Using Taste Aversion as a Tool to Explore Context Conditioning and Perceptual Learning

Geoffrey Hall
Department of Psychology
University of York

I want to write about two things here, and neither, it should be admitted immediately, concerns flavor aversion learning in the strict sense of the term. That is, neither deals with the mechanisms, psychological or physiological, that generate conditioned aversions to tastes or odors. Both, however, take the fact of conditioned aversion as their starting point and use it, in different ways, to explore issues of practical and theoretical interest. The first deals with flavors only indirectly, and focuses, rather, on the possibility that nausea might act as reinforcer that can condition aversions more generally; the second deals directly with flavors, but uses aversion learning as a tool to supply information about how these, and other stimuli, are perceived. In each case I have picked out one experiment that seems (at least to its authors) to merit being called a highlight, prefacing the description of the experiment with some necessary background material.

Nausea-Based Context Conditioning

Background

It has often been suggested that the anticipatory nausea, sometimes developed by patients undergoing chemotherapy for cancer, is a consequence of classical conditioning, in which the context (the clinic) serves as the conditioned stimulus (CS) and the state of nausea, produced by the infusion of cytotoxic drugs, functions as the unconditioned stimulus (US) (see, e.g., Stockhorst, Klosterhalfen, & Steingrüber, 1998a). The fact that nausea can support the acquisition of conditioned flavor aversions lends plausibility to the suggestion; but the assertion that such aversion learning is restricted to flavors constitutes a direct challenge. Following in the footsteps of some other investigators we (the work was done mostly in collaboration with Michelle Symonds) took up the challenge, and set about trying to demonstrate the reality of context conditioning in the rat.

Table 1
Blocking test for context aversion conditioning

	Context Conditioning	Compound Conditioning	Test (in home cage)	
E	A+Li & B-	Suc -> A+Li	Suc	8.6 ml
C	A+LI & B -	Suc -> B+Li	Suc	1.9 ml

E and C are experimental and control groups; A and B are distinctive contexts; Suc refers to sucrose solution; Li, an injection of lithium chloride. Context conditioning consisted of four trials in each context. Full details are given in Rodriguez et al. (2000).

The basic conditioning procedure that we have used is exceedingly simple; it consists of giving the rat an injection of LiCl in conjunction with exposure to a novel context (a cage different from the home cage). The challenge was to devise a test capable of showing that this treatment results in a context that evokes a state of nausea. We devised several different procedures (a summary of these is to be found in Hall & Symonds, 2006), but I will concentrate here solely on the *blocking* test, as thus is the procedure used in the experiment to be highlighted below. Table 1 summarises the design and results of one of our experiments (Rodriguez, Lopez, Symonds & Hall, 2000). All subjects received initial training with two distinctively different contexts, one of which (A) was associated with an injection of LiCl whereas the other (B) was not. They then received flavor aversion conditioning in which consumption of a sucrose solution was followed by LiCl. For subjects in the experimental condition (E in the table) this occurred in context A; for control (C) subjects it occurred in the B context. Finally we tested the strength of the aversion established to sucrose with a test given in a different context (the home cage). As the table shows, the aversion was attenuated in the E group (consumption was greater in this group then in the C group). We concluded that the initial pairings of context A with LiCl had allowed the context to block acquisition of the aversion to sucrose in the E group, and thus, that these pairings had established the context aversion that we were looking for.

Overshadowing and Potentiation

Our next step was to make use of this experimental paradigm to investigate procedures that might restrict the formation of context aversions, procedures that might, eventually, be used in the clinic to limit the development of anticipatory nausea in chemotherapy patients. In spite of the use of modern antiemetic medication, cytotoxic drugs still produce unpleasant side-effects in a substantial number of patients and, for these, the pairing of the context with nausea is an unavoidable consequence of the treatment. But the contiguous occurrence of the CS and the US does not necessarily mean that a strong association will be formed between them. In *overshadowing*, for example, the presentation of a salient cue along with the target CS will restrict the acquisition of associative strength by the latter. Perhaps such a cue could be presented during chemotherapy sessions to overshadow the context and thus restrict the development of anticipatory nausea. (This cue would itself acquire aversive properties, but this would not matter if we used a novel-flavoured drink, say, that the patient would never need to encounter again.)

There is, however, a major potential problem with this suggestion. Although overshadowing is well established for many training procedures, there are others, and context aversion conditioning is one of them, in which the addition of the extra cue appears to have quite the opposite effect. Rather than producing overshadowing, so it has been claimed, the added cue may act to *potentiate* learning about the context – quite the reverse of the effect we want (and one with possibly disastrous clinical consequences). But before giving up on this idea we (Symonds & Hall, 1999) conducted a review of the relevant literature and came to the conclusion that the evidence for potentiation in context conditioning was weaker than we had supposed, and usually open to alternative explanations. For example, evidence in favor of potentiation has been sought from experiments in which the aversive properties of the context are assessed by mean of a consumption test – by measuring the extent to

which consumption of a novel flavor is suppressed in the pretrained context (e.g., Best, Brown, & Sowell, 1984). Presenting a salient flavor during the initial phase of context conditioning has been found to result in enhanced suppression of consumption. But this outcome is ambiguous – it might reflect a potentiation of context conditioning, but equally it could be a simple consequence of direct generalization from the pretrained to the test flavor. To resolve the issue, we need evidence from an experimental procedure (such as our blocking test) to which this objection will not apply.

Table 2
Overshadowing of context aversion conditioning

	Context Conditioning	Compound Conditioning	Suc (in home cage) Test 1	Test 2
E	A(H)+Li & B(W)+Li	Suc -> A+Li	4.6 ml	5.3 ml
C	A(W)+Li & B(H)+Li	Suc -> A+Li	6.2 ml	8.1 ml

E and C are experimental and control groups; A and B are distinctive contexts; Suc refers to sucrose solution; H to an acid solution; Li, an injection of lithium chloride. Context conditioning consisted of three trials in each context; compound conditioning of two trials. Full details of this experiment are given in Symonds & Hall (1999).

Table 2 presents the design and results of such an experiment (Symonds & Hall, 1999). In this study two groups of rats received compound conditioning in which sucrose was presented in the pretrained context A and followed by an injection of LiCl. Blocking can be expected to occur in both groups; that is, the aversion acquired to A during the first stage of context conditioning should act to block acquisition to sucrose, and both groups might be expected to consume it fairly readily in the final test given in the home cage. The groups differed, however, in the treatment given in the first stage of training. The E group received the overshadowing (or potentiation) treatment in that a salient flavor (the sour taste of acid) was available in context A during this stage, whereas the C group received only water. (The C group experienced acid too, but in a different context, B; to balance the books, the E group was given access to water in this other context.) If the added cue overshadows conditioning to context A, that context should be less able to block acquisition to sucrose and consumption on test should be less in the E group than in the C group. This is just the pattern of result obtained.

Implications

I have chosen to highlight this experiment as it seems to me to be important for two reasons. The first is theoretical. According to some, nausea-based learning must be regarded as a special phenomenon, exempt, to some extent, from the laws that govern other forms of learning. Part of the evidence for this suggestion comes from the notion that tastes are uniquely associable with nausea and that exteroceptive

cues (such as those that constitute a context) will support aversion learning only in special circumstances – specifically when there is also a taste present to potentiate the learning. Our results contradict this view. They show that context aversion learning, like other forms of conditioning is susceptible to overshadowing; and in doing so they help to bring nausea-based learning back into the fold of general learning theory. Second, the results of the experiment have practical relevance. Secure in the knowledge that context conditioning is susceptible to overshadowing we may go on to attempt to devise interventions that can be applied in the chemotherapy clinic to limit the development of the unwanted side-effects of treatment (see Stockhorst et al., 1998b).

Perceptual Learning

Background

The classic examples of abilities that are assumed to be the product of perceptual learning are to be found in the realm of taste discrimination – the refined abilities of expert wine (or tea, or whisky, tasters) are legendary. But it was not for this reason that we turned to flavour-aversion learning in the rat as our preferred technique for investigating the phenomenon in the laboratory. Rather, it was because we were particularly interested in the effects of mere exposure to stimuli, and flavour stimuli turn out to be ideal for this. To ensure that a rat is exposed to visual (and to a lesser extent auditory) stimuli it is necessary to arrange that the stimuli in question are associated with significant consequences. The associations that will be formed in such circumstances will transfer to subsequent tests of discriminability, and thus will complicate the analysis. With flavors, on the other hand, mere exposure is easy to arrange. A rat must drink from time to time and thus must necessarily expose itself to any flavor that the experimenter adds to its drinking water. The sequence in which the stimuli are experienced can be easily controlled, as can important aspects of their properties – we were particularly interested in the effects of exposure to similar stimuli and the similarity of two tastes, say sugar and salt (A and B) can readily be increased by adding a third taste (X, e.g., acid) to each.

Table 3
Within-subject perceptual learning effect

Preexposure	Conditioning	Test	
AX/BX _ CX	AX+	BX (15.0 ml)	CX (12.0 ml)

A, B, C and X are flavours; + refers an injection of lithium chloride. AX and BX were presented on alternate trials, CX in a separate block of trials. Full details are given in Blair and Hall (2003).

Our initial experiments (e.g., Symonds & Hall, 1995) showed that AX and BX were indeed difficult to discriminate, in that an aversion established to AX generalized well to BX. Prior exposure to the flavors, however, was found to reduce generalization (to enhance discrimination). This was particularly true when the flavors were presented in alternation in the preexposure phase (i.e., AX/BX/AX/BX...);

preexposure in which the flavors were presented in separate blocks of trials (i.e., AX/AX...BX/BX) was much less effective in this regard. A more recent example of this instance of a perceptual learning effect (using a within-subject design) is presented schematically in Table 3. In this, all the rats received alternating presentations of two compounds, AX and BX, and a block of trials with a third (CX). An aversion was then established to AX and finally generalization to BX and CX was tested. As the table shows, BX was consumed more readily than CX, indicating that BX was better discriminated from AX than was CX.

Testing Possible Explanations

This result is what might be expected if the alternating preexposure procedure (perhaps because it promotes stimulus comparison) engaged a perceptual learning process of the sort envisaged by Gibson (1969). Such a process might be postulated to enhance the perceptual effectiveness (the effective salience) of features that distinguish between the preexposed stimuli (the A and B features), thus facilitating discrimination between AX and BX. The mechanism, in our generalization test procedure would be twofold – a salient A stimulus during conditioning with AX would detract from the strength acquired by the X element; a salient B stimulus on test would detract from the ability of X to elicit such conditioned responding as it had come to control.

This interpretation requires the postulation of a novel learning process (that responsible for salience change), and before pursuing it, it would be well to be sure that the results cannot be explained in terms of associative learning mechanisms with which we are familiar. And, in fact, an associative interpretation has been proposed (McLaren & Mackintosh, 2000). Rather than going into (the ingenious) details of this account, it will be enough to say that this explanation depends on the suggestion that alternating exposure to AX and BX seems capable of establishing inhibitory associations between the features A and B. There is some evidence to support the possibility such associations can be formed, but they provide the basis for the perceptual learning effect must be doubted, given the experiment I will describe next.

Table 4
Testing the role of feature A

	Preexposure	Conditioning	Test	
	X/BX _ CX	X+	BX (9.3 ml)	CX (4.8 ml)

B, C and X are flavours; + refers an injection of lithium chloride. X and BX were presented on alternate trials, CX in a separate block of trials. Full details are given in Blair et al. (2003).

The experiment summarized in Table 4 is essentially a replication of that shown in Table 3, with one important difference – in this the feature A was omitted. With this design, inhibitory associations between A and B can play no part, but the opportunity to compare the compound BX against its 'background' (X) might still be

expected to enhance the salience of the distinctive feature, B. In this case the feature B should still be better able to interfere with the expression of an aversion acquired to X than is the control stimulus C, and this is just what the test results showed. Consumption was low on test (there was no A stimulus in the conditioning phase to overshadow conditioning to X); but the aversion to X was much less evident in testing with the BX compound than in testing with the CX compound.

Implications

I have chosen to highlight this last experiment because it seems to show (in conjunction with a body of related work; see Hall, 2003) the need to allow the existence of a further learning process additional to that responsible for the formation of associations. Associative learning principles concern the processes that generate a link between the central representations of two events (such as a taste and nausea, in the case of taste aversion learning). The further process appears to one that modulates the effectiveness with which an event is capable of activating its representation. That the effective salience of a stimulus might decline over the course of repeated presentations is not in itself a contentious notion – the familiar phenomenon of habituation can be construed in just these terms. Work on perceptual learning raises the intriguing prospect that habituation, as normally understood, may be only part of the story and that experience with a stimulus is capable not only of lowering but, in some circumstances, of maintaining or even raising its effective salience. We are currently working (using taste aversion techniques) to try to specify what these circumstances are, and thus to specify the mechanism involved.

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Addendum

What I have written contains none of the autobiographical detail that has characterized other contributions to this series, so I thought I would add a little here. I first came across taste-aversion learning in the early 1970s when I was a postdoc at the University of Sussex. A research group led by David Booth was investigating (among other things) diet selection by rats, and talking to members of that group introduced me to the phenomenon. That 'bait shyness' might be an instance of learning seemed to me at that time, as to many others, to be no more than a curious quirk, and not one to distract us from the real business of formulating general theories of learning based on studies of discrimination in the pigeon and conditioned suppression in rats. My confidence began to falter with the advent of other examples of what were then sometimes called 'constraints on learning' -- Shettleworth's demonstrations of the variable effectiveness of food reinforcement; Bruce Moore's studies of the newly discovered autoshaping (that I saw close up during a further postdoctoral period at Dalhousie University). It was with some relief that I observed, over the years, the success with which (for the most part) effects like these were incorporated within an expanded and strengthened general learning theory. (Our own work on overshadowing in context aversion learning can be seen as a contribution to this effort.) But even before this theoretical realignment was complete, learning theorists had taken to taste aversion conditioning as a standard technique for testing their general theories. I recall on a visit in about 1980 to Bob Rescorla's lab (then in Yale), being impressed by the effectiveness of the technique for investigating basic questions about within-compound association and related matters. I went back to my, fairly new, job at York with the notion of using the phenomenon in the same way, and it has been an important part of my experimental armoury ever since. The experiments described above are a sample of the results.