seen in humans and rats reflect the operation of quite different mechanisms (see Hall, 2009; Mitchell & Hall, 2014). Here, we examined whether perceptual learning with complex tastes could be observed in rats with timescales more like those used in humans (cf. Recio et al., 2018, 2019); and provided a concurrent analysis of both consumption and licking microstructure to assess whether perceptual learning is equally evident in different assays of flavor aversion: consumption and lick-cluster size. This form of analysis of perceptual learning has not been undertaken in either rat or human, but it has been used in the context of a theoretically related phenomenon: sensory preconditioning (Dwyer et al., 2012).

When rats receive pairings of BX with LiCl it results two changes: later presentations of BX result in lower consumption and a reduction in lick-cluster size (for a review, see Dwyer, 2012). There is already some evidence that these different conditioned behaviors are dissociable. For example, if rats receive a sensory preconditioning procedure in which BX is first exposed and then X is paired with LiCl, the reduction in consumption of X generalizes to B, but the reduction in lick-cluster size does not (Dwyer et al., 2012). This is interesting because it suggests anew (cf. Rescorla, 1988) the need for models of Pavlovian conditioning and higher-order conditioning to provide a more sophisticated analysis of the translation of (associative) learning into different forms of conditioned behaviors (see Honey et al., 2020; Honey & Dwyer, 2021, 2022). Here, we used the standard measures of avoidance (i.e., consumption) and aversion (i.e., lick cluster size)

to assess perceptual learning generated by different schedules of exposure to two complex tastes: AX and BX.

On each of four exposure days, rats received successive 10-min presentations of compound tastes separated by 5 min. Some rats received alternating exposure where the successive presentations were of different flavors, AX and BX; whereas other rats received blocked exposure where the same number of exposures to AX and BX but arranged so that within a day the flavors were the same (e.g., AX and AX on 2 days and BX and BX on 2 days). Across Experiments 1 and 2 it was shown that when the rats had access to water during the 5-min intervals between compounds, there was less generalization at test from BX to AX after alternating than blocked exposure (using a one-tailed test in Experiment 1 and a two-tailed test in Experiment 2); but this effect was only evident in the measure of avoidance (i.e., consumption) and not aversion (i.e., lick-cluster size). However, in Experiment 2, when access to water occurred after the second of the successive presentations there was no difference between the two schedules of exposure; with a tendency for alternating exposure to result in more generalization (as measured by consumption). There is a simple explanation for the effect of water placement between AX and BX: It prevents the remnants of one taste (e.g., AX) being present when the next is presented (e.g., BX), which would otherwise allow AX and BX to become linked and increase generalization from BX to AX (cf. Dwyer et al., 2012; Rescorla & Cunningham, 1978; cf. James, 1890). This interpretation suggests that there are at least two processes in play when two compounds are presented close together in time: a process of perceptual learning process that reduces generalization and an associative process that enhances it (cf. Honey & Bateson, 1996; see also, Rodríguez & Alonso, 2008). But, why should perceptual learning be evident in one measure of generalization, but not another? The fact that the difference in perceptual learning, between alternating and blocked exposure, was only evident in consumption scores is potentially important: Without additional assumptions, it is not captured by two popular theoretical accounts of perceptual learning.

Hall (2009) suggested that alternating exposure to AX and BX, unlike blocked exposure, will mean that A and B will be repeatedly activated in their absence, which was taken to maintain the salience of A and B (but see, Dwyer & Honey, 2007): Associations formed between A and X (on AX trials) and between B and X (on BX trials) will mean that A will be activated on BX trials and B will be active on AX trials. If the salience of A and B is greater after alternating than blocked exposure, B should limit the development of the aversion established to X, when BX is paired with LiCl, and A should interfere (through a process of external inhibition; see Pavlov, 1927) with the aversion otherwise evoked by X or indeed any other effective (CS; e.g., Y). As we saw in Experiment 1, there was no evidence of the latter influence in the groups given conditioning with Y and tested with AY: No evidence that the perceptual learning effect resulting from rapid alternation reflected a change in the salience of A. Moreover, the fact that when there was a scheduling effect (in both Experiments 1 and 2) it was only evident statistically in one measure of generalization (e.g., consumption) is not consistent with the idea that B is more likely to overshadow the formation of an association between X and LiCl. As noted in the preceding paragraph and in the beginning of the article, without further assumptions such an effect should be evident in those conditioned behaviors that are established through pairing BX with LiCl.

Another popular account of perceptual learning is that it reflects, at least in part, the development of inhibition between the unique features of the AX and BX compounds (i.e., A and B). McLaren et al. (1989) noted that an application of the Rescorla and Wagner (1972) learning rules to a procedure in which AX and BX were alternated would result in inhibition between A and B. Thus, initial AX and BX trials should result in the formation of associations between A and X, and between B and X, which should then provide the basis for the development of inhibition between A and B: X will activate B on trials on which it was absent (i.e., AX trials) and X will activate A on trials on which it is absent (i.e., BX trials). This inhibition could impact generalization by preventing B from becoming associatively activated by X on AX test trials, and generating a conditioned response via the associative chain: X-B-LiCl. However, this theory does address why such a process should not impact both consumption and lick-cluster size.

One possibility, open to both accounts of perceptual learning considered above, is that lick-cluster size is simply a less sensitive measure than is consumption (cf., Dwyer et al., 2012). The fact that pairing BX (and Y) with LiCl had effects on consumption and lick cluster size that were similar in magnitude here suggests that the sensitivity of the two measures is not a general issue. If the dissociation observed in Experiments 1 and 2 between the two measures of performance was reliable and representative across a broad range of parameters, then one would need a more nuanced analysis of how perceptual learning is translated into performance. A recent model of Pavlovian conditioning and higher-order conditioning has developed such an analysis (Honey et al., 2020; Honey & Dwyer, 2021, 2022). While detailed application of this model to perceptual learning is beyond the scope of this article, it is relevant to note that the model provides a formal analysis of the translation of learning into different forms of conditioned responding: Responding that is based on the properties of the (CS) or CSs (e.g., consumption) and responding that is based on the properties of the US (e.g., lick cluster size; see Honey & Dwyer, 2021,

2022). It affords a natural basis for when and why different forms of conditioned response diverge across different conditions (e.g., higher-order conditioning and Pavlovian conditioning).

In more general terms, the results presented here suggest that the conditions under which perceptual learning is observed using tastes are similar in rats and humans (Dwyer et al., 2004; Mundy et al., 2006), encouraging the possibility that similar theoretical mechanisms might be at work (cf. Hall, 2009; Mitchell & Hall, 2014). However, the results also suggest that there is a need for any theoretical analysis to consider how perceptual learning is translated into performance.

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AUTHOR QUERIES


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1


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