

Can Theories of Animal Discrimination Explain Perceptual Learning in Humans?

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We present a review of recent studies of perceptual learning conducted with nonhuman animals. The focus of this research has been to elucidate the mechanisms by which mere exposure to a pair of similar stimuli can increase the ease with which those stimuli are discriminated. These studies establish an important role for 2 mechanisms, one involving inhibitory associations between the unique features of the stimuli, the other involving a long-term habituation process that enhances the relative salience of these features. We then examine recent work investigating equivalent perceptual learning procedures with human participants. Our aim is to determine the extent to which the phenomena exhibited by people are susceptible to explanation in terms of the mechanisms revealed by the animal studies. Although we find no evidence that associative inhibition contributes to the perceptual learning effect in humans, initial detection of unique features (those that allow discrimination between 2 similar stimuli) appears to depend on an habituation process. Once the unique features have been detected, a tendency to attend to those features and to learn about their properties enhances subsequent discrimination. We conclude that the effects obtained with humans engage mechanisms additional to those seen in animals but argue that, for the most part, these have their basis in learning processes that are common to animals and people. In a final section, we discuss some implications of this analysis of perceptual learning for other aspects of experimental psychology and consider some potential applications.

Keywords: perceptual learning, discrimination, attention, habituation, association

Mention of human perceptual learning immediately brings to mind the refined discriminative skills of “experts” of various kinds—wine tasters, tea tasters, chicken-sexers, and so on. William James gave us some impressive examples:

In the purely sensorial field we have the well-known virtuosity displayed by the professional buyers and testers of various kinds of goods. One man will distinguish by taste between the upper and lower half of a bottle of old Madeira. Another will recognize, by feeling the flour in a barrel, whether the wheat was grown in Iowa or Tennessee. The blind deaf-mute, Laura Bridgman, had so improved her touch as to recognize, after a year’s interval, the hand of a person who had once shaken hers; and her sister in misfortune, Julia Brace, is said to have been employed in the Hartford Asylum to sort the linen of its multitudinous inmates, after it came from the wash, by her wonderfully educated sense of smell. (James, 1890, pp. 509–510)

On the face of things, it may seem unlikely that laboratory studies of discrimination learning by rats or pigeons would have much to say about the development of skills like these. On the

other hand, we should note that, although these experts may be naturally gifted, they have refined their skills only over the course of prolonged experience and practice. That is, their abilities are a product of a learning process, making it at least reasonable to use our well-developed accounts of animal discrimination learning as the basis of an account of the mechanisms involved. We next offer a preliminary justification for this view.

Preliminary Considerations

In fact, one of the earliest experimental studies of perceptual learning (that by Gibson & Walk, 1956) was conducted using animal subjects (we use “animal” to refer to nonhuman animals). The stimuli used in this study were (relatively) complex (shapes—a triangle and a circle), and the training procedure consisted merely of prolonged exposure to them; experiments of this general type form the bulk of the review that follows. However, in both these aspects (the complexity of the stimuli; training that involved mere exposure), Gibson and Walk’s (1956) procedure differs from that used in a substantial number of studies of human perceptual learning, studies conducted for the most part, by researchers whose primary interest has been in mechanisms of perception rather than in learning itself.

Simple Sensory Discriminations

Although there have been exceptions (see, e.g., Furmanski & Engel, 2000) studies of human perceptual learning conducted in the context of perception and psychophysics have used simple

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stimuli, often differing only along a single dimension. Experience with such stimuli, usually involving very many training trials, has been demonstrated to produce an improvement in discrimination. For example, positive effects have been obtained in motion direction discrimination (Ball & Sekular, 1982), orientation judgments (e.g., Vogels & Orban, 1985), vernier acuity (e.g., McKee & Westheimer, 1978), and texture discrimination (Karni & Sagi, 1991). In some of these studies it has been found that improved sensitivity generated by training with stimuli presented in one part of the visual field will fail to transfer to stimuli presented in a different part. This has prompted the proposal that the important change reflects plasticity in early or basic processing mechanisms (e.g., in area V1 of the visual cortex). Such a mechanism would be rather different from the general learning processes postulated by animal learning theory, in which case, insights from studies of perceptual learning in animals might be restricted to effects obtained with more complex stimuli (in humans, perceptual learning effects with complex visual stimuli do not show retinotopic specificity, e.g., Furmanski & Engel, 2000).

It would be premature, however, to conclude on the basis of these data that central processing changes are responsible for perceptual learning effects with complex stimuli but that more peripheral changes operate for simpler stimuli. Recent evidence has cast doubt on the idea that training-induced improvements in simple sensory thresholds occur solely in early visual cortex (for a review see Lu, Hua, Huang, Zhou, & Doshier, 2011). One particularly ingenious experiment provides a clear demonstration. Xiao, Zhang, Wang, Klein, Levi, and Yu (2008) trained participants on two tasks (a visual contrast discrimination task and an orientation discrimination task), one at each of two retinal locations. They found that training on one task (e.g., contrast) at Location 1 transferred perfectly to Location 2, at which the other task (e.g., orientation) had been previously trained. That is, as long as some kind of discrimination had been trained at the Location 2, transferring the discrimination task from Location 1 to Location 2 did not affect performance. This suggests that contrast sensitivity improved as a consequence of changes in central processing (and some other change occurred that enhanced performance at specific locations but was not stimulus specific). As Dwyer (2008) has pointed out, if perceptual learning about both simple and complex stimuli occurs centrally, this opens the possibility that the same mechanism is at work in both cases. Of particular interest in the present context is that the mechanisms of animal discrimination learning might be responsible for perceptual learning in humans, perhaps with both complex and simple stimuli. One possible mechanism will be considered straightaway.

Learning With Feedback

In experiments on human sensory discrimination, the participants are customarily given feedback (knowledge of results) during training (i.e., they are told if they are right or wrong when they report the presence or absence of a difference between the stimuli). The same is true for the “experts”—that is, the wine taster can check his guess by reading the label on the bottle; the chicken-sexer will soon hear about it if she classifies a cock as a hen; and so, presumably, did Julia Brace when she gave the wrong item of linen to one of the inmates. This fact means that many examples of perceptual learning are readily accommodated by the (associative)

theories that have emerged from study of discrimination learning in animals.

Perceptual learning training with feedback is not formally different from that experienced by a rat required to choose between a triangle and circle, say, when one of these is followed by a given outcome (e.g., access to food) and one is not. Contemporary associative theories of animal discrimination learning (e.g., that proposed by Rescorla & Wagner, 1972) provide an explanation of such learning. Thus the Rescorla-Wagner account of discrimination learning treats the stimuli as being compounds, call them AX and BX, where A and B represent those features unique to a given stimulus (the sharp corner of the triangle, the curve of the circle) and X represents features they hold in common (e.g., black shape). If AX is followed by food and BX is not, then the associative learning principle used by the Rescorla-Wagner model predicts that A will gain positive associative strength, and B negative strength. In this, as in many similar models of learning, stimuli compete for associative strength with the result that the incidental, X, features, which lose the competition, end up with little strength and responding will be controlled by A—the feature that predicts food. Another contemporary model of associative learning, proposed by Mackintosh (1975), predicts that, because A is a better predictor of food than X, attention to A will be higher than to X. This will lead to more learning about A than X, and so, again, responding will be controlled by A on AX trials and will not generalize to BX. Discrimination produced by differential reinforcement is what such theories have been designed to explain.

Theories of this sort can be applied to simple sensory discriminations—a given tone and a slightly higher tone (say) can be construed as having distinctive features (comparable to A and B) and features in common (X). It is worth noting, then, that an associative learning model has recently been proposed in the perception literature to account for changes in simple sensory thresholds. Petrov, Doshier, and Lu (2005) described a Hebbian learning model in which the discriminating features are selectively reweighted according to their predictive value. Consistent with Xiao et al. (2008), Petrov et al. suggested that these changes in weights occur at the level of the decision about the stimulus (central processing) not in the early sensory representations. It is clear that this model, which was tested in a simple orientation-discrimination experiment by Petrov et al. (2005), has much in common with the Rescorla-Wagner (Rescorla & Wagner, 1972) and Mackintosh (1975) analyses of discrimination learning. When it comes to perceptual learning with feedback, therefore, associative learning theory, or theories of animal discrimination, have much to offer the human perceptual learning theorist. There are other perceptual learning phenomena, however, that present a greater challenge.

Mere Exposure: Perceptual Learning With No Feedback

What is more difficult to explain in associative terms is perceptual learning that occurs as a consequence of mere exposure to stimuli, in the absence of any reinforcement. In the study by Gibson and Walk (1956), mentioned above, rats were raised from infancy in cages in which cut-out figures (geometrical shapes—triangles and circles) were displayed on the walls. When tested in adulthood these preexposed animals were much better than a

nonpreexposed control group in solving a discrimination test in which one shape but not the other was associated with food reward. The finding evoked considerable interest and generated a large number of follow-up studies (reviewed by Hall, 1980). These successfully confirmed the reliability of the effect, helped define its boundary conditions, and demonstrated that it was not a phenomenon found only in immature animals (Hall, 1979). A major reason for the interest in this finding was that it was taken to constitute an important challenge to the theories of learning then current. These associative theories (e.g., that proposed by Spence, 1936, which is a direct precursor of the Rescorla & Wagner, 1972, theory) emphasized the role of reinforcement. But what the Gibson and Walk (1956) result shows is that learning (during the exposure phase) occurs without differential reinforcement.

Perceptual learning in the absence of informative feedback has also been observed in humans, with both simple and complex stimuli (e.g., Herzog & Fahle, 1997). Particularly interesting examples can be found in the categorization literature. Thus, Goldstone (1994) asked his participants to categorize squares of subtly different size and brightness. There were four different sizes and four different levels of brightness (16 stimuli in total). Half the participants were asked to categorize according to size; squares of the two lower values on the size dimension (regardless of brightness) required one response, larger squares required a different response. Feedback was given for this aspect of the task. This training created a categorical boundary between the two smaller and the two larger sizes. The remaining participants categorized according to brightness. As can be predicted from the models described above (e.g., Mackintosh, 1975; Petrov et al., 2005), for participants given the size discrimination, size became a major determinant of perceived similarity; squares of the two low values on the size dimension were seen as very different from the larger types of square (training on the brightness dimension had the same effect with respect to brightness). Interestingly, however, the stimuli categorized *together* were also perceived as more different after training; that is, exposure in which the stimuli were not associated with different consequences was also effective in facilitating discrimination (McLaren, Leavers, and Mackintosh, 1994, reported a similar result using more complex stimuli).

Conclusions

Exposure to difficult-to-discriminate stimuli can improve subsequent discrimination performance, both for humans and animals, and both for simple and for complex stimuli. The change produced by mere exposure is not to be explained in terms of the formation of associations of the sort described by the Rescorla-Wagner model—rather, there appears to be a change in the perceptual properties of the stimuli that makes them more discriminable. According to Gibson and Levin (1975), “the simple and ancient notion [of learning by association] does not work for perceptual learning, because what is learned is not the addition of something but the extraction of something” (p. 23). This does not, however, mean that animal learning research has nothing to contribute to perceptual learning research. Having acknowledged what it was not, animal learning theorists have since taken up the challenge of attempting to specify what mechanisms are in fact responsible for the perceptual learning effect generated by mere exposure to the stimuli.

Although the specific procedures have been rather different (the majority of modern animal perceptual learning experiments have used flavors as the critical stimuli and Pavlovian conditioning in the test phase), the general design has been that used by Gibson and Walk (1956)—simple preexposure to a pair of similar stimuli followed by a test of discrimination. A review of this work is presented in the first main section of this article. We focus mainly on material published since 2000, as earlier work has already been reviewed by Hall (1991, 2001). These more recent findings suggest that there is a set of mechanisms that are jointly responsible for the perceptual learning effects seen in animals. Subsequent sections of this article will examine the applicability of these mechanisms to perceptual learning effects in humans. The last 10 years has seen the publication of a set of experimental studies using human subjects and complex stimuli that parallel, in their essentials, the Gibson-Walk paradigm. We review these experiments in the second major section of the article, offering interpretations based on conclusions from the animal work. To anticipate, this survey will reveal some intriguing differences between the effects obtained in animals and those seen in people. Analysis of the mechanisms responsible for these differences, in the next section of the article, prompts the conclusion that studies of human perceptual learning can engage mechanisms additional to those at work in studies with animal subjects. Finally we consider the possibility that these additional mechanisms are the product simply of procedural differences between the animal and human studies and examine the extent to which they can be accommodated by generally applicable learning principles.

Perceptual Learning in Animals

With just a few exceptions, recent experiments providing homologues of the Gibson-Walk (Gibson & Walk, 1956) perceptual learning effect have used mature animals as the subjects (but see Chotro & Alonso, 1999, for a study with infant rats), and flavors as the stimuli (but see Prados, Artigas, & Sansa, 2007, for an example using spatial cues; Mondragón & Murphy, 2010, for a study using auditory cues). The basic procedure was introduced by Honey and Hall (1989) and developed by Mackintosh, Kaye, and Bennett (1991). In these experiments the critical stimuli, referred to as AX and BX, are constructed from the three distinct flavors A, B, and X. For example, in Mackintosh et al.’s (1991) experiment, lemon juice was used as the common element (X); salt and sugar (elements A and B) were then added to the lemon juice to produce two similar flavors—salty lemon and sweet lemon. These were added to the rat’s drinking water, a procedure that ensured that the stimuli were fully experienced during the preexposure phase, as the rat must necessarily drink. Discrimination performance after preexposure was tested by examining the generalization of a conditioned aversion. Thus in the study by Mackintosh et al., one group of rats was given preexposure to AX and BX, another experienced only unflavored water. Following this treatment, the animals were allowed access to AX (e.g., sweet lemon) and were then injected with lithium chloride (LiCl) to induce nausea. This conditioning resulted in an aversion to AX (shown as suppression of consumption of this flavor). The question of interest was the extent to which this aversion would generalize to BX (salty lemon). Mackintosh et al. found that the rats given preexposure to AX and BX drank more BX on test than did the rats given no

preexposure to the target flavors; that is, the aversion generalized rather poorly for the preexposed animals. Reduced generalization was equated with an enhanced ability to discriminate between AX and BX.

The Role of Latent Inhibition

The degree of generalization between AX and BX will depend, in part, on the amount learned about AX during the conditioning phase. If, to take an extreme example, preexposed subjects failed to learn about AX during conditioning, then an absence of generalization to BX could scarcely be taken as evidence of an increased ability to discriminate between the stimuli. McLaren and Mackintosh (2000; see also McLaren, Kaye, & Mackintosh, 1989) have offered just such an explanation for results of the sort reported by Mackintosh et al. (1991). They pointed out that when animals are exposed to AX and BX on multiple occasions, the common X element is presented twice as often as either of the unique elements A or B. Hence X will be more familiar than A and B. Familiar stimuli are learned about less readily than (otherwise equivalent) novel stimuli, an effect termed *latent inhibition* (Lubow & Moore, 1959).

Latent inhibition is multiply determined (see Hall, 1991); but an important component appears to be a reduction in the ability of the stimulus to command that aspect of attention required for new associative learning (the *associability* of the stimulus; Pearce & Hall, 1980; Hall & Rodriguez, 2010). The fact that X will suffer more latent inhibition than A or B is enough to explain why preexposure should reduce generalization of an aversion from AX to BX. When AX is paired with LiCl, the rats will readily learn the relationship between the relatively novel A and nausea but not that between the more familiar X and nausea. It is the associative strength of the common element X that determines the degree of generalization of the taste aversion from AX to BX. Therefore, following preexposure, generalization between AX and BX will be low because X is highly latently inhibited and acquires little associative strength on the conditioning trials with AX. It may be noted that this simple process is enough to explain the enhanced discrimination shown by the rats in the original Gibson and Walk (1956) procedure.

The implication of this account, that generalization between AX and BX is importantly determined by the effects of preexposure on the X element, has been confirmed in further experiments by Mackintosh and his colleagues. Thus, Bennett, Wills, Wells, and Mackintosh (1994) found that preexposure to X alone is capable of reducing generalization of an aversion from AX to BX. Conversely, preexposure in which the elements A and B are presented alone, is far less effective in restricting generalization from AX to BX than is preexposure to AX and BX themselves (e.g., Scahill & Mackintosh, 2004).

It should be stated immediately, however, that although it supplies a satisfactory explanation for these cases, latent inhibition is capable of explaining only a limited set of perceptual learning effects. First, not all perceptual learning procedures, in particular those conducted with human participants, involve a conditioning phase of the kind described above. Second, there are now many examples of perceptual learning from experiments that use a generalization test but that control for stimulus familiarity. We consider these next.

The Intermixed-Blocked Effect

The contribution of latent inhibition to the perceptual learning effect can be eliminated by comparing two groups given an equivalent amount of preexposure to the stimuli, but on different schedules. The intuition underlying this suggestion (first introduced by Honey, Bateson, & Horn, 1994) was that a schedule in which the critical stimuli were presented in alternation would (perhaps because it would aid comparison between them) be especially likely to produce a perceptual learning effect. This intuition has been amply confirmed experimentally by studies demonstrating what has become known as the *intermixed-blocked effect*.

Animals given preexposure to AX and BX in an *intermixed* fashion (i.e., given the trial sequence: AX BX AX BX . . .) perform better on test than animals preexposed to AX and BX according a *blocked* schedule, in which all AX presentations are given prior to BX presentations (AX AX . . . BX BX . . .), or vice versa. This intermixed-blocked effect has been obtained in a range of procedures—for example, with visual stimuli in chicks (Honey et al., 1994), flavor stimuli in rats (Symonds & Hall, 1995), auditory stimuli in rats (Mondragón & Murphy, 2010), maze learning in rats (Prados et al., 2007), and perceptual learning of outcomes in an instrumental conditioning procedure in rats (Blair, Blundell, Galtriss, Hall, & Killcross, 2003).

It is difficult to explain the intermixed-blocked effect in terms of the latent inhibition mechanism discussed earlier, as the amount of exposure given to the various elements of the stimuli is the same in both schedules. Admittedly, given our partial understanding of the mechanisms responsible for latent inhibition, it might be argued that, for some reason, the intermixed arrangement generates more latent inhibition to X than the blocked schedule (see Mondragón & Hall, 2002; Mondragón & Murphy, 2010). This cannot, however, explain the results of a within-subject version of the intermixed-blocked effect demonstrated by Blair and Hall (2003). In this experiment, rats were given intermixed exposure to two similar flavor stimuli AX and BX. They were also given exposure to a third flavor CX, either before or after all AX and BX presentations. Thus, with respect to AX, presentations of BX were intermixed, but presentations of CX were blocked. A generalization test showed that discrimination between AX and BX was better than discrimination between AX and CX. The critical feature of this design is that the X element was common to all three stimuli. Therefore, latent inhibition of the common element cannot explain any differences between the intermixed (BX) and blocked (CX) conditions.

Stimulus comparison. The superior effectiveness of the intermixed preexposure schedule accords well with the fact of everyday experience that the opportunity to compare similar stimuli makes it easier to tell them apart (see Gibson, 1969, for a more formal statement of this notion). The obvious implication is that increasing the opportunity for comparison, by presenting the stimuli more closely together in space and time, should enhance the magnitude of the perceptual learning effect. Unfortunately, experiments with animals have failed to support this suggestion.

Honey and Bateson (1996) varied the interval between stimulus presentations for the intermixed (AX/BX) preexposure trials in their chick imprinting procedure. A short delay between presentations might be expected to allow greater opportunity for comparison, and therefore produce a greater perceptual learning effect. In

fact, when the chicks were later required to learn a discrimination between the preexposed stimuli, the reverse result was observed. That is, long intervals between trials during preexposure produced better discrimination performance than short intervals. Similar results have come from experiments using flavor-aversion procedures in which the interval between presentations has been reduced to near zero by presenting two bottles, one containing flavor AX and one BX, concurrently (in which circumstances the rats are permitted to move freely between the two bottles). Such experiments (e.g., [Alonso & Hall, 1999](#); [Bennett & Mackintosh, 1999](#)) have uniformly found that generalization of a conditioned aversion between AX and BX was greater when the flavors were presented concurrently than when they were spaced according to an intermixed schedule.

None of these results provides support for the idea that an increased opportunity for stimulus comparison will promote perceptual learning. Indeed, it now becomes necessary to explain why the opposite appears to be true. [Honey and Bateson \(1996\)](#) suggested that although short intervals between stimulus presentations might increase the opportunity for comparison, they would also allow the formation of direct associations between the two stimuli. These associations between AX and BX would reduce later discrimination performance, as the response established to AX would tend, by way of the AX-BX association, to be evoked by BX (and vice versa). Support for this interpretation comes from experiments by [Rodríguez and Alonso \(2008\)](#) and by [Rodríguez, Blair, and Hall \(2008\)](#), who made use of procedures designed to preclude the formation of direct associations between the unique features, A and B. These procedures eliminated the deficit seen in previous studies on concurrent preexposure. But it remained the case that concurrent exposure conveyed no special advantage; the experiment by [Rodríguez et al. \(2008\)](#) found no difference between concurrent exposure and standard (spaced) intermixed exposure—both were better than blocked preexposure, and to the same extent.

Using a very different procedure, [S. Wills and Mackintosh \(1999\)](#) provided support for the idea that direct stimulus comparison can enhance discrimination learning, but only under very specific circumstances. They trained pigeons on a pair of simultaneous discrimination tasks, between rectangles that differed in luminance and between stars that differed in the number of points they possessed. In one condition (that we may call the comparison condition) the two similar stimuli (e.g., two rectangles) were presented together; in another the choice was between a rectangle and a star (see also, [Saldanha & Bitterman, 1951](#)). The opportunity for comparison bestowed an advantage, although, significantly, this was true only for the luminance discrimination. Their interpretation was that the results were best explained in terms of a low-level sensory process (likely to operate only in some stimulus dimensions, such as luminance) that allows contrast between simultaneously presented similar stimuli to enhance the difference between them. This process would act to facilitate acquisition of the discrimination but would not necessarily produce the longer-term changes that constitute the perceptual learning effect of interest here. In a further experiment, S. Wills and Mackintosh confirmed that initial training on a luminance discrimination in which the stimuli were presented concurrently did not bestow a benefit when the pigeons were given a further test in which the stimuli were presented individually.

The conclusion that emerges from these experiments with animal subjects is that the extent to which comparison facilitates perceptual learning is, at best, limited. Presenting the critical stimuli in alternation is clearly beneficial (as shown by the basic intermixed-blocked effect), and presenting both concurrently will facilitate the acquisition of some forms of discrimination. But the longer term changes in the perceptual effectiveness of stimuli that characterize perceptual learning do not benefit from the opportunity to compare the stimuli directly. The theoretical interpretations of perceptual learning in animals, discussed next, make use of learning principles that can accommodate this conclusion.

Theoretical Interpretation of the Intermixed-Blocked Effect

The intermixed-blocked effect has been investigated intensively over the last decade (mostly in experiments using rats, the generalization test, and flavors as the stimuli), and its source is thought now to be well understood. Two mechanisms have been argued to be involved, both of which can be introduced by reference to [Figure 1](#). This shows, schematically, a schedule of stimulus preexposure of the sort used in an experiment like that by [Blair and Hall \(2003\)](#), described previously. The figure depicts the procedure in which rats are given access, twice a day, to compound flavor solutions; each is presented four times, the compounds AX and BX according to an intermixed schedule, and CX as a separate block of trials. Recall that after conditioning with AX, generalization to BX was less than to CX (the intermixed-blocked effect that we need to explain).

Although no explicit reinforcement is given, various forms of learning can be expected to occur during such preexposure. That responsible for latent inhibition has already been discussed and has been shown not to be relevant to the explanation of this form of perceptual learning. We focus here on two others, one associative and one nonassociative. The latter is the well-known phenomenon of *habituation*—the observation that repeated nonreinforced exposure to a stimulus will reduce its ability to evoke a response. According to [Hall \(2003\)](#) this effect may be taken to reflect a change in the effective salience of the stimulus, in which case all the components of the stimuli (A, B, C, and particularly X, which is experienced more often) will be effectively less salient at the end of the preexposure phase than at the beginning. The associative process, within-compound conditioning, is equally well established (e.g., [Rescorla & Durlach, 1981](#)). According to standard associative principles, the cooccurrence of the two elements A and X on the first trial can be expected to establish an associative link between them; this may weaken or extinguish on the next trial, on which X occurs in the absence of A, but on this trial an association between B and X will form (and so on). The “thought bubbles” added to the figure are an attempt to represent one consequence of this learning. The associations governed by the X element will result, during the intermixed phase, in activation of the representation of the unique feature, now absent, that was present on the preceding trial. Thus, on AX trials, B will be activated associatively, and on BX trials A will be activated associatively.

We now need to specify how these learning processes might result in subjects showing less generalization between AX and BX than between AX and CX. There is evidence to support the

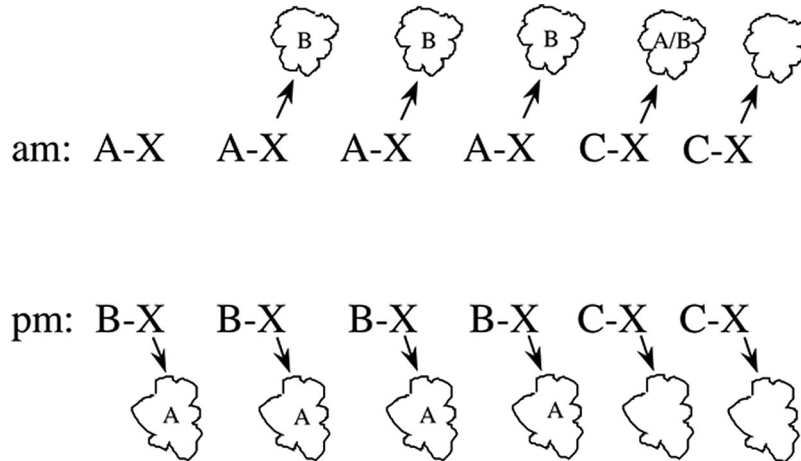


Figure 1. Representation of the preexposure procedure used with rats (e.g., Blair & Hall, 2003), in which access to a compound flavor is given twice a day, there being four presentations each of AX and BX, presented in alternation, and a block of four CX trials. The “bubbles” indicate that the formation of within-compound associations will allow associative activation of the representations of features that are absent.

operation of two processes, which we refer to as *associative inhibition* and *saliency modulation*.

Associative inhibition. McLaren and Mackintosh (2000; see also McLaren et al., 1989) have pointed out that the within-compound associations just described do not exhaust the list of associative connections that will be formed during preexposure. Specifically, standard associative theory (e.g., Wagner, 1981) predicts that, as a consequence of intermixed preexposure, inhibitory links might form between the representations of the unique features A and B. In simple terms, the within-compound associations ensure that A is expected (its representation is activated associatively) on trials when B occurs, and B is expected on trials on which A occurs; B will thus become a signal for the absence of A, and A for the absence of B. With sufficient training A will come to inhibit activation of the B representation, and B of the A representation. Admittedly most demonstrations of inhibitory associative learning have come from experiments involving an event of motivational significance, but experiments by Espinet, Gonzalez, and Balleine (2004) and by Espinet, Artigas, and Balleine (2008) have shown that the effect can be found when neutral stimuli are used (and in the second of these reports, the stimuli were flavors of the sort used in studies of perceptual learning).

This analysis explains the results obtained from generalization testing as follows. When, after conditioning with AX, animals are tested with the blocked stimulus, CX, responding will occur both because this stimulus contains the conditioned X element and because an excitatory X-A link will activate the representation of the A element (a stimulus that has also undergone conditioning). This second source of generalization will be denied to subjects that are tested with the intermixed stimulus BX. For these, the presence of the B element in BX will inhibit activation of the A element. Associative activation of the A representation will, therefore, be unable to contribute to responding. More generally, discrimination between AX and BX is superior to discrimination between AX and CX, because the first pair of stimuli has fewer elements in common than does the second pair. For AX and BX the only elements activated will be those actually presented (others being suppressed

by associative inhibition) so that the only common element will be X. CX, on the other hand, will be able to activate A (and B) associatively and will thus have both X and A in common with AX.

Evidence in favor of this hypothesis comes from demonstrations that intermixed exposure to AX and BX can indeed establish inhibition between A and B. One early finding taken to support the inhibition hypothesis has become known as the “Espinete effect.” Espinet, Iraola, Bennett, and Mackintosh (1995; see also Artigas, Chamizo, & Peris, 2001) presented rats with the flavor compounds AX and BX in an intermixed fashion and then conditioned an aversion to A alone with an injection of lithium chloride. Subsequent tests of B (using both retardation and summation test procedures; Rescorla, 1969) indicated that B had acquired the power to act as an inhibitor for the unconditioned stimulus (US) of illness. Given certain assumptions, this outcome is consistent with the notion that the initial training had established mutual inhibition between A and B. Bennett, Scahill, Griffiths, and Mackintosh (1999) took the analysis a step further by demonstrating that this effect requires intermixed preexposure and was not observed in control subjects given blocked preexposure to AX and BX. (The implications of a further study by Prados, Hall, & Leonard, 2004, showing that under certain preexposure conditions a perceptual learning effect can be obtained when the Espinete effect is quite absent, are taken up later).

Bennett et al. (1999) sought further support for the associative inhibition hypothesis using a preexposure procedure in which the stimuli were presented in pairs, in quick succession on each trial (e.g., AX immediately followed by BX, or vice versa). The arrangement in which BX follows AX should be especially effective in establishing B as an inhibitor of A (Wagner & Larew, 1985); and, indeed, Bennett et al. found that generalization from AX to BX was poor after AX→BX preexposure, a result consistent with the notion that B was able to inhibit the representation of A on test. It should be acknowledged, however, that an alternative explanation of this particular effect in terms of habituation is possible. Artigas, Contel, Sansa, and Prados (2012) have argued that habit-

uation to A is likely to proceed less well in subjects given the AX→BX sequence than in those given BX→AX. Habituation to A will be disrupted by the presence of a salient X in the former case but not in the latter, in which X itself has already undergone habituation. If so, then the salience of A will be greater following AX→BX than BX→AX preexposure. It further follows that the presence of A during conditioning with AX will be more likely to interfere with (*overshadow*) acquisition by X in the former condition. The poor generalization to BX observed by Bennett et al., following AX→BX preexposure and subsequent conditioning with AX, could, therefore, simply indicate that the common X element had acquired little associative strength.

Clearly it would be useful to have a more direct measure of the ability of intermixed exposure to establish inhibition between A and B. This has been supplied in a series of experiments by Dwyer et al. (Dwyer, Bennett, & Mackintosh, 2001; Dwyer & Mackintosh, 2002). In the first of these studies, Dwyer et al. (2001) gave their rats intermixed or blocked exposure to sweet lemon (AX) and salty lemon (BX). They then presented rats with a solution containing both sucrose and salt (AB). Their aim was to examine the ease with which an A-B association would be formed; inhibition between A and B should slow the formation of such an association. To test this, they induced in the animals a state of salt need through an injection that is known to render salt, and other flavors associated with salt, more palatable (Fudim, 1978; Rescorla & Durlach, 1981). Thus, animals that have learned a strong sucrose-salt association might be expected to consume more sucrose solution on test. Dwyer et al. found that animals given intermixed preexposure to AX and BX drank less sucrose (A) on test than those given blocked preexposure. This result is consistent with the idea that intermixed preexposure to AX and BX led to the formation of an inhibitory link between A and B.

Further support comes from a subsequent study in which Dwyer and Mackintosh (2002) again gave rats preexposure to compounds of saline and lemon and of sucrose and lemon (AX and BX) in an intermixed or blocked fashion. They then presented a peppermint-saline solution and induced a salt need in order to increase the tendency to consume peppermint. On test, the rats were given access to a mixture of sucrose and peppermint; those in the blocked condition consumed more of this than those in the intermixed condition. Dwyer and Mackintosh argued that the presence of sucrose in the intermixed but not the blocked condition served to inhibit the representation of salt that would otherwise have been activated by the peppermint flavor. This inhibition of the representation of the desired salt rendered the sucrose-peppermint compound less attractive for subjects given intermixed preexposure.

Taken together, the various experiments described in this section provide reasonably convincing evidence that intermixed exposure to AX and BX can result in inhibition between A and B. We conclude that such inhibition is one likely source of the intermixed-blocked effect obtained in flavor-aversion leaning in rats. But, as we have said, this does not preclude the possibility that other processes contribute to the effect. We turn next to a direct consideration of the roles of habituation and salience modulation.

Salience modulation. Discrimination between two similar stimuli (such as AX and BX) requires that behavior be controlled by their unique and distinctive features (A and B) rather than by features they hold in common (X). Preexposure to the stimuli would thus result in a perceptual learning effect if it succeeded in

enhancing the effective salience of the distinctive features A and B relative to that of the common features X. This is the essence of the salience-modulation theory proposed by Hall (2003). It accepts, in common with the McLaren and Mackintosh (2000) theory, that preexposure to stimuli will establish within-compound associations as depicted in Figure 1 and that these will allow the associative activation of certain stimulus elements on trials when the stimulus itself is not presented (essentially, presentation of X will make the animal think about A and B). For Hall, however, the important consequence of the associative activation of A and B representations is not that it might allow the development of inhibition between them; rather he suggested that associative activation of a stimulus representation can increase its effective salience. This mechanism is explained in more detail next.

Repeated presentation of a stimulus results in a reduction in its effectiveness—the well-known phenomenon of habituation (see, e.g., Hall, 1991). Hall (2003) has characterized this effect as reflecting a reduction in the effective salience of the stimulus. The preexposure procedures used in perceptual learning experiments might thus be thought of as tending to produce a reduction in the effective salience of all the stimulus features presented. Hall suggested, however, that in some circumstances this habituation effect could be reversed. Specifically he suggested that this reversal will occur when a stimulus representation is activated, but the stimulus is not itself present. That is, associative activation of a stimulus representation will lead to an increase in the salience of that stimulus. How does this explain the intermixed-blocked effect?

Intermixed AX/BX presentations will lead to the formation of X-A and X-B associations, each of which will be strengthened on every alternate trial. As a consequence, the representations of A and B will be activated in the absence of A and B on BX and AX trials, respectively. That is, animals will be reminded of A on BX trials and of B on AX trials. On these trials, therefore, the salience of A and B will increase; the salience of X will continue to decline. In contrast, on the blocked schedule (all AX presentations followed by all BX presentations, or vice versa) the X-A and X-B associations are not maintained throughout preexposure as they are in the intermixed condition. There will, therefore, be little associative activation of A and B and therefore little reverse habituation of these elements; all elements (A, B, and X) will suffer a loss of effective salience. Overall then, the A and B features will have been associatively activated on many BX and AX trials in the intermixed but not the blocked schedule. The A and B features will, therefore, be more salient following intermixed than blocked exposure.

Hall (2003) did not propose a mechanism for this reverse habituation process but one emerges from the McLaren and Mackintosh (2000) model. This model views habituation as being, in part, the consequence of a *unitization* process in which associative links are formed among the various components of a stimulus. Thus, exposure to AX and BX will lead not only to links between elements (X-A and X-B) but also to links within the various components that constitute the stimuli A, B, and X. The various components that go to make up, for example, element A will become connected to each other (unitized) and A will become habituated. This is because one element of A (call it *a1*) will prime, via an associative link, another element of A (*a2*), and so the salience of *a2* will be reduced (priming of one stimulus by another leads to habituation—a reduction in salience—in the model). A

further feature of the model is that simultaneous *associative* activation of more than one stimulus will weaken any associative links between those stimuli. Thus, if stimulus A is activated associatively when BX is presented (via an X-A link), the links within A (among the various components that make up A, such as *a1* and *a2*) will be weakened—the habituation process will be reversed, and the salience of A will be maintained.

Support for the proposal that intermixed exposure to AX and BX will maintain the effective salience of the features A and B has come from experiments using Blair and Hall's (2003) within-subject design described previously (see Figure 1), in which rats were exposed to intermixed trials of AX and BX as well as a separate block of CX trials (AX/BX_CX). According to the hypothesis, such training should leave stimulus C with low effective salience, whereas that of A and of B should be higher. One way to test this theory is to examine whether the *associability* of A and B is higher than C following preexposure (see e.g., Dwyer & Honey, 2007). Thus, the greater the salience, the greater the ease with which the stimulus will become associated with some biologically significant outcome such as nausea following injection of LiCl. We shall not, however, take this approach here. This is because the associability of A, B, and C might be affected by factors other than stimulus salience (e.g., associations formed in preexposure might interfere with new learning). More direct measures of salience have, however, been developed, and these will be the focus of the following survey.

Blair and Hall (2003) tested Hall's (2003) hypothesis using what they referred to as a *superimposition* test. In this test, following AX/BX_CX preexposure, the compound stimuli BX and CX were presented. Between preexposure and test, the X element was paired with the administration of LiCl, rendering it aversive. In these circumstances, the expression of the aversion to X will be determined on test, all else being equal, by the salience of the other element of the compound. Thus, if B, for example, is very salient, the animal may not notice the aversive X and will readily drink BX. Conversely, if B is not very salient, X will be more prominent, and the animal will avoid BX. Blair and Hall found that the rats consumed more of BX than CX; that is, the ability of stimulus X to evoke its conditioned response was reduced by the presence of B in the compound. They concluded that the more salient B was better able to interfere with the perception of the X stimulus than was the less salient C element. It may be noted that this result is not readily explained in terms of inhibition between A and B as a consequence of AX/BX preexposure. Specifically, this test procedure does not involve conditioning of A, and so inhibition between A and B should not affect consumption on test.

In a related study, Blair and Hall (2003) gave AX/BX_CX preexposure in which the X element was saline. They again found that after an aversion had been conditioned to X, consumption of BX was greater than that of CX. However, when a salt need was induced prior to the test in another group of rats, rendering X highly palatable, consumption of BX was *lower* than that of CX. Both of these results are consistent with the idea that the presence of the highly salient B element interfered with the perception of X. This reduced the aversiveness of BX when X was aversive but also reduced the palatability of BX when X was palatable.

In a series of follow-up studies Blair, Wilkinson, and Hall (2004) gave rats the same preexposure schedule (i.e., AX/BX_CX) but assessed its impact on the effective salience of the elements B

and C in a range of different ways. In one study they examined the unconditioned response controlled by these stimuli. Rats find quinine aversive and sucrose appetitive, and this effect is related (within limits) to the strength of the solution. Following AX/BX_CX preexposure, rats consumed less quinine on test if quinine had served as the B (intermixed) element in preexposure than if it had served as the C (blocked) element. Conversely, rats consumed more sucrose on test if sucrose had served as B than if it had served as C. This suggests that flavors that had served as unique elements on an intermixed preexposure schedule (element B) were functionally more salient than those preexposed on a blocked schedule (as element C).

The complementary roles of associative inhibition and salience modulation. There is evidence to confirm the viability of both associative inhibition and salience modulation in generating the intermixed-blocked effect in animals. There is reason to think, however, that the contribution of each varies according to the conditions (specifically, the extent) of training. To develop this analysis we begin by considering examples of the intermixed-blocked perceptual learning effect that are not to be explained in terms of the associative inhibition mechanism.

We have already mentioned two instances: Recall that Blair and Hall (2003), with their superimposition test, found a perceptual learning effect in circumstances in which associative inhibition could not be operating; also that Prados et al. (2004) found an intermixed-blocked effect in flavor perceptual learning in rats, but no evidence for the Espinet effect (a test for inhibition) using exactly the same preexposure parameters. Even more telling is a study by Artigas, Sansa, Blair, Hall, and Prados (2006) that demonstrated the intermixed-blocked effect in perceptual learning alongside an effect that was quite the opposite of that predicted by the inhibition account. In brief, they found that, following AX/BX_CX preexposure, rats learned a B-A association faster than they learned a B-C association—quite the opposite of what would be expected if an inhibitory link had formed between B and A but not between B and C. The details of the experiment are presented below.

In Artigas, Sansa, Blair, et al.'s (2006) Experiment 1, rats received preexposure to three compound flavors AX/BX_CX (the design used by Blair & Hall, 2003) and generalization between AX and BX was found to be weaker than between AX and CX—a standard intermixed-blocked effect. In Experiment 2, AX/BX_CX preexposure was again given. For some rats element A was salt, whereas for other rats C was salt. In a second phase, B was paired with salt. That is, B-A pairings were given in group intermixed, whereas B-C pairings were given in group blocked. A salt need was then induced in all rats. Artigas et al. were interested in the degree to which the palatability of B changed as a result of pairings with salt (A or C) after the induction of this salt need. They found that consumption of B was higher in the intermixed group, for whom element A was salt, than it was in the blocked group for whom C was salt. Thus the B-A association in the intermixed group appeared to have been learned faster than the B-C association in the blocked group. As noted above, this result is the opposite of that predicted by the notion that A and B entered an inhibitory relationship in the first phase of training. It may be added that this result is what would be expected on the basis of the salience-modulation account of the intermixed-blocked effect. According to that account the perceptual learning effect seen in

Experiment 1 reflects the fact that the salience of A and B is high, whereas that of C is low; this notion readily predicts the result of Experiment 2 in which A is better able to form the association with salt than is C.

The experiments just described establish that the intermixed-blocked perceptual learning effect can be obtained when the pre-exposure conditions are such that inhibition between A and B is not generated (and the last of them is supportive of the salience modulation account). It is important to note, however, that in all of them, relatively few trials were given during the preexposure phase (usually four presentations of each, as in Figure 1). As we have already said, the development of inhibition between A and B may require extensive initial exposure to AX and BX, and in the experiments that demonstrated such inhibition (Dwyer et al., 2001; Dwyer & Mackintosh, 2002) much more exposure was given. Could it be that the intermixed-blocked effect obtained after restricted initial preexposure depends on changes in effective salience, whereas that obtained after prolonged exposure depends on the inhibitory mechanism?

Answering this question requires direct comparison the effects of brief and of more prolonged exposure on associative inhibition and on salience modulation. Artigas, Sansa, and Prados (2006) have examined the first of these. They gave rats intermixed or blocked exposure to two flavor compounds AX and BX. Half of the animals were given four presentations each of AX and BX (the short-exposure groups). The remaining animals were given 10 presentations each of AX and BX (the long-exposure groups). Artigas et al. then tested both for a perceptual learning effect and also for evidence of inhibition between A and B (by testing for the Espinet effect). Although an intermixed-blocked effect appeared in perceptual learning in both the short and the long groups, evidence of inhibition between A and B was seen only in the long-exposure groups.

The implication that salience modulation effects should be less evident after lengthy preexposure has been tested and confirmed by Contel, Sansa, Artigas, and Prados (2011). They assessed the effective salience of the A feature by testing the response it governed after conditioning with AX as the CS (a more salient A would be expected to have acquired conditioned strength more readily). They found, by this measure, that A was more salient after intermixed than after blocked preexposure in subjects given just four trials each of AX and BX during preexposure (but see also Mondragón & Hall, 2002). Increasing the number of preexposure trials to eight each of AX and BX led to a reduction in the salience of A in the intermixed conditioned and a reduction in the difference between intermixed and blocked groups. Contel et al. (2011) concluded that salience modulation effects are evident only after relatively short preexposure.

Perceptual Learning in Animals: Conclusions

This survey of the literature reveals that several processes are likely to be active in generating the perceptual learning effect observed with animal subjects. First, exposure to the stimuli will result in varying degrees of latent inhibition of their various components. Exposure to AX and BX will mean that X in particular will suffer extensive latent inhibition, and this is enough to explain why generalization to BX after conditioning with AX (which will depend on the associative strength acquired by X)

should be limited. But this mechanism cannot be the only source of perceptual learning. Most important, it cannot explain why intermixed preexposure should be so much more effective than the blocked arrangement, and attempts to explain this difference have constituted the main focus of research into perceptual learning in animals over the past decade.

That intermixed preexposure should be especially effective fits well with the common-sense view that perceptual learning will be promoted by a procedure that increases the opportunity for the relevant stimuli to be compared. But, as we have seen, the mechanism responsible for the effect does not appear to depend on comparison as it is usually conceived; in particular, the advantage bestowed by intermixed exposure is not enhanced by reducing the interval between successive presentations of the stimuli. We turned, therefore, to interpretations that depend on longer-term, associative, learning processes. We have considered two of these—salience modulation and associative inhibition.

Both of these accounts assume that exposure to AX and BX will allow the formation of associations between the component parts of the stimuli: between X and A, and between X and B. Both also suggest that these associations can generate effects that might aid discrimination between AX and BX following exposure on an intermixed schedule. The salience-modulation account accepts that exposure to a stimulus will reduce its effective salience by way of habituation. It proposes, however, that this effect will be reversed when a stimulus representation is activated in the absence of the stimulus itself. The within-stimulus associations established and maintained by intermixed preexposure ensure that A is activated on BX trials and that B is activated on AX trials—the effective salience of the unique features A and B (critical for discrimination between AX and BX) is thus maintained. The associative-inhibition account addresses the fact that the existence of within-stimulus associations is, in itself, likely to hinder discrimination between A and B—these associations will mean that the representation of B will be activated on AX trials as will the representation of A on BX trials. But the standard principles of associative theory predict that intermixed exposure to AX and BX will (given sufficient training) establish inhibitory links between A and B. The disadvantage created by the ability of AX to activate the B representation (and of BX to activate A) will therefore be nullified.

These two theories should not be thought of as alternatives (Contel et al., 2011). Salience modulation effects appear to operate only early in training. With extended exposure, the habituation process may well reduce the salience of all components of the stimuli. That is, the reverse-habituation process of Hall (2003) may only attenuate, rather than abolish, the effects of exposure on salience. Associative inhibition effects, on the other hand, appear to be important only when exposure to the stimuli is prolonged. Indeed, for animals to detect that A predicts the absence of B, and vice versa, they must be able detect the unique features A and B and in this, the salience modulation process may be helpful. The experiments we have discussed support the implication that both processes operate but do so at different stages of training.

In the next major section of this article, the principles of perceptual learning identified in the animal experiments are investigated in experiments with human participants. Given the extensive differences between the procedures used in the animal experiments and those typically used with humans, the reader may be skeptical that the mechanisms outlined above (latent inhibition, conditioned

inhibition, and salience modulation) could, in principle, also operate in studies of human perceptual learning. The proof of the pudding will be in the eating, but the issue deserves some preliminary consideration.

One difference between human and animal experiments is that the former have relied largely on the generalization test as a measure of perceptual discriminability, whereas the latter have usually used more direct measures (e.g., a same-different task or the ability to detect a discriminating feature). The potential problem here is that, generalization of a conditioned response will be affected by factors, such as the strength of the association responsible for that response, that are unrelated to perceived stimulus similarity (see Mitchell, 2009). Only when these other factors are carefully controlled will the results of a generalization test give information relevant to understanding performance on (e.g.) the same-different task. We are confident, however, that such control has been achieved in most of the experiments described above (and, in addition, interpretations generated by studies using the generalization test have been confirmed by experiments using other testing procedures, e.g., by the superimposition test of Blair & Hall, 2003).

A further, quite striking, difference concerns the amount of training employed. Studies with human participants have commonly given very extensive training involving hundreds of trials. The animal experiments have used much less—Hall's salience modulation mechanism, for example, requires only four presentations of each stimulus to be demonstrated. This difference may seem to imply that different mechanisms are involved in the two procedures, but it does not require this conclusion. It may, for instance, simply be a parametric matter, to do with the nature of the stimuli used. The animal experiments have used stimuli that, although they are imperfectly discriminated to start with, are none the less rather different from one another; experiments with humans have used stimuli that are very similar indeed (thus requiring more training for an effect). Moreover, with some stimuli, perceptual learning effects in people can be obtained quite rapidly; Mundy, Honey, and Dwyer (2007), using pictures of faces as the stimuli, showed a reliable perceptual learning effect after only five presentations of each stimulus.

There remains one inevitable difference between the human and animal procedures—only in the former are the subjects intentionally seeking to detect differences between the stimuli. In many procedures, the human participants are given instructions telling them to look for differences between the stimuli; in some they are specifically informed what sort of differences to concentrate on (the apprentice chicken-sexer is told that the key feature is the distance between the anal and genital papillae). In such cases the participants know exactly what the target stimulus is; in a sense, they are experts at the task before they begin training. Animals cannot be instructed what to look out for in the task ahead of them. It could be argued, then, that the mechanisms of animal perceptual learning will not be the same as those in operation in humans who have been given such instructions because, for animals, the central task must be to discover what that critical, discriminating feature is.

We take up this last point later in the article. But to begin the analysis, in the next section, we concentrate on human experimental procedures that are broadly analogous to those used with animals; they use complex multidimensional stimuli, and partici-

pants are not instructed in advance as to the precise nature of the distinguishing stimulus features. The initial question, therefore, is whether the results of experiments in humans, that are procedurally similar to those conducted in animals, can be explained in terms of the mechanisms of animal perceptual learning described above.

Application to Perceptual Learning in Humans

Mackintosh and Bennett (1998) presented a review assessing the extent to which principles derived from studies of the phenomenon in animals might be successfully applied to the explanation of perceptual learning in people. Their conclusion was generally positive—that the principles derived from animal learning theory seem well fitted to explain human perceptual learning (or at least those instances of it that appear to derive from implicit or unintentional learning processes). Our intention here is to update this review in the light both of theoretical developments that have come from continued experimentation with animals and also of the body of experimental evidence on human perceptual learning that has become available only since Mackintosh and Bennett wrote their review. Their review briefly discussed the classic instances—the abilities of the expert (e.g., the chicken-sexer; Biederman & Shiffar, 1987), the effects of familiarity on face recognition (e.g., Chiroro & Valentine, 1995), and training effects in simple sensory discriminations (e.g., Poggio, Fahle, & Edelman, 1992). But these were presented simply as examples of the phenomena to be explained, and the argument offered was that, *in principle*, an explanation of human perceptual learning in terms of animal learning theory is possible. But work conducted since 1998 means that we now have available a set of experimental studies with human participants that not only demonstrate the phenomena but have been explicitly arranged to allow the testing of explanatory theories. Next we outline the main findings to come from this body of work, before going on to attempt to apply to it the theories based on animal studies that were described in the previous section.

Method

Most of the experiments to be discussed have made use of artificially constructed visual stimuli (exceptions are the studies by Dwyer, Hodder, & Honey, 2004, and Mundy, Dwyer, & Honey, 2006, who used compound flavors in a procedure that closely paralleled the experiments done with rats). The stimuli have been devised so as to be difficult to discriminate (at least when first met with). This has usually been arranged by ensuring that they share a large number of irrelevant, nondistinguishing features. An example is provided by the checkerboard displays illustrated in Figure 2 (from Mitchell, Kadib, Nash, Lavis, & Hall, 2008). These all have the same background pattern, shown at the bottom of the figure; each of the other four checkerboards shown in the figure, used as the experimental stimuli, has a unique feature added (outlined in black for illustrative purposes in Figure 2). In the terminology applied to the animal experiments, the background constitutes the common component, X; the added features generate four different compound stimuli, AX, BX, CX, and DX (where A–D refers to the added distinctive feature). Other experiments have made use of pictures of faces—somewhat more natural, but again artificially manipulated for the purposes of analytic study. Modern morphing techniques allow a picture of a face to be

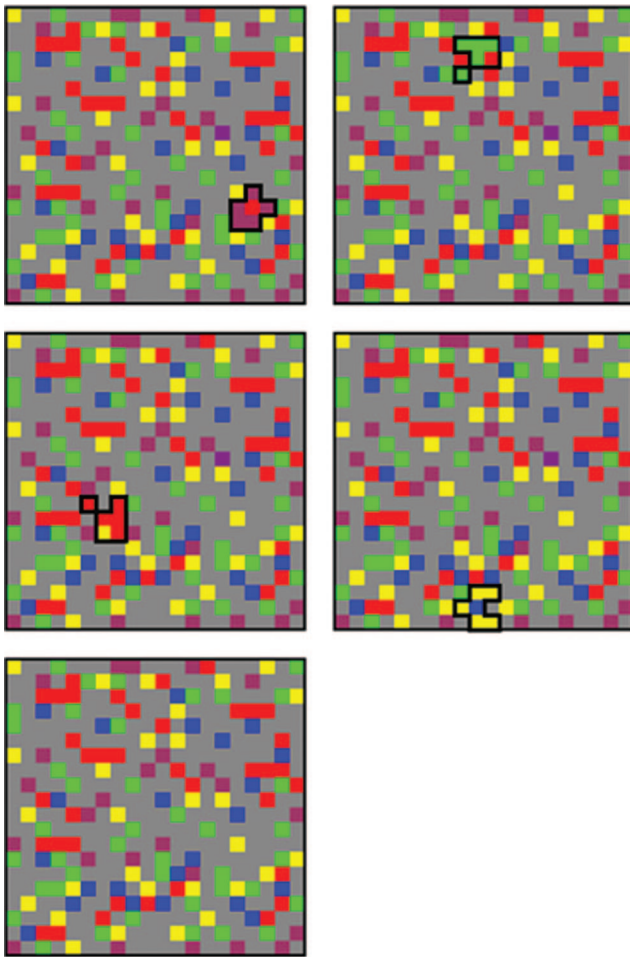


Figure 2. Checkerboard stimuli, as used in the experiments by Mitchell, Kadib, Nash, Lavis, and Hall (2008). The display at the bottom is the common background (X) used for all stimuli. In the other four, a distinctive feature (A, B, C, or D), consisting of pattern of six adjacent squares, has been added. The features are outlined in black for illustrative purposes only. Reprinted from “Analysis of the Role of Associative Inhibition in Perceptual Learning by Means of the Same–Different Task,” by C. Mitchell, R. Kadib, S. Nash, Y. Lavis, and G. Hall, 2008, *Journal of Experimental Psychology: Animal Behavior Processes*, 34, p. 476. Copyright 2008 by the American Psychological Association.

modified marginally, producing two images that are very similar (an example, taken from Mundy et al., 2007, is shown in Figure 3). These stimuli can still be conceptualized, however, as possessing a set of common features (X) and distinctive features (A and B).

The basic procedure has involved preexposure to these stimuli, followed by a test of discrimination. In some studies this test has taken essentially the same form as that used with animals. That is, it has involved explicit discrimination training in which the stimuli are associated with different events and consequences. For example, the participant might be required to learn (by way of feedback) to perform a categorization in which one response key must be pressed when AX is presented, and a different key when BX is presented. An alternative procedure, less readily available for animal subjects, is to use the same-different task, in which partic-

ipants are presented with stimuli in pairs (usually in quick succession) and are instructed to say whether the two are the same or different.

Preexposure Facilitates Discrimination

A simple example of the basic preexposure effect is supplied by Wang and Mitchell (2011, Experiment 1). The stimuli were two checkerboards similar to those shown in Figure 2. Participants received initial exposure in which AX and BX were presented in alternation, 60 times each; each presentation lasted 480 ms, and the interval between trials was 2 s. Discrimination was tested by way of the same-different task that showed that the participants were better able to discriminate the preexposed AX and BX than novel stimuli, CY and DY (stimuli with different distinctive features, C and D, superimposed on a different common background, Y). (See also Goldstone, 1994; A. J. Wills & McLaren, 1998; A. J. Wills, Suret, & McLaren, 2004, for related results).

As was true for studies done with animals, an effect of this sort can be explained without recourse to the mechanisms (inhibition and salience modulation) influencing the effectiveness of the distinctive features of the stimuli that are our primary concern. Preexposure to AX and BX may enhance discrimination, simply because it involves extensive exposure to the X element. As we have noted, Bennett et al. (1994) have shown for rats, that preexposure to X alone is enough to restrict generalization from AX to BX. Wang and Mitchell (2011; Experiment 2) have demonstrated a parallel effect in their procedure, finding enhanced performance (again on the same-different, AX-BX discrimination) when preexposure consisted simply of 120 presentations of X. Mundy et al. (2007) have obtained a similar result using pictures of faces as the stimuli. In the test phase the participants were required to categorize two faces, AX and BX (like those shown in Figure 3), one as left-handed and one as right-handed. Initially they had to guess, but feedback was given allowing a reliable discrimination to be established. Prior to this test, the participants were preexposed to the morphed average of two faces, which can be conceptualized as X (i.e., the features that the two hold in common). Performance was found to be better for AX, and BX than for a novel pair of similar faces CY and DY.

The effect of preexposure to X in the animal studies (e.g., Bennett et al., 1994) was interpreted in terms of latent inhibition, which was equated with a reduction in the associability of the preexposed stimulus. A stimulus that is low in associability will condition only slowly, thus explaining why generalization between AX and BX should be poor. The same process can explain why performance should be enhanced on the categorization task of Mundy et al. (2007); if X is low in associability it will be poor at forming an association with a given response (left-handed, say) and performance based on learning about the critical features, A and B, will be correspondingly enhanced. It should be noted, however, that this interpretation of the latent inhibition effect would not be relevant for performance on the same-different task of Wang and Mitchell (2011), in which no new associative learning is required. To explain this result it is necessary to assume that a preexposed stimulus suffers a reduction in its ability to command attention more generally (rather than in just that aspect of attention necessary to support further associative learning).



Figure 3. Two of the faces used in the study by Mundy et al. (2007). Reprinted from "Simultaneous Presentation of Similar Stimuli Produces Perceptual Learning in Human Picture Processing," by M. E. Mundy, R. C. Honey, and D. M. Dwyer, 2007, *Journal of Experimental Psychology: Animal Behavior Processes*, 33, p. 126. Copyright 2007 by the American Psychological Association.

The Intermixed-Blocked Effect and Stimulus Comparison

The difference demonstrated for animal subjects, between the effects of intermixed and blocked schedules, indicates that preexposure has effects beyond those to be explained in terms of amount of experience of the common X elements. Accordingly, explanation of the intermixed-blocked effect has been a central concern of recent theorizing. It is important to establish, therefore, that the effect is to be found with human participants just as with rat subjects.

An example comes from an experiment by Lavis and Mitchell (2006) using checkerboard stimuli similar to those shown in Figure 2. In preexposure the participants saw 60 presentations of each of these stimuli: AX and BX were presented in alternation (the intermixed schedule); the CX trials constituted a separate block, as did the DX trials. (The order of these phases of stimulus presentation was counterbalanced across subjects, as was the identity of the checkerboard that was designated as AX, BX, CX, or DX.) The subsequent test showed that the participants were better able to discriminate between AX and BX than between CX and DX. This was true both when the test involved new learning (as in the generalization test used for rat subjects) and when it did not. In the former the participants were required to learn to make different responses to AX and BX, and to CX and DX (feedback was given), and performance was found to be much superior with the intermixed pair. In the latter they were simply required to make a same-different judgment when presented with two stimuli, one after the other; they proved to be much better at responding "different" to the AX/BX pair than to the CX/DX pair. Other demonstrations of the superiority of intermixed over blocked preexposure have come from experiments using flavors (Dwyer et al., 2004), pictures of faces (Mundy et al., 2007), and colored shapes (Nelson & Sanjuan, 2009) as the stimuli.

We noted with respect to the animal experiments that, although presenting the stimuli in alternation is beneficial, there is no extra

benefit to be gained by presenting them concurrently. Indeed, the formation of associations between two stimuli displayed together might serve to retard subsequent discrimination between them. Parallel experiments with human participants have produced a different pattern of results. Mundy et al. (2007, Experiments 3 and 4) presented pairs of similar faces either simultaneously (side by side) or successively (on an alternating schedule). Performance on a categorization task was better for the face pairs that had been presented simultaneously than those that had been presented successively. Mundy, Honey, and Dwyer (2009), demonstrated essentially the same effect using checkerboard stimuli.

Further confirmation of the importance of comparison comes from a recent experiment by Dwyer, Mundy, and Honey (2011), in which a distractor stimulus (e.g., a checkerboard) was inserted, during intermixed preexposure, between successive presentations of the two displays (two similar faces) that subsequently had to be discriminated. The distractor, which might be assumed to prevent direct comparison of AX and BX, attenuated the advantage normally bestowed by intermixed preexposure.

In contrast, for animal subjects, even when any effects of within-display associations were eliminated, simultaneous stimulus presentation did not lead to greater perceptual learning. It appears then that humans, but not rats, can benefit from the opportunity to compare the stimuli very directly during preexposure. The implications of this conclusion are taken up later. For the time being it is enough to note that in the experiments to be described shortly (designed to evaluate the application of inhibition and salience modulation theory to the intermixed-blocked effect in humans) the stimuli have been presented successively during preexposure.

Self-Generated Feedback

Before turning to a description of these experiments, it will be useful to address the argument that, in the tasks employed for human participants, the form of learning that goes on during

exposure to the stimuli is necessarily different from that at work in the animal experiments. The theories developed to account for the results of the animal experiments described above are specifically devised to deal with the effects of *mere exposure*, it being acknowledged at the outset that other, or additional, mechanisms will operate when differential feedback is given. The argument has been made, however, that many of the procedures devised for the study of human perceptual learning (e.g., Lavis & Mitchell, 2006; Mundy et al., 2007) have failed to exclude the operation of feedback, so that the learning produced is potentially a consequence of reinforcement rather than the form of perceptual learning we are primarily interested in (Mackintosh & Bennett, 1998; see also Mackintosh, 2009).

People subjected to a set of presentations of similar stimuli will inevitably try to detect differences among them. In many of the experiments described here, they are instructed to do so (e.g., Wang and Mitchell's, 2011, participants were "instructed to pay attention to the presented stimuli and that any differences detected would be useful later in the experiment," p. 438). But even in the absence of explicit instruction, the social psychology of the situation seems certain to be enough to make people look for differences. In these circumstances we can reasonably assume that detecting a difference will generate a feeling of mild satisfaction (i.e., will constitute a small reward). It is the likely occurrence of this "self-generated feedback" that led Mackintosh (2009) to argue that the effects seen in the human experiments were produced by a different mechanism from those at work in the animal experiments.

Mackintosh (2009) was particularly concerned with the possibility that differential reinforcement could teach subjects to attend to some aspects of a stimulus array rather than other aspects. For example, for a complex visual display having a distinctive yellow feature, the reward of spotting this feature will reinforce the tendency to look for yellow features, and future discrimination performance could be facilitated. (There is evidence from studies of eyegaze, described later, that is entirely consistent with this possibility.) That is, deliberate search for the discriminating features can support associative learning relevant to those features, via reinforcement, even in the absence of any externally supplied feedback. This same point has been made in the perception literature. Thus, when participants perform reasonably well on a simple stimulus threshold task, the self-generated feedback produced by regular detection of the target stimulus will serve as reinforcement and lead to reweighting of the target stimulus feature in Petrov et al.'s (2005) Hebbian learning model.

If as Mackintosh (2009) suggests, this kind of self-generated feedback operates in the human experiments but not with animals, then differences could be expected in the perceptual learning effects observed in the two cases. It is important to note, however, that self-generated feedback cannot operate in the way that externally applied feedback is thought to. With the latter there is differential reinforcement, with different stimuli being associated with different outcomes; and theories have been developed (e.g., Mackintosh, 1975) that specify mechanisms by which this arrangement can produce enhanced attention to distinctive features. But self-generated feedback must be the *result* of detecting a difference, it cannot be the initial cause of it. Once a feature has been detected, a reinforcement process may act to increase the tendency to attend to it, but this process does not explain how the feature

was spotted in the first place. Thus, processes dependent on self-generated feedback will enhance performance once exposure has allowed the distinctive features to be identified, but the notion supplies no explanation as to why intermixed exposure should be superior to blocked in this respect. The theories derived from animal experiments, on the other hand, provide some possible answers.

Associative Inhibition

When people are required to make a same-different judgment between two successively presented checkerboards (AX and BX), emitting the correct response would be rendered more difficult if AX activated a representation of B, and BX activated a representation of A. Inhibition between A and B, so that each could suppress associative activation of the other, would be helpful. Thus, the associative inhibition notion can be applied to the human same-different task just as to generalization tests in animals. But although the notion can supply a theoretical account of the intermixed-blocked effect in humans, the experimental evidence suggests that this mechanism plays little role in producing the effect actually observed.

An example is provided an experiment by Lavis and Mitchell (2006). In this study the participants were preexposed to six checkerboards, two pairs in an intermixed fashion (AX/BX and CX/DX), the remaining stimuli (EX and FX) being presented on a blocked schedule. The test compared discrimination between pairs that had been presented together (e.g., AX vs. BX) with that between pairs that had been intermixed with other stimuli (e.g., AX vs. CX). In both cases performance was better than for discrimination between the blocked stimuli, EX and FX, and, critically, there was no difference between the two. Associative inhibition can be expected to form during preexposure between A and B (and also between C and D). Whatever other mechanisms might contribute to the intermixed-blocked effect, this inhibitory association could thus facilitate discrimination between AX and BX (and between CX and DX). It will not play a role, however, when the test discrimination is between AX and CX. For this test, the superiority over the blocked control must be acknowledged to be the result of some other process. Furthermore, inhibition might be expected to bestow some extra advantage for the AX versus BX test, making performance in this discrimination superior to performance on AX versus CX. No such advantage was observed. Further evidence for the occurrence of perceptual learning in the absence of any contribution from mutual inhibition between distinctive features can be found in the experiments reported by Mitchell, Kadib, et al. (2008).

The associative inhibition mechanism of McLaren and Mackintosh (2000) requires that within-display excitatory associations (e.g., A-X) first be formed and then that sufficient training be given to allow inhibition to form between the distinctive features of the displays. Whether the procedures and stimuli used in studies of human perceptual learning are conducive to the formation of such associations is an empirical matter. The failure to find evidence for this mechanism with the checkerboard stimuli does not mean that it will not operate when other stimuli and procedures are used. Indeed, an experiment by Mundy et al. (2006), more closely modeled on those done with rats, has produced evidence said to

demonstrate a role for inhibitory associations in perceptual learning in humans.

The participants in the study by Mundy et al. (2006) drank water to which tastes or odors had been added. One pair of stimuli (e.g., AX and BX) was made up of weak acid (X) mixed with either sucrose or saline (A or B); another pair of stimuli (e.g., CY and DY) was made up of the odor of lemon (Y) mixed with either a raspberry or a strawberry odor (C and D). These compounds were each experienced six times, with presentations following this sequence: AX BX DY CY AX BX DY CY. There followed a conditioning phase in which AX and CY were presented again, this time with an unpleasantly bitter-tasting substance added to the mix. When subsequently asked to evaluate these flavors, the participants (unsurprisingly) rated AX and CY less pleasant than when tasted initially. The same was true of the DY compound, but not of BX. That is, the aversion conditioned to AX and CY generalized to DY but not to BX.

Mundy et al. (2006) argued that this result was consistent with the inhibition account in the following way. The scheduling of trials in preexposure was arranged to ensure that BX always followed AX, and CY followed DY. Thus, B signaled the absence of A, and C the absence of D. In these conditions standard associative theory (e.g., Wagner & Larew, 1985) predicts that inhibitory links will form from B to A, and from C to D (but not in the other direction, i.e., not from A to B or from D to C). When tested with BX, the inhibitory B-A link would suppress any contribution to the response from activation of the A representation; but when tested with DY, D would not have a tendency to inhibit C, and associative activation of the C representation could contribute to the negative reaction observed to DY on this test.

This result is encouraging for those seeking common principles underlying animal and human perceptual learning, and Mundy et al. (2006) presented it as establishing a fundamental similarity between the mechanisms that operate in the two cases. They did not claim, however, that inhibition is a mechanism of major importance in producing perceptual learning effects. An effect consistent with associative inhibition can be demonstrated under the special training conditions of this experiment, but, as Mundy et al. acknowledged, the results of most other experiments with human subjects are not readily explained in terms of inhibition. It is worth adding that the results, even of this study, do not *require* an explanation in terms of inhibition; in common with the results of the related study with rats by Bennett et al. (1999), described earlier, they can be explained in terms of habituation. As Artigas et al. (2012) have argued, when subjects receive a trial sequence like AX→BX, habituation of the second feature (B) is likely to proceed more readily than habituation of the first. This is because B will suffer less competition from the recently presented X element (see Wagner, 1981). Such considerations mean that in the experiment by Mundy et al. the salience of A would be higher than that of C after preexposure. Thus, when AX and CY were conditioned, A would tend to overshadow X more effectively than C would overshadow Y. The resulting difference in strength between X and Y could then explain the test results obtained with BX and DY.

Saliency Modulation

If intermixed preexposure to a pair of checkerboards maintains or enhances the effective salience of their distinctive features (and reduces that of the common background) then performance on a same-different task (which critically depends on responding being controlled by the distinctive features) will be enhanced. This notion of saliency modulation is also capable of explaining the results described in the previous section, some of which proved problematic for the associative inhibition theory. For example, inhibition between A and B produced by AX/BX preexposure cannot explain why a discrimination between AX and CX should be facilitated (the result obtained by Lavis & Mitchell, 2006), but the result follows readily from the notion that such preexposure will enhance the effective salience of A. But although the experiments discussed so far disconfirm the idea that inhibition between unique stimulus features plays an important role in the intermixed-blocked effect in human perceptual learning, they support the alternative, saliency-modulation theory, only to the extent that they are consistent with it. We now consider some recent attempts to find direct evidence that different schedules of preexposure (e.g., intermixed as opposed to blocked) can produce differences in saliency in the unique of the stimuli.

Evidence for saliency modulation. An advantage of using visual stimuli like those depicted in Figure 2 is that it is possible, by monitoring eyegaze, to assess the extent to which the subject is looking at the localized distinctive feature. A more salient feature, it may be assumed, will be more likely to attract gaze than a less salient feature. Wang and Mitchell (2011, Experiment 4) gave their participants intermixed preexposure to AX and BX and separate blocks of CX and DX. They then confirmed, using a same-different test, that discrimination between displays containing A and B was superior to discrimination involving C and D. Monitoring eyegaze during this test showed that, from the outset, the participants spent more time on each trial looking at A or B than at C or D. In a further experiment, Wang and Mitchell showed that eyegaze was greater to the unique features (A and B) of stimuli (AX and BX) that had been preexposed on an intermixed schedule than it was to the novel features C and D, presented as CY and DY (with a familiar Y background). Discrimination of AX and BX was also better on test than was discrimination of CY and DY. Consistent with the notion of saliency modulation, therefore, intermixed preexposure to AX and BX renders the unique features A and B more salient. In fact, preexposure appeared to have increased the salience of A and B relative to that of the novel stimuli C and D. This finding will be taken up later, where we discuss the role of strategic attentional processes in human perceptual learning.

Further evidence for a saliency modulation mechanism comes from a study by Lavis, Kadib, Mitchell, and Hall (2011). They argued that a stimulus feature with enhanced saliency would be better learned about and better represented in memory than a less salient feature. In particular, the various aspects of such a feature, all being high in saliency, should become strongly associated with each other (i.e., unitization should occur readily). Accordingly, unitization should be more evident for the distinctive features of stimuli presented on an intermixed schedule than for those of stimuli presented on a blocked schedule (i.e., the opposite of the effect predicted by McLaren and Mackintosh (2000), an issue to

which we return below). The experiment designed to test this again used checkerboards, but (as is shown in Figure 4) these were slightly different from those described previously, in that the unique features (A–D) were distinctively shaped blocks, each of a different color. Participants received intermixed exposure to two of them (AX/BX) and blocked preexposure (CX_DX) to the others. A standard, same-different, test confirmed that participants were better able to discriminate between the intermixed than between the blocked stimuli. In a further test, the shapes of the unique features A–D were shown without their color, and participants were asked to match the shape of the unique feature to the color in which it was presented during preexposure. Performance on this test was better for the intermixed than the blocked features. That is, knowledge of the intermixed feature was better than of the blocked feature, consistent with the proposition that elements of the former had a higher level of salience than those of the latter.

This finding was confirmed in a related experiment by de Zilva and Mitchell (2012) that used stimulus displays of the sort shown in Figure 5. Of the 12 shapes in the display, one was a unique feature, the rest formed a common background. After intermixed or blocked preexposure, participants were given a recognition memory test in which selected shapes were presented individually. Participants proved better able to recognize a shape that had been

the distinctive feature in the intermixed arrangement than one that had been presented in the blocked arrangement. Interestingly, the pattern of memory performance was reversed when the test shape had been part of the background, suggesting that intermixed preexposure can reduce the effectiveness of common features (see Carvalho & Albuquerque, 2012, for related results).

Problems for salience modulation. We are now in position to conclude with some confidence that, in human perceptual learning, intermixed preexposure is effective because it leaves the distinctive features of the stimuli with more effective salience than do other forms of preexposure. To this extent, notions derived from animal learning are helpful in understanding the effects seen in humans. But we must now acknowledge that the specific account of the mechanism responsible for salience modulation that has come from the animal work runs into difficulties when it is applied to the results obtained from studies with humans.

To recap briefly, the central feature of the account offered by Hall (2003) was that habituation occurring during exposure to stimuli will produce a loss in the effective salience of all stimulus elements. However, intermixed preexposure, since it results in repeated associative activation of the unique features of the stimuli, allows the effects of habituation to be attenuated or reversed for these features. McLaren and Mackintosh (2000) specified the

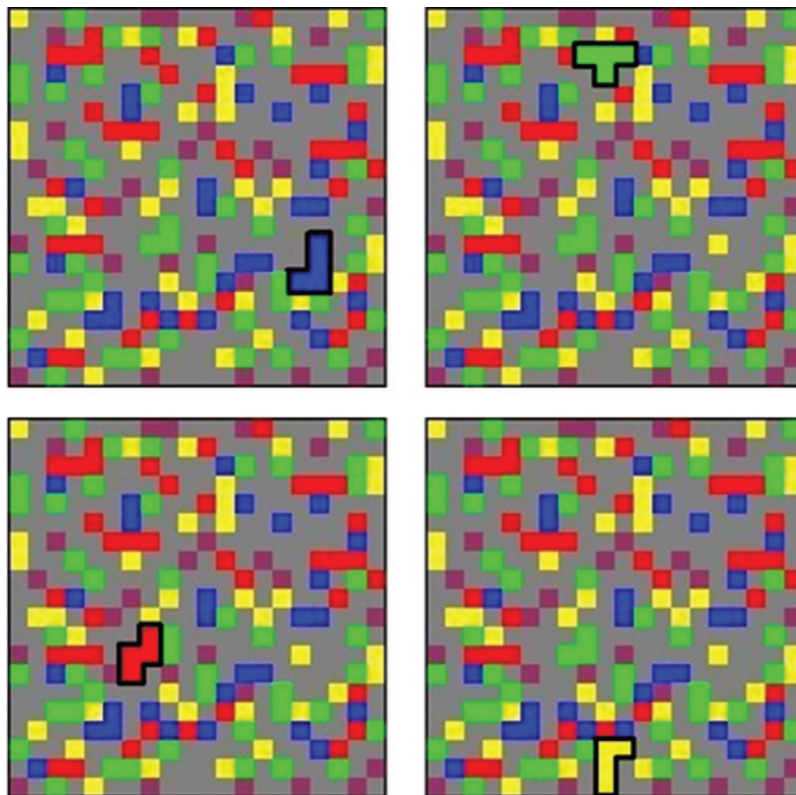


Figure 4. Checkerboard stimuli, as used in the experiments by Lavis et al. (2011). All had a common background on which a distinctive feature (outlined in black in this figure, for the purposes of illustration) was superimposed. Each feature had a simple distinctive shape and was of a uniform color. Reprinted from “Memory for, and Salience of, the Unique Features in Perceptual Learning,” by Y. Lavis, R. Kadib, C. J. Mitchell, and G. Hall, 2011, *Journal of Experimental Psychology: Animal Behavior Processes*, 37, p. 213. Copyright 2011 by the American Psychological Association.

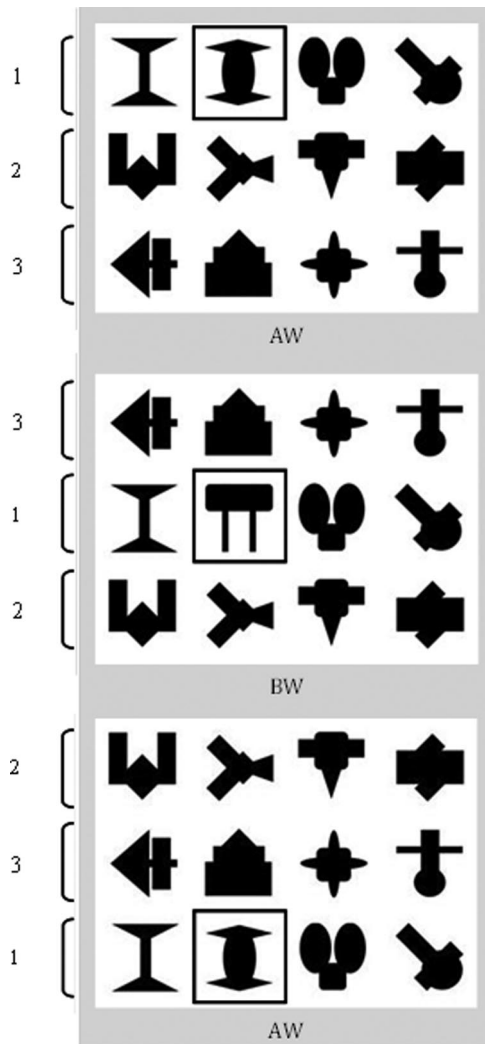


Figure 5. An example of the shape stimuli used by de Zilva and Mitchell (2012). The unique shapes A and B are the shapes that appear within the black squares of AW and BW, respectively (the black squares are shown here for illustrative purposes only). A sequence of three trials is shown (AW, BW, AW). The rows of shapes, labeled on the left, shift by one row between each trial. Reprinted from “Effects of Exposure on Discrimination of Similar Stimuli and on Memory for Their Common and Unique Features,” by D. de Zilva and C. J. Mitchell, 2012, *Quarterly Journal of Experimental Psychology*, 65, p. 1125. Copyright 2012 by Taylor & Francis.

mechanism by which associative activation has its effect. According to their account, a stimulus undergoes habituation (loses salience) as repeated presentation causes its various elements to become associatively linked; associative activation causes a reduction in the strength of these links, thus restoring salience. It may already be apparent that some of the observations just described as demonstrating a salience modulation effect are problematic for this particular interpretation.

The experiment by Lavis et al. (2011), just discussed, can be seen as providing a direct test of McLaren and Mackintosh’s (2000) suggestion that intermixed preexposure leaves the distinc-

tive feature of the stimulus with a high level of salience because it weakens their within-compound (in this case, shape-color) associations. If intermixed preexposure leads to extinction of links among the various components of the unique features then participants should not be able to match the shape to the color of the intermixed unique elements. But, as we have seen, the opposite was observed—shape-color matching was better for the unique elements presented on the intermixed than the blocked schedule. The intermixed schedule appears, if anything, to result in stronger associations between the component parts of the unique elements. According to the tenets of the theory, the unique features of intermixed stimuli should actually be lower in salience than those of the blocked stimuli.

It should be acknowledged that the supposition that the intermixed features have lowered salience does not in fact preclude the McLaren and Mackintosh (2000) theory from predicting the basic intermixed-blocked effect. If the salience of A (an intermixed feature) is low, it will be less able to form an association with the background (X) than would a more salient blocked feature (C). So the X - A link would be weaker than the X-C link.¹ This difference could determine performance in a test procedure in which compound stimuli are presented. The presence of X can be expected to produce activation of the representation of a feature with which it is associated (to “prime” that feature) and will do so more effectively for the C feature than the A feature. Given the further assumption that priming reduces salience, or the ability of a representation to respond to external stimulation (see Wagner, 1981), it can follow that, in the context of X, presentation of A might be more salient or effective than presentation of C. In short, it is possible that the salience of A might be less than that of C when these features are presented alone but that the position is reversed when they are presented as the compounds AX and CX. This account can therefore accommodate the results of Wang and Mitchell (2011) in which levels of eyegaze to the unique features were found to be high in participants tested with AX and BX after intermixed preexposure to these stimuli.

What remains problematic for this ingenious account are the other results reported by Wang and Mitchell (2011). Specifically, the salience of A and B, as assessed by eyegaze, was higher even than that of novel features, C and D (presented on a familiar Y background). This observation, and the fact that discrimination between AX and BX was better than that between CY and DY, is not to be expected on the basis of any of the salience modulation processes to be derived from McLaren and Mackintosh’s (2000) theory. These processes can generate differences between the intermixed and blocked preexposure schedules, but there is nothing in the theory to suggest that with either form of preexposure the salience of the unique stimuli will come to exceed that of novel stimuli. The most one can expect is that the salience of the features

¹ A similar notion, but using a configural representational system, rather than the elemental system of McLaren and Mackintosh (2000), is presented by Dwyer et al. (2011). They proposed an account in terms of a three-layer network in which a bias in attention to the unique features A and B (referred to by them as a and a’) during preexposure “could reduce the likelihood that a and a’ would be drawn (by the presence of the common element, x) into the same configural unit within a connectionist system, or increase the likelihood that a and a’ will be linked to different hidden layer units” (Dwyer et al., 2011, p. 305).

might be restored to (or maintained at) the level seen when they were novel, before any links between the representational units had formed.

The problems just described are specific to the McLaren and Mackintosh (2000) version of salience modulation. Hall's (2003) reverse habituation theory remains a possibility. The observation of Lavis et al. (2011), that associations between the components of the unique features are better formed with intermixed preexposure, is consistent with the suggestion that reverse habituation has restored the salience of each of the various components (e.g., shape and color) of the feature. And (admittedly only by virtue of the fact that no mechanism was specified) it is open to the theory to suppose that the reverse-habituation process will not merely oppose loss of salience but will actually increase its salience beyond the point at which it started out, thus accommodating the results of Wang and Mitchell (2011).

But even this flexible theory has problems with the results of a further study reported by Lavis et al. (2011). In their Experiment 2, they gave intermixed exposure to four compound stimuli, AX, BX, CX, and DX. In addition, intermixed with presentations of these compound stimuli, separate exposures were given of A and of B (i.e., to the unique features, of AX and BX, in the absence of the X background). Recall that, in the animal case it has been shown that presentations of A and B alone are ineffective in producing perceptual learning (Scahill & Mackintosh, 2004). And according to Hall's (2003) account, these additional trials can only act to reduce the salience of A and B—they are, after all, further opportunities for habituation to occur. On this account, therefore, discrimination between AX and BX must thus be predicted to be worse than between CX and DX. In fact, the reverse was observed; additional presentations of A and B improved discrimination performance to AX and BX.

Application to Human Perceptual Learning: Conclusions

The procedures used to demonstrate perceptual learning effects in animals have been found to be effective in generating equivalent effects in humans. Importantly, in both animals and humans, intermixed preexposure of similar stimuli also conveys an advantage (compared to blocked preexposure) when subsequently a discrimination between the stimuli is required. This is true not only when the discrimination test is a categorization task (with differential reinforcement) akin to the test procedure used with animal subjects but also when it requires a simple same-different judgment.

The attempt to apply to the human case the theoretical mechanisms proposed to explain animal perceptual learning has produced mixed results. There was no support for the view that associative inhibition between the unique features of the preexposed stimuli (as might be produced by intermixed preexposure) plays a major role in the perceptual learning effect in humans. But as we have seen, the perceptual learning effect can be obtained in animals in circumstances in which such inhibition is unlikely to develop. These examples have been explained in terms of the salience-modulation account, and this account seems to apply, in general terms, to the results of the human experiments. That is, appropriately scheduled preexposure to similar stimuli will not only reduce the effectiveness of features they hold in common but

will maintain or enhance that of their distinctive features. Clearly, having distinctive features that are high in effective salience and likely to command attention and are thus able to control learning and performance, will promote success in both categorization and same-different tests. Direct evidence that the features have acquired such properties comes from the results of Lavis et al. (2011; see also de Zilva & Mitchell, 2012) and of Wang and Mitchell (2011). The first of these shows that intermixed preexposure leaves people with an accurate representation of the unique features; the latter that such features are indeed good at attracting attention, as assessed by the overt response of eyegaze.

This may seem a satisfactory state of affairs, but there are results from experiments with humans that challenge important aspects of the salience modulation notion. In its general form (e.g., as proposed by Hall, 2003), the idea is that habituation processes will tend to reduce the effective salience (and hence, the attention-getting properties of) preexposed stimuli but that associations formed among components of the stimuli during intermixed preexposure will attenuate or reverse this process for the unique features of the stimuli. First, the role played by habituation is challenged by the results of the study, just described, by Lavis et al. (2011), showing that additional exposure to features A and B will increase the discriminability of AX and BX. On the face of things, the opportunity for habituation provided by these additional presentations can work only to retard subsequent discrimination. Second, the role given to associative processes is challenged by the evidence on the importance of comparison in human perceptual learning (e.g., Dwyer et al., 2011; Mundy et al., 2007). The theory proposed by Hall (2003) was designed to deal with the fact that intermixed preexposure was especially effective in producing a perceptual learning effect and, to that extent, was seen as accommodating the notion of comparison. But because it relies on associative links, which are assumed to be permanent or at least long-lived, the theory must suppose that the comparison effect will be independent of the interval between presentations. The demonstration that the opportunity for immediate comparison facilitates human perceptual learning implies the operation of some other or additional mechanisms.

The next section of this article will focus on these phenomena—the effects of comparison, and of additional exposure to unique features—in an attempt to determine what these other mechanisms might be.

Additional Mechanisms in Human Perceptual Learning?

We take as our starting point the observation (Lavis et al., 2011) that additional exposure to A and B will improve discrimination of AX and BX. The immediate implication is that the human perceptual effect depends on the effectiveness of the preexposure procedure in allowing the participant to learn about the unique features of the stimuli. This conclusion prompts two questions. First, what is the mechanism by which intermixed preexposure to AX and BX (or, more generally, exposure that allows close comparison) promotes learning about the unique stimulus features A and B? Second, how does what is learned about these features act to facilitate subsequent discrimination between AX and BX?

Short-Term Habituation

An answer to the first question follows directly from consideration of habituation effects, and forms the basis of the account offered by Dwyer et al. (2011) to explain their effects of stimulus comparison. The notion was first proposed by Honey and Bateson (1996, with respect to an experiment with animal subjects in which the stimuli were closely spaced) and developed, in slightly different ways, by Mundy et al. (2007) and by Mitchell, Nash, and Hall (2008). Honey and Bateson pointed out, following Wagner (1981), that when representational elements have been activated recently, they are not easily reactivated. Thus, when AX and BX are intermixed, the common X element will always have been presented more recently than the unique elements A and B and will suffer greater short-term habituation. On a BX trial for example, X will have been presented on the preceding AX trial and will have suffered short-term habituation. In consequence, there will be preferential processing of B elements. In contrast, on a blocked schedule, both the unique and common features will have been presented on the immediately preceding trial, so both kinds of feature will suffer from short-term habituation. The unique features will not, therefore, be especially well processed during blocked preexposure.

It may be apparent that this mechanism does not, in itself, supply an answer to the second question (indeed, quite the reverse). Habituation of the X background during intermixed preexposure may well facilitate processing of the unique features A and B, but the processing that occurs will itself result in habituation. It is possible, then, that the intermixed procedure will be especially effective in causing habituation of A and B (see Artigas et al., 2012), and a reduction in the effective salience of these features can be expected only to retard discrimination between AX and BX. Another mechanism is required to account for the improvement in discrimination performance resulting from preferential processing of A and B. We consider two possibilities that have recently been advanced: The first postulates the development of an attentional bias; the second uses the notion of unitization. Neither account denies the reality of the habituation processes just described; both postulate the operation of other processes during intermixed preexposure that can overcome any disadvantage consequent on loss of salience by A and B during intermixed preexposure.

Attentional Bias Toward Unique Features

Mundy et al. (2007) argued that the short-term habituation effects described above might have “enduring repercussions for the attentional weighting given to the unique and common features” (p. 136). More specifically, they proposed that “higher level attentional or representational processes” might act to maintain the advantage of A and B over X across the delay from preexposure to test. This attentional process can be conceived of in a variety of ways. For example, one may postulate an interaction between bottom-up and top-down attentional processes (Schneider & Shiffrin, 1977). Thus, initially, habituation of X during intermixed preexposure to AX and BX will allow automatic detection of A and B; attention to these unique features is then maintained, from preexposure to test, by the operation of a top-down, deliberate, attentional process. An alternative, that makes use only of automatic processes, is also possible. Given that the detection of unique features can be assumed to be rewarding for the human

participant, (Mackintosh, 2009), an attentional response could be acquired, by reinforcement during preexposure. Thus, if the unique features A and B attract attention over the course of the preexposure trials, because they are presented on the habituated X background, participants may begin to orient to A and B habitually and would carry this reinforced response-tendency over to the test phase.

Unitization of Unique Features

The second proposal has also been expressed in a range of different ways. Thus, Mitchell, Nash, and Hall (2008) proposed that the critical consequence of the short-term habituation process described above was that, because it allows A and B to stand out more clearly from the background when preexposed on an intermixed schedule, it results in these features being readily encoded in memory. The availability of a well-formed representation of the feature allows that feature to be easily recognized when presented later (de Zilva & Mitchell, 2012) and for one aspect of the feature to cue retrieval of another (Lavis et al., 2011). A “well-formed representation” may be taken to be one in which the various aspects have become integrated. McLaren and Mackintosh (2000) have proposed a similar interpretation of unitization as the formation of a network of associative links among these aspects. How might such unitized representations aid discrimination on test?

Consider the task faced by a participant required to make a same-different judgment between two novel stimuli AX and BX. On presentation of AX the various features of A ($a1$, $a2$, and so on) and of X ($x1$, $x2$, $x3$, and so on) will be activated. A correct response (“different”) requires a system that compares a memory of the details of the first-presented stimulus with the current input (the second presented stimulus), so that, for example, the absence of any a elements in the current input (and the absence of the b elements in the stored representation) can serve to control the response. It is possible to imagine a variety of comparator systems that might be devised to perform this task, but all of them are likely to find it difficult, given the large number of stimulus elements to be sampled in a limited time, and the massive preponderance of nondiscriminating, x elements. Only if the system happens to hit on the critical elements of the displays will discrimination be successful. The situation will be different, however, for subjects given intermixed preexposure to AX and BX and for whom, therefore, A and B are unitized. For these, presentation of AX on test is likely to activate all of the representational elements of A. In the language of associative links, even if only $a1$ is detected on presentation, the links among its components will mean that all aspects of A will be activated. Similarly the subsequent presentation of BX will be likely to activate the unitized representation of B. Thus, the critical features of the stimuli will be activated enabling the comparator to detect the difference between the displays.

It may be noted, that the comparator process will be able to detect a difference between the current input (e.g., BX) and the preceding stimulus (e.g., AX) only to the extent that the details of the former are retained over the interval between stimulus presentations. This factor, too, could play a role. We may assume, simply, that activation in each of the critical stimulus elements ($a1$, $a2$, etc.) will decline independently on stimulus offset, if the A features have not been unitized. But, for a unitized A stimulus,

activation of one element will supply further activation to the others, thus increasing the chances that these elements will be available for use when it comes to making a comparison with BX. The likelihood of responding “different” will thus be increased.

Given the same assumptions concerning stimulus sampling, unitization of A and B can also be expected to improve performance on a categorization task (e.g., Mundy et al., 2007). In this task, participants are required to learn (following preexposure) to respond with a left button press (R1) to AX and right button press (R2) to BX. If *a1* is sampled on Trial 1 and becomes associated with R1, then *a2*, which happens to be sampled on the next trial, will be able to evoke the correct response by way of its association with *a1*. Therefore, unitization of A and B will improve performance on this categorization task.

Experimental Evidence

A recent experiment by Wang, Lavis, Hall, and Mitchell (2012) has produced evidence that lends support to the attentional-bias theory. Using the checkerboard stimuli of Lavis and Mitchell (2006) they found that following preexposure to checkerboard stimuli AX and BX, performance on test was good only if the unique features were presented in the locations within the X background occupied by A and B during preexposure. Importantly, it did not matter what those features were. That is, once A and B were detected in the preexposure phase, and their locations identified, any stimuli that appeared in those locations (e.g., C and D) were easily detected on test, leading to good discrimination performance. This result is in full accord with the suggestion that intermixed preexposure is effective in facilitating AX/BX discrimination because it establishes an attentional bias (in this case, a tendency to direct overt attention to specific locations in the stimulus display). It can also accommodate the eye gaze data of Wang and Mitchell (2011), and other results, such as those from Lavis et al. (2011), showing that additional presentations of A and B alone improve performance on test. On the additional trials, the locations of A and B within the square normally occupied by X were the same as those occupied by those unique features on AX and BX trials. Thus, additional exposure to A and B would be helpful to the participant in identifying the location in which A and B appeared on the checkerboard.

We should note that the evidence for the attentional-bias process comes from a study using stimuli in which the unique features are presented in a given location. Feature location may well be the most salient dimension for these stimuli; and it is possible, then, that other mechanisms (such as unitization) play a more important role for stimuli in which the discriminating features are less obviously localized. Perfectly clear perceptual learning effects are obtained with such stimuli; for example with the morphed faces of Mundy et al. (2007; Figure 2) or with the shapes of Figure 5, used in the experiment by de Zilva and Mitchell (2012), in which the position of the distinctive feature in the display was changed from one trial to another. This is not to say that an attentional-bias mechanism could not operate in these cases. An attentional bias toward unique features could occur even when these features are not localized; that is, participants could maintain attention to unique features previously detected, even when those features are distributed across the stimulus, as they are in the case of morphed faces (see Mundy et al., 2007). It remains the case, however, that

the evidence in favor of the hypothesis comes solely from a study of stimuli with localized features.

Finally, there is direct evidence for the occurrence of unitization from the experiment by Lavis et al. (2011), which demonstrated that associations between different aspects of the distinctive features of preexposed stimuli were particularly strong after intermixed preexposure. Attentional bias could well play a part in generating this effect; that is, a tendency to attend to the locations in which the features are presented would enhance exposure to them and facilitate the formation of associations among their components. From this perspective attentional bias and unitization are not to be regarded as alternatives. There is evidence to show (at least for stimuli of the type used by Lavis et al., 2011, and Wang et al., 2012) that both can develop during intermixed preexposure; and, under the right conditions, both might contribute to the enhanced discrimination seen on test.

Conclusions

This analysis leads to the conclusion that the procedures used in studies of human perceptual learning bring into play mechanisms that are not usually engaged in experiments on perceptual learning in animals. Results from animals can be explained in terms of two processes, one involving associative inhibition and one involving long-term habituation that enhances the relative salience of unique stimulus features. We find no evidence of a role for the former process in human perceptual learning. And although salience modulation and habituation are important for the human case, the mechanism appears to be different—initial detection of the unique features is to be explained in terms of a short-term habituation process, and the subsequent change in their properties on mechanisms that have not been applied (attentional bias) or have been applied differently (unitization) to the animal case. We now consider whether these differences imply a fundamental difference between species in the processes of perceptual learning.

Resolving the Differences

Although the experimental designs are formally equivalent, the procedures used to demonstrate, for example, the intermixed-blocked effect are necessarily different for rats and for people. It is possible, then, that the same range of general mechanisms is at work in the different species but that the contribution made by one process rather than another is modified by these procedural differences. As we have already acknowledged, the absence of effects expected on the basis of the associative inhibition account may simply reflect the fact that the procedures used with checkerboard stimuli are not conducive to the formation of inhibitory associations. Effects may, therefore, be obtained with humans when the stimuli and trial spacing are arranged to be more similar to those used with rats (Mundy et al., 2006). To take this argument further, however, it is necessary to consider whether procedural differences can account for the role played in human perceptual learning by the additional mechanisms that we identified in the previous section.

Role of Procedural Differences

The short-term habituation effect (that the element A is more salient—“stands out”—if it appears on a recently presented X

background), which we identified as the basis for the additional mechanisms seen in humans, is clearly not restricted to our species. It was devised on the basis of experimental work with animal subjects (Wagner, 1981), and its effects have been demonstrated in several of the experiments with rats already discussed (e.g., Artigas et al., 2012; Bennett et al., 1999). That these effects should play a more major role in human than in animal perceptual learning is to be expected simply on the basis of procedural differences—in most of the experiments with people the critical stimuli have been presented briefly, just a second or so apart; in the experiments with rats the interval between presentations has been much greater (usually several hours in experiments using flavors as the stimuli). What remains a problem is that it has proved difficult to demonstrate *any* clear role for the short-term habituation process in the animal perceptual learning experiments. As we have noted, when the procedure used with animals is modified so that the stimuli are presented in close temporal proximity during preexposure, subsequent discrimination performance is no better than that seen after intermixed preexposure with widely spaced presentations (Rodríguez et al., 2008). If short-term habituation effects can occur in both species, some additional factor must be operating to determine whether these processes will influence stimulus discriminability. One possibility comes from a consideration of the nature of the stimuli used.

The stimuli used in studies of human perceptual learning are, very often, complex and initially extremely hard to tell apart. In experiments using the checkerboard stimuli of Figure 2, unless participants have had the benefit of intermixed preexposure, their dominant tendency is to respond “same” when given a same-different test. The situation appears to be different in the animal experiments. Here the stimuli appear to be rather simpler, and although naïve rats will show substantial generalization from (e.g.) salty-lemon to sweet-lemon, the effect is not total, showing that even animals given no preexposure can discriminate between such cues, to some extent, from the outset. This difference between the stimuli will alter the balance of the processes we have identified as sources of perceptual learning.

With very similar stimuli, the first requirement of an effective preexposure procedure is that it should allow the distinctive features to be discriminated from the background. The short-term habituation process, which allows this to happen, will thus be of prime importance for the experiments with human participants in which these features are not evident on first inspection. The consequence of this process will be the creation of unitized representations of the unique features. Once these representations have been established, the mechanisms thought to be at work in animals, mechanisms that depend on the formation of associations involving these representations, could begin to operate. But the contribution of these mechanisms may not be substantial, and, as we have seen, unitization, combined with the development of an attentional bias, is enough to explain the perceptual learning effect in humans.

The short-term habituation process will be much less important for the stimuli used in the animal experiments in which the unique features may be detectable from the start. Here unitization and added exposure to the unique features (Lavis et al., 2011) will play a lesser role, given that effective representations can be assumed to be already available. In this case, the learning processes (the development of associative inhibition, modulation of salience) that

act to reduce generalization will be able to begin to operate immediately, and their effects will dominate.

Self-Supervised Learning Revisited

The analysis presented in the previous section leads to the conclusion that the same general learning processes may be at work in studies of human and animal perceptual learning and that differences between the species are largely a consequence of procedural factors. The implications of this analysis are readily testable—for example, studies of preexposure effects in animals using stimuli that are more similar and more complex than those used so far should reveal evidence for the kinds of mechanisms seen to operate in human perceptual learning. There is, however, a feature of human perceptual learning that no study of mere exposure effects in animals, whatever the procedural modification, could succeed in reproducing.

As noted earlier, Mackintosh (2009) has argued that work on human perceptual learning is not comparable to that on mere exposure in animals because human participants will inevitably tend to “look for differences” between the stimuli during preexposure in a way that animals do not. When they detect the stimulus differences (perhaps, indeed, as a consequence of the short-term habituation process) they will experience reinforcement, and this will increase attention to those features. That is, the learning that takes place is, to use Mackintosh’s term, “self-supervised.” It follows that these human experiments are equivalent to animal experiments in which reinforcement is given, rather than to those involving nonreinforced preexposure. According to this reasoning, we should look elsewhere for examples of human perceptual learning following mere stimulus exposure. One comes from the experiment by Goldstone (1994) discussed earlier.

In Goldstone’s (1994) study, the perceptual learning effect of interest was a consequence of incidental learning, with explicit feedback being given for another aspect of the task. In brief, he gave feedback for a categorization task in which one aspect of the stimuli (saturation, for example) was critical; the participants were thus, presumably, not looking for differences in the other aspect in which the stimuli differed (brightness). Nonetheless, the results showed that the brightness discrimination was facilitated by this form of training. This outcome is thus readily accommodated by the assumption that one or other of the unsupervised forms of learning responsible for perceptual learning after mere preexposure is at work in this case. Unfortunately, the design of the experiment does not allow us to determine which. It can be explained, for example, solely in terms of the simple notion that exposure to common features will facilitate discrimination (McLaren & Mackintosh, 2000), without recourse to the other mechanisms that are needed to explain the intermixed blocked effect. These results do serve, however, to confirm the plausibility of the notion that a mechanism demonstrated in research with animals (Bennett et al., 1994) is likely to be operating in equivalent experiments carried out with humans (see Wang & Mitchell, 2011).

Another experiment with the potential to demonstrate perceptual learning in humans in the absence of self-supervised learning has been reported by Watanabe, Náñez, and Sasaki (2001). The task involved of detecting the direction of motion in dynamic random dot displays. Their participants could detect coherent motion when

10% of the dots moved in the same direction (90% were in random directions), but not when only 5% of dots moved in the same direction (with 95% random). Participants were given many exposures to 5% coherent motion displays, all in the same direction, and with no feedback given. On test, they were presented with 10% coherent motion displays in a variety of directions. Participants showed significantly greater sensitivity to 10% motion in the direction of the 5% motion presented during preexposure (even though they were unable to detect coherent motion in those 5% displays). Thus, exposure to the distinguishing feature (the direction of motion used in preexposure) increased the effectiveness of that feature in a subsequent discrimination. This result parallels the finding of Lavis et al. (2011) that additional exposure to the A and B elements of checkerboard stimuli made participants more sensitive to these cues in a subsequent discrimination of AX and BX. In Watanabe et al.'s experiment, however, as the participants were unable to perceive the stimuli during preexposure, the result cannot be explained in terms of self-supervised learning.

What these experiments demonstrate is that perceptual learning effects can be observed when self-supervised learning is not possible. What they cannot show, of course, is that the effects observed when self-supervised learning *is* possible are a consequence of the various processes identified in studies of mere exposure. We would make two observations with respect to this. First, unless it is supposed that self-supervised learning, if it occurs, somehow suppresses the operation of other learning processes, it is reasonable to assume that these other processes will contribute to the effects obtained in humans when self-supervised learning is possible. Second, we have highlighted two principal ways in which human perceptual learning (in which self-supervised learning is possible) differs from animal perceptual learning (in which it is not). In explaining these differences (in the role played by stimulus comparison and of the effects of additional exposures to the unique features of the stimuli) we have made use of a range of mechanisms. One of these, we have acknowledged, could involve a form of self-supervised learning (as when the rewarding effects of detecting a unique stimulus feature promotes the development of an attentional bias). But the full explanation of the differences involves other processes (short-term habituation, unitization, and so on) that are a consequence of mere exposure.

Concluding Comments

It is clear that, as well as striking similarities, there are important differences between the mechanisms thus far identified responsible for perceptual learning in humans and animals. A number of ways in which these remaining differences might be resolved in future studies have been described in the previous section. In this final section we draw out some of the implications of animal and human perceptual learning research for psychology more broadly. We end with a more direct attempt to answer the question in the title.

Applications

We have already touched on two areas of research in which perceptual learning effects are acknowledged as having relevance. One is the study of the process of categorization (see Goldstone, 1994; Welham & Wills, 2011) in which (not surprisingly, given the central role of stimulus similarity in models of categorization)

perceptual learning effects have become a major focus of interest (see Goldstone, 1998; Pothos & Wills, 2011). The second is visual face-processing. Mundy et al. (2007) used pictures of faces as the stimuli in their perceptual learning experiments, and the effects seen in those experiments (e.g., the intermixed-blocked effect, the effects of comparison) must form part of any complete theory of face processing (see also Dwyer, Mundy, Vladeneau, & Honey, 2009). We turn now to some other instances in which work on perceptual learning can make a contribution.

Recognition memory. In the memory literature, the term perceptual learning has been used to describe the idea that exposure to a stimulus (usually a word), allows easier (or more fluent) subsequent processing of that word (e.g., Jacoby & Dallas, 1981). This allows an explanation of the well-known superiority of spaced over massed practice. Specifically, Jacoby (1978) has suggested that if a stimulus is presented twice, then the resources required to process the stimulus on the second presentation will be reduced. Thus, if the first presentation of the stimulus is remembered well (because it was presented very recently, in the case of massed practice), then fewer resources will be required to process it on the second occasion. This reduced processing then translates into poorer memory for the item in the long term. Hence, massed practice produces poorer memory because each stimulus presentation after the first can be processed more easily.

The parallel with our analysis of the effects of blocked and intermixed exposure to similar visual stimuli (AX and BX) will be evident. Blocked presentations of AX will permit fluent processing of both aspects of the stimulus (A and X), whereas intermixing AX with BX should allow fuller processing of the A and B features so that they become well encoded in memory. Although there is reason to think that the intermixed-blocked effect is not simply a consequence of the difference between massed versus spaced training (see Mitchell, Nash, & Hall, 2008), this general notion accords well with the results of Lavis et al. (2011) and de Zilva and Mitchell (2012), which showed that memory for the distinctive feature is particularly good after intermixed preexposure. It would be worth testing the implication that recognition memory for lists of related items that share features should be importantly determined by the schedule of presentation during the study phase.

Contextual interference effects. This interpretation of the intermixed-blocked effect also has application to the contextual interference effects seen in verbal learning and motor learning (Battig, 1972; Shea & Morgan, 1979). If participants are required to learn, for example, a set of motor tasks, then performance is affected by the order in which the different tasks are practiced. In particular, if each task is practiced in a separate block, then performance is very good during acquisition. If trials on each of the tasks are randomly intermixed, acquisition performance is poorer, an effect attributed to contextual interference. When given a later test, however, the opposite pattern is observed; participants in the random practice condition show superior performance. A perceptual learning process could contribute to this effect. If we assume that different motor actions, like different stimuli, have parts in common and parts that are unique, then the random training schedule will allow better identification of the unique aspects. These features may then be better encoded in long term memory, thus improving performance after a retention interval.

Education and training. Shea and Morgan (1979) argued that their contextual interference data had important implications

for educational issues. Thus, even though progress may be slow at first, they argued that there might be long-term benefits to be gained from teaching a number of different tasks within each session. More generally, the principles of perceptual learning will be important in developing training for professions in which detection of subtle stimuli from complex backgrounds is required. Obvious areas of application include medicine (e.g., in the detection of tumors in mammograms; Gur et al., 2004) and security (e.g., in enhancing the ability to detect weapons in X-ray images of luggage; Wolfe, Horowitz, & Kenner, 2005). An understanding of the psychological mechanisms by which experts acquire their skills, both through feedback (or self-supervised learning) and mere stimulus exposure should allow more effective training in future.

Clinical matters. Last, research concerning mere stimulus exposure should have implications for our understanding of some clinical disorders, in particular, those that have been characterized as reflecting a dysfunction in some aspect of attention. Schizophrenia is the prime example, and indeed, abnormal attentional learning after nonreinforced stimulus exposure has been observed in those suffering from the disorder (e.g., Gray & Snowden, 2005). Perceptual learning effects of the sort discussed here have not yet been investigated in schizophrenia. They have, however, been used in the study of autism. Plaisted, O’Riordan, and Baron-Cohen (1998) found that individuals with autism were actually better than controls at discriminating complex similar stimuli when those stimuli were novel. When given preexposure, however, the group with autism failed to benefit so that their performance with the familiar stimuli was now worse than that of the controls. With further research we should be able to identify which of the mechanisms responsible for the normal perceptual learning effect is dysfunctional in autism, something that, we may hope, would allow a fuller understanding of the nature of the disorder.

The list above suggests that an understanding of human perceptual learning may have important implications for a wide variety of areas in psychology. Of course the importance of the mechanisms identified in studies of animal learning in this respect depends on whether those mechanisms also operate in humans. This takes us back to the original question.

Can Theories of Animal Discrimination Explain Perceptual Learning in Humans?

The answer to the question posed in the title of this article is (perhaps not surprisingly): Yes—but only in part. When it comes to training procedures in which explicit feedback is given, the analysis that is provided by theories of discrimination learning in animals is directly relevant. The convergence that is evident between these theories (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972) and accounts emerging from human psychophysics (e.g., Petrov et al., 2005) confirms this conclusion. The conclusions to be drawn for studies of mere preexposure are more mixed.

Experiments on mere preexposure effects with people have demonstrated some of the phenomena (notably the intermixed-blocked effect) that have been central to the analysis of perceptual learning in animals, and this is enough to encourage the view that it is worthwhile to look for a common set of explanatory mechanisms. One mechanism, based on latent inhibition of the common features of similar stimuli seems to operate in both species—prior

exposure to X improves discrimination of AX from BX, both in humans (McLaren et al., 1994; Mundy et al., 2007; Wang & Mitchell, 2011) and in rats (Mackintosh et al., 1991). But neither of the other major mechanisms to come out of studies with animals works well for the human case. Although associative inhibition effects can be demonstrated with people under certain conditions of training (Karazinov & Boakes, 2004; Mitchell, Livesey, & Lovibond, 2007), there is no indication that it contributes to the effect produced by repeated exposure to closely spaced alternating presentations of complex visual stimuli. The second mechanism, salience modulation, fares a little better in that many of the results obtained with humans are consistent with the suggestion that preexposure is effective because it enhances the salience of the distinctive features. But the mechanisms thought to be responsible for salience modulation in animals do not readily apply to the procedure used with humans. In animals, these mechanisms involve long-term habituation and associative processes. In humans, we have argued, identification of the unique features of the stimuli depends on a short-term habituation process that allows the formation of a unitized representation of the feature and the development of an attentional bias toward it.

To acknowledge these differences is not to assert, however, that human perceptual learning involves processes quite different from those seen in animals. Self-generated reinforcement may contribute to the development of an attentional bias in humans only. The other processes involved, short-term habituation, within-stimulus association formation, however, are mechanisms that have been derived from, and validated by, studies of animal learning. Given that these mechanisms operate generally, in animals as well as people, we can expect them to contribute, when circumstances are appropriate, to the perceptual learning effects shown in animals. Adapting the procedures used with animals to reproduce the essential features of that used with humans may demonstrate a role for unitization, attentional bias, and so on, in this case too. It will take a program of research to confirm this. The program would be essentially an exercise in “back-translation,” in which the outcome of applying an animal model to people is used to refine the animal model, making it yet more useful as a source of information of general applicability.

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