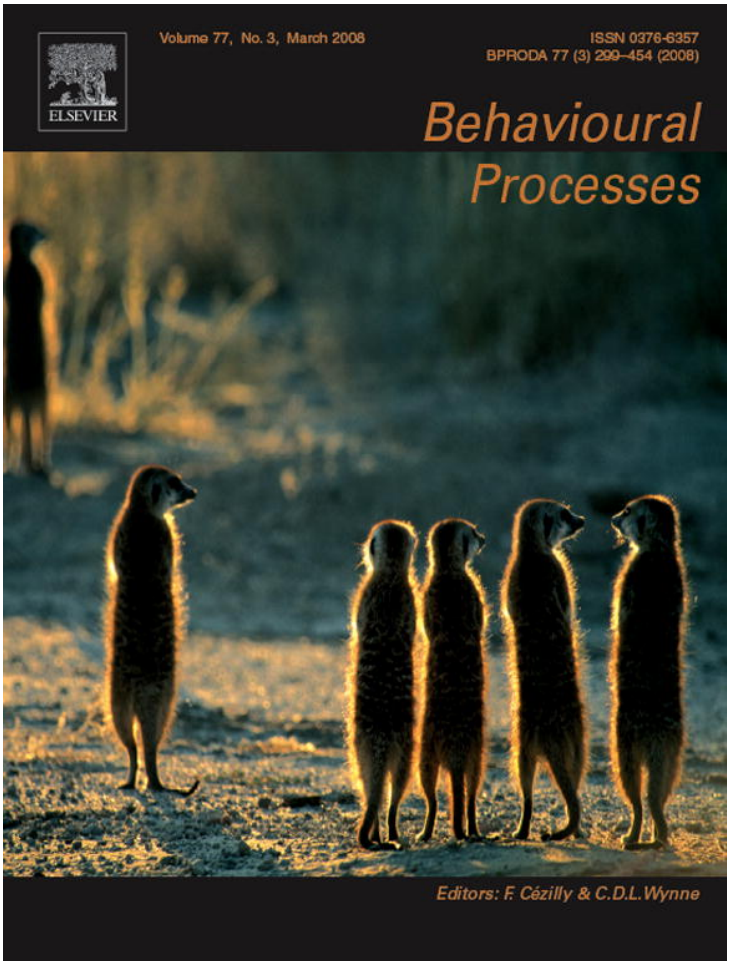
ELSEVIER
Volume 77, No. 3, March 2008
ISSN 0376-6357
BPRODA 77 (3) 299–454 (2008)
Behavioural Processes
Editors: F. Cézilly & C.D.L.Wynne

Available online at www.sciencedirect.com
ScienceDirect
Behavioural Processes 77 (2008) 400–404
BEHAVIOURAL PROCESSES
www.elsevier.com/locate/behavproc

Short report

Stimulus comparison in perceptual learning: Roles of sensory preconditioning and latent inhibition

Gabriel Rodríguez [a,*], Gumersinda Alonso [b]

[a] *Department of Psychology, University of York, York YO10 5DD, United Kingdom*
[b] *Facultad de Psicología, Universidad del País Vasco, Avenida de Tolosa 70, 20018 San Sebastián, Spain*

Received 2 April 2007; received in revised form 24 June 2007; accepted 26 June 2007

Abstract

Rats were given exposure to a compound flavour (AX) and to one element of that compound (X). Two drinking tubes were made available to the rat on each exposure trial. For group concurrent (CNC) one tube contained AX and the other X. For groups alternating (ALT) and blocked (BLK), however, both tubes contained the same flavour (AX or X). Group ALT received AX and X on alternate trials; group BLK received AX in the first block of trials and X on the second, or vice versa. After an aversion had been established to X the groups were tested with AX. It was found that group ALT showed less generalization from X to AX than did group BLK. This difference was not accompanied by a parallel difference in the level of conditioning to X. However, group CNC showed both stronger conditioning to X and greater generalization from X to AX than groups ALT and BLK. Implications for the role of stimulus comparison in the perceptual learning effect are discussed.

Keywords: Perceptual learning; Stimulus comparison; Generalization; Flavour-aversion

Under certain conditions, exposure to two similar stimuli facilitates subsequent discrimination between them (i.e., reduces the extent to which generalization occurs between them). Examples of this perceptual learning effect have frequently been observed in experiments that make use of the flavour-aversion learning procedure. In this type of experiment rats are generally given non-reinforced exposure to two compound flavours (call them AX and BX, where A and B represent distinctive features of the stimuli and X is a feature common to both). The ability of the animals to discriminate between these flavours is then assessed by establishing an aversion to one of them (AX) and measuring the extent of generalization to the other (BX). It has been consistently found that the effect of such pre-exposure is to attenuate the extent to which such generalization occurs (e.g., Mackintosh et al., 1991; Sanjuán et al., 2004; Symonds and Hall, 1995).

There is evidence that the schedule according to which the stimuli are pre-exposed is important in generating a perceptual learning effect. For instance, if AX and BX are presented on alternate trials during pre-exposure (i.e., AX, BX, AX, BX, etc.) then generalization between them is attenuated to a greater extent than if AX and BX are presented equally often but in separate blocks of trials (AX, AX, etc., BX, BX, etc., e.g., Bennett and Mackintosh, 1999; Mondragón and Hall, 2002; Symonds and Hall, 1995). Controversy has arisen concerning the nature of the process or mechanism responsible for this perceptual learning effect. One possible candidate can be found in the influential theory of perceptual learning proposed by Gibson (1969). According to this, mere exposure to two or more similar stimuli (e.g., AX and BX) brings into play a *differentiation* process, which allows the animals to detect more easily the distinctive features of the stimuli (A and B), thus enhancing their perceptual dissimilarity and reducing generalization between them. Critically, Gibson (1969, p. 145) stated that this differentiation process would be more likely to occur in pre-exposure conditions that favour stimulus comparison. Within this framework, it has been suggested that the reason why alternating pre-exposure is more effective than blocked pre-exposure in reducing generalization is that such alternation provides a better opportunity for stimulus comparison, and thus for stimulus differentiation (e.g., Mondragón and Hall, 2002; Symonds and Hall, 1995).

An implication of this account is that, if comparison drives the perceptual learning effect, then a pre-exposure schedule in which

* Corresponding author.
E-mail address: gr509@york.ac.uk (G. Rodríguez).

0376-6357/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.beproc.2007.06.010

AX and BX are presented simultaneously should generate a particularly strong effect. Animals under this *concurrent* schedule would have the opportunity to sample the flavours in quick succession, and thus the conditions for comparison to occur (and for perceptual learning to be generated) should be better than in the standard alternating or blocked schedules, in which the minimum interval between the presentations of AX and BX is of several hours. However, previous studies examining this hypothesis have shown that far from reducing generalization, concurrent pre-exposure actually results in more generalization than the alternating (Bennett and Mackintosh, 1999; experiment 2) and blocked (Alonso and Hall, 1999) schedules. Although this is the opposite of what is predicted by Gibson's account, it might be premature to dismiss the possibility that concurrent pre-exposure may promote differentiation.

It has been suggested that the enhanced generalization found after concurrent pre-exposure might be caused by two possible processes. The first is sensory preconditioning. As some authors have proposed (e.g., Alonso and Hall, 1999; Honey and Bateson, 1996) the simultaneous presentation of two stimuli (e.g., AX and BX) during pre-exposure could allow the formation of excitatory associations between their unique features (A and B). Consequently, when animals given concurrent pre-exposure are tested after conditioning to AX, the presentations of BX could activate (by way of the B–A association) the representation of A, which would be itself associated with the unconditioned stimulus (US), thus increasing the aversion observed (i.e., enhancing the generalization between AX and BX). This source of generalization would not be available to animals given alternating or blocked pre-exposure, for whom the longer interval between the presentations of AX and BX would serve to preclude the formation of any excitatory association between A and B.

The second possible process is suggested by the results of an experiment reported by Bennett and Mackintosh (1999; experiment 2). They found that concurrent pre-exposure to AX and BX (*near simultaneous presentations* of AX and BX, in their terminology) resulted in an increase in the generalization between them, that was accompanied by an increase in the conditioning to X. They suggested, in explanation, that concurrent pre-exposure might disrupt the development of latent inhibition to the common X element. Stimulus generalization, which depends largely on the strength acquired by the stimulus common features, would thus have been enhanced after concurrent pre-exposure.

The fact that the enhanced generalization found after concurrent pre-exposure can be accounted for by either or both of the processes just mentioned might make it possible to rescue Gibson's (1969, p. 145) comparison hypothesis. As Honey et al. (1994) first noted, concurrent pre-exposure might foster two kinds of processes with opposing effects on stimulus generalization. On the one hand, the sensory preconditioning and the disruption of latent inhibition to the common stimulus features would act to enhance generalization. On the other hand, the comparison process would promote perceptual learning and act to decrease generalization. Whether concurrent pre-exposure will result in an increase or decrease in the stimulus generalization would depend on the balance between these two types

Table 1
Experimental design

Pre-exposure	Conditioning	Test
CNC group: AX-X/AX-X	X+	AX
ALT group: AX-AX/X-X	X+	AX
BLK group: AX-AX/AX-AX...X-X/X-X...	X+	AX

Note: A and X refer to flavors. During pre-exposure, stimuli separated by a dash (-) were presented simultaneously within the same trial, and those separated by a forward slash (/) were presented on alternate trials within a day; + refers to the administration of LiCl.

of opposing processes. It remains possible that in the previous studies examining the effects of concurrent pre-exposure (Alonso and Hall 1999; Bennett and Mackintosh, 1999), the decrease in generalization resulting from the comparison process was counteracted by the increase in the generalization resulting from those two opposing processes. What follows from this suggestion is that the use of a procedure in which the influence of either or both of these generalization-enhancing processes was neutralized might allow for the observation of the benefits of concurrent pre-exposure on perceptual learning (i.e., a generalization-reducing effect). The experiment to be reported here attempted to follow this strategy.

Previous studies examining the effects of concurrent pre-exposure in flavour-aversion learning have used either two primary flavours (A and B; Alonso and Hall, 1999) or two flavour compounds each with a unique element (AX and BX; Bennett and Mackintosh, 1999) as stimuli. In contrast, in the present experiment (its design is outlined in Table 1) we chose to use a flavour compound (AX) and an element of this compound (X). Two drinking tubes were made available to the rat on each experimental trial. There were three groups that differed in the pre-exposure they received. Group concurrent (CNC) received pre-exposure in which one tube contained AX and the other X. Groups alternating (ALT) and blocked (BLK) received equivalent pre-exposure to the flavours but for them both tubes contained the same flavour (AX or X) on each trial. Group ALT received AX and X in alternate trials; group BLK received AX in the first block of trials and X on the second, or vice versa. All rats then received aversion conditioning with X as the conditioned stimulus (CS), followed by a generalization test with AX. We made use of this experimental design for two main reasons.

The first is derived from the recent finding (Rodríguez and Alonso, 2004; see also Hall et al., 2006) that alternating pre-exposure to AX and X generates a generalization-reducing effect comparable with that produced by alternating pre-exposure to AX and BX (e.g., Symonds and Hall, 1995). Gibson's (1969) comparison hypothesis can accommodate both perceptual learning findings. The greater opportunity for comparison offered by the alternating pre-exposure will facilitate the detection of the unique features of the stimuli (A and B when AX and BX are pre-exposed, or A when AX and X are pre-exposed), thus enhancing their perceptual dissimilarity and reducing the generalization between them. To test the adequacy of this explanation, it would obviously be of interest to examine the effect of a concurrent pre-exposure to AX and X. Will generalization be reduced or enhanced after such a pre-exposure schedule? What will be the impact of using this procedure on the two processes that might enhance stimulus generalization after concurrent pre-exposure?

The answer to this latter question leads us to the second reason for choosing the present experimental design. Using this design will eliminate the possible enhancing effect of sensory preconditioning on generalization. This effect, it will be recalled, depended on the formation of an association between the unique features of the two pre-exposed stimuli. This will not be possible when the flavours used are AX and X (i.e., when one has no distinguishing unique feature). With such stimuli the simultaneous presentations of AX and X during concurrent pre-exposure will only affect, if anything, the strength of the within compound association between A and X, and this association should not have an influence on test performance since both A and X are presented during the generalization test with AX. With sensory preconditioning neutralized, the stimulus differentiation process that hypothetically would be operating during concurrent pre-exposure should become more easily evident as a perceptual learning effect. Such a reduction in generalization might still be counteracted by a possible attenuation of latent inhibition (i.e., an increase in the conditioning) to X. The present design does not eliminate this second generalization-enhancing process but, at least, conditioning with X alone will provide a direct assessment of its possible influence.

To summarize, according to Gibson's (1969) differentiation account, the differing opportunities for stimulus comparison afforded by concurrent, alternating and blocked schedules should result in differing amounts of perceptual learning. On these grounds, first we expected to find a perceptual learning effect of the sort demonstrated by Rodríguez and Alonso (2004), with group ALT showing less generalization from X to AX than group BLK. And second, and more important, we expected to find an even more substantial perceptual learning effect when stimuli could be directly compared during pre-exposure, with group CNC showing less generalization than groups ALT and BLK. However, if concurrent pre-exposure results in an attenuation of latent inhibition to the common stimulus features, then a stronger aversion to X during the conditioning stage, and perhaps to AX during the generalization test, should be evident in group CNC.

1. Method

1.1. Subjects and apparatus

The subjects were 24 experimentally naïve Wistar male rats with a mean ad lib weight of 288 g at the start of the experiment. 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.

Solutions were administered, in the home cages, at room temperature through 50-ml graduated cylinders fitted with a metal spout. The solutions were counterbalanced. For half the animals in each group, flavor A was 0.3% (w/v) saline and X was 5% (w/v) sucrose. The remaining animals received the opposite arrangement. Consumption was measured by weighing to the nearest 0.01 ml. The unconditioned stimulus for the conditioning trials was an intraperitoneal injection of 0.3 M lithium chloride (LiCl) at 10 ml/kg of body weight.

1.2. Procedure

1.2.1. Water deprivation

The water deprivation regime was initiated by removing the standard water bottles in the morning. On the next 4 days access to water was restricted to two daily sessions of 30 min, beginning at 13:00 (afternoon session) and 18:00 (evening session). This schedule was in place throughout the experiment. Two drinking tubes (separated from one another by 15 cm) were presented on each session. The rats were then randomly assigned to one of the three equal-sized experimental groups matched for their consumption of water.

1.2.2. Pre-exposure

Over the next 4 days, the rats were given access to fluid in two drinking tubes, each containing 5 ml of the appropriate fluid (AX or X). For group CNC, one tube contained solution AX and the other solution X on each session. The left/right position of the tubes was counterbalanced. For groups ALT and BLK, the two drinking tubes contained the same solution on each session. Animals in group ALT were given access to the flavors in alternation. For half the animals in this group, AX was presented during the afternoon session and X in the evening; for the remainder the arrangement was reversed. Animals in group BLK received the solutions in two blocks of trials. For half the animals in this group, AX was presented on the first 2 days in both daily sessions and X on the last 2 days. The remaining animals received the opposite sequence.

1.2.3. Conditioning

After pre-exposure, animals received two conditioning trials. The first was given in the afternoon session of the next day. It consisted of a 30-min presentation of the two drinking tubes, each containing 5 ml of X, followed immediately by an injection of LiCl. The next day was a recovery day on which animals had unrestricted access to water for 30 min during both afternoon and evening sessions. The second conditioning trial was given in the afternoon session of the next day. It was identical to the first except that the animals were given free access to X for 30 min prior to the injection. Water was available for the rats in the evening session next to this conditioning trial. After the second recovery day, a non-reinforced test trial was given in which all the subjects were given unrestricted access to X in two tubes for 30 min in the afternoon session. Water was available during the evening session following this test.

1.2.4. Generalization test

On the afternoon session of the next day, the animals received a single test trial in which they were given unrestricted access to AX in two tubes for 30 min.

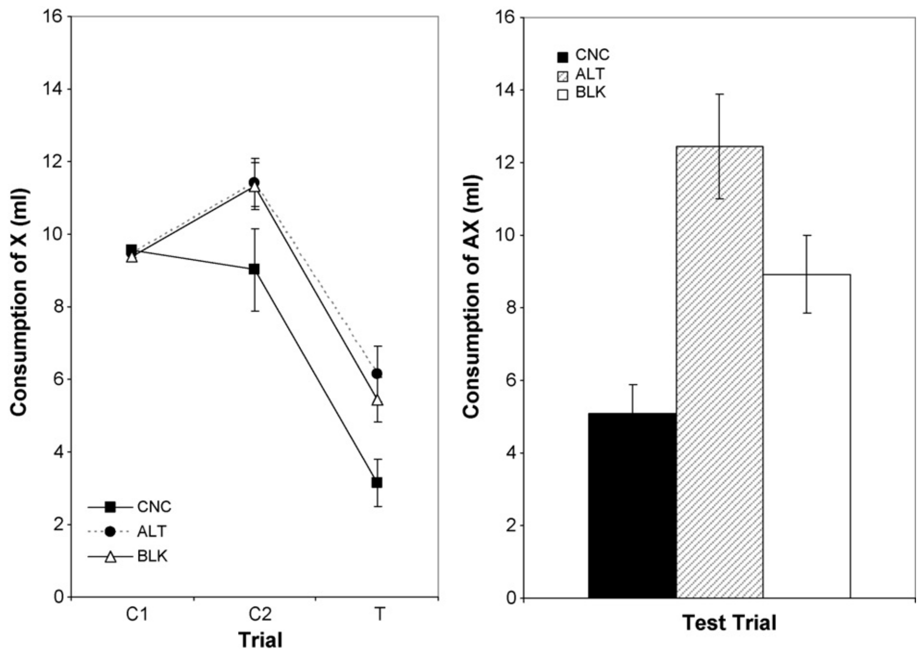

Fig. 1. Left panel: group mean consumption of flavour X during two conditioning trials (C1 and C2), and one non-reinforced test trial (T). Right panel: group mean consumption of the compound flavour AX on the generalization test trial. Group names refer to the pre-exposure schedule (CNC: concurrent; ALT: alternating; BLK: blocked). Vertical bars represent the standard error of the mean.

2. Results

The rats consumed all the fluid offered throughout the pre-exposure phase, with no evidence of neophobia. The left-hand panel of Fig. 1 shows the group mean consumption of X on the two conditioning trials and on the subsequent X-test trial (during this phase and the final generalization test, scores for each subject were the total consumption from both tubes presented on each trial). It is evident that the conditioning procedure was effective, as consumption in all three groups declined by the final X-test trial. However, acquisition of aversion to X appeared to occur more readily (and to be finally more profound) in group CNC than in groups ALT and BLK. There was no sign of a difference between the latter two groups. This pattern of results presumably reflects an attenuation of latent inhibition to X in subjects given concurrent pre-exposure. Our description of the data was supported by an analysis of variance (ANOVA), with group, trial and the counterbalanced factor of conditioned solution (saline or sucrose as X) as the variables. This revealed significant main effects of group, $F(2, 18) = 3.58$, trial, $F(2, 36) = 121.68$, and a significant interaction between this factors, $F(4, 36) = 3.59$ (here and elsewhere, a significance level of $p < 0.05$ was adopted). An analysis of simple effects revealed that groups differed significantly on the X-test trial, $F(2, 54) = 6.14$. Subsequent pairwise comparisons using Duncan's test showed that that group CNC drank significantly less than groups ALT and BLK on this trial. There were no other significant effects (largest $F < 1.05$).

The right-hand panel of Fig. 1 shows the group mean consumption of AX on the generalization test. It is clear that subjects in group ALT drank more than those in group BLK. The performance of these two groups confirms the finding that alternating pre-exposure to a pair of stimuli, in this case AX and X, reduces the generalization between them to a greater extent than blocked pre-exposure. Animals in group CNC, however, showed greater generalization (less consumption) than those in groups ALT and BLK. This difference mirrors those observed previously during the conditioning stage. That suggests that the enhanced generalization observed in group CNC relative to groups ALT and BLK can be explained in terms of parallel differences in the level of conditioning to X. Statistical analysis confirmed all these impressions. An ANOVA conducted on these data, with group and conditioned solution as the variables, revealed a main effect of group, $F(2, 18) = 11.14$. Pairwise comparisons using Duncan's test showed that group ALT differed significantly from groups CNC and BLK, and that these two groups also differed significantly from one another. No effect of conditioned solution was observed, nor was there any interaction between group and conditioned solution, F's < 2.45.

3. Discussion

The results of the present experiment confirm Rodríguez and Alonso's (2004) finding that alternating pre-exposure to a compound flavour (AX) and to one element of that compound (X) is more effective than blocked pre-exposure in reducing generalization between them (see also Hall et al., 2006). This finding is consistent with Gibson's (1969) suggestion that alternating pre-exposure to two stimuli enhances their discriminability (and thus reduces generalization between them) by allowing animals to compare them. One implication of this account is that if the opportunity for comparison between the stimuli is increased, then a stronger generalization-reducing effect should be observed. The present experiment aimed to test this prediction by presenting AX and X simultaneously throughout pre-exposure (and thus providing the best conditions for comparison to occur) in the concurrent pre-exposure condition. Contrary to Gibson's comparison hypothesis, it was found that this concurrent pre-exposure schedule resulted in more generalization than alternating and blocked schedules, thereby replicating previous results reported by Alonso and Hall (1999) and Bennett and Mackintosh (1999; experiment 2).

As noted in the Introduction, it has been suggested that two processes might underlie this enhanced generalization. One is sensory preconditioning, and the other is the attenuation of the latent inhibition to the stimulus common features. We argued above that the experimental design used here neutralized sensory preconditioning, and allowed (by giving conditioning to X alone) a direct assessment of the contribution made by latent inhibition to X to the test performance. It was observed that concurrent schedule resulted in stronger conditioning to X than alternating and blocked schedules. This clearly suggests that the reason why concurrent pre-exposure resulted in enhanced generalization was that simultaneous presentations of the stimuli (AX and X) reduced latent inhibition to their common features (X).

One possible explanation for this attenuation of latent inhibition emerges from the well established finding that latent inhibition is attenuated by a change of context between pre-exposure and conditioning. Animals in a concurrent condition experienced the presentation of two different stimuli (AX and X) on each pre-exposure trial. By contrast, they experienced the presentation of one single stimulus (X) during conditioning. It follows that the transition from pre-exposure to conditioning could be accompanied by some sort of context change for these animals, but not for those given alternating or blocked schedules, who receive presentations of one single stimulus in both pre-exposure (AX or X) and conditioning (X) phases. This context change would be expected to attenuate latent inhibition and so explain the stronger level of conditioning to X that was observed in the concurrent condition.

There is nothing in the results presented here (nor in those reported by Bennett and Mackintosh, 1999) to test the validity of this explanation. However, this is not a crucial question here. What is important for present purposes is only that whatever process is allowing faster acquisition to the common stimulus features (and is mediating enhanced generalization) in the concurrent condition, the same process is not at work (or, at least, to the same degree) in the alternating and blocked conditions. Under these circumstances, the enhanced generalization found in this condition cannot be taken as a convincing disproof of the notion that the opportunity for stimulus comparison promotes the occurrence of perceptual learning. Clearly, future experiments should be specifically designed to address this issue. That would help in elucidating whether the process responsible for the generalization-reducing effect found after alternating pre-exposure depends or not on stimulus comparison.

Acknowledgements

This research was supported by a grant from the Spanish Ministerio de Ciencia y Tecnología (PB98-0230). The experimental work for this paper took place while the first author was at the University of the Basque Country, and was supported by a postdoctoral fellowship from the Basque Government (Programa de Formación de Investigadores del Departamento de Educación, Universidades e Investigación). We thank G. Hall for helpful discussion.

References

Alonso, G., Hall, G., 1999. Stimulus comparison and stimulus association processes in the perceptual learning effect. Behav. Process. 48, 11–23.

Bennett, C.H., Mackintosh, N.J., 1999. Comparison and contrast as a mechanism of perceptual learning? Quart. J. Exp. Psychol. B 52, 253–272.

Gibson, E.J., 1969. Principles of Perceptual Learning and Development. Appleton-Century-Crofts, New York.

Hall, G., Blair, C.A.J., Artigas, A.A., 2006. Associative activation of stimulus representations restores lost salience: Implications for perceptual learning. J. Exp. Psychol. Anim. Behav. Process. 32, 145–155.

Honey, R.C., Bateson, P., Horn, G., 1994. The role of stimulus comparison in perceptual learning: an investigation with the domestic chick. Quart. J. Exp. Psychol. B 47, 83–103.

Honey, R.C., Bateson, P., 1996. Stimulus comparison and perceptual learning: Further evidence and evaluation from an imprinting procedure. Quar. J. Exp. Psychol. B 49, 259–269.

Mackintosh, N.J., Kaye, H., Bennett, C.H., 1991. Perceptual learning in flavour aversion conditioning. Quart. J. Exp. Psychol. B 43, 297–322.

Mondragón, E., Hall, G., 2002. Analysis of the perceptual learning effect in flavour aversion learning: evidence for stimulus differentiation. Quart. J. Exp. Psychol. B 55, 153–169.

Rodríguez, G., Alonso, G., 2004. Perceptual learning in flavor-aversion learning: alternating and blocked preexposure to a compound and to an element of that compound. Learn. Motiv. 35, 208–220.

Sanjuán, M.C., Alonso, G., Nelson, J.B., 2004. Blocked and test-stimulus exposure effects in perceptual learning re-examined. Behav. Process. 66, 22–33.

Symonds, M., Hall, G., 1995. Perceptual learning in flavor aversion conditioning: Roles of stimulus comparison and latent inhibition of common stimulus elements. Learn. Motiv. 26, 203–219.