Intermodal blocking in honeybees

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Previous findings of intramodal but not of intermodal blocking in foraging honeybees prompted a new series of experiments with colours, odours, a proximal visual landmark, and a localized geomagnetic anomaly as stimuli. In Experiments 1–2, the landmark was blocked by both colour and odour. In Experiments 3–6, the anomaly was blocked by both colour and odour, but the anomaly failed to block either colour or odour. In Experiments 7–8, the anomaly failed again to block either colour or odour even though it could be shown to develop substantial associative strength in the course of the training. The several instances of intermodal blocking bring the results for honeybees into closer agreement than before with the results for vertebrates. The failures of blocking seem understandable in terms of the relative salience of the stimuli employed without reference to modal relationships. An attentional interpretation is suggested.

In experiments on compound conditioning in free-flying honeybees trained to discriminate targets labelled with colours and odours, Funayama, Couvillon, and Bitterman (1995) failed repeatedly to find blocking of odour by colour. In subsequent experiments, Couvillon, Arakaki, and Bitterman (1997) found blocking in compounds of two colours and of two odours and blocking of colour by position, as defined in terms of proximity to a distinctive visual landmark, but not blocking of odour by the landmark. The possibility that the negative results for colour and odour and for landmark and odour might be traced in some way to heteromodality was considered by Couvillon et al. (1997), who noted that intermodal and intramodal compounds had seemed to function differently also in overshadowing experiments with honeybees (Couvillon, Mateo, & Bitterman, 1996) and in summation experiments with rabbits and pigeons (Kehoe, Horne, Horne, & Macrae, 1994; Rescorla & Coldwell, 1995). The experiments now to be reported show that heteromodality is not, in fact, a bar to blocking in honeybees and suggest instead that the discrepant results can be understood in terms of the properties of the component stimuli apart from modal relationships.

As in our previous experiments, a concurrent blocking strategy was employed in the sense that independent experience with the prospective blocker accompanied experience with the compound of blocker and stimulus to be blocked. The procedure in Experiments 1–2 was to
train a blocking group with A+, C– and the compound AB+ (A+/C–/AB+ training), to train a control group with A–, C+ and AB+ (A–/C+/AB+ training), and then to test both groups with B. A and C were two colours or two odours, and B was a landmark, with + and – signifying reinforcement and nonreinforcement. The C+ trials for the control group equate the number of reinforcements for the two groups, whereas the C– trials for the blocking group equate the number of nonreinforcements as well as exposure to the stimuli. The design of Experiments 3–8 was simplified by the elimination of stimulus C. The blocking group was trained A+/–/AB+; the control group was trained A–/+/AB+ (– alone representing nonreinforced exposure to the context, + alone representing unsignalled reinforcement in the context); and the test again was with B. A was a colour or an odour, and B was a magnetic anomaly in Experiments 3–4, and the roles of the stimuli were reversed in Experiments 5–8. Again in this design, which was employed also by Couvillon et al. (1997) in the demonstration of blocking with two colours and two odours, the blocking and control groups have the same exposure to the stimuli and the same experience with reinforcement and nonreinforcement.

With respect to the traditional definition of blocking—A+ training impairs the conditioning of B in AB+ training (Kamin, 1969)—both these designs have a disadvantage. The difficulty is that response to B may be less in the blocking group than in the control group at least in part because A– training enhances the conditioning of B in the control group; such enhancement is clearly to be expected, for example, from the theory of Rescorla and Wagner (1972). Backward conditioning and explicitly unpaired training, which have been used as control treatments in blocking experiments on conditioned proboscis extension in harnessed honeybees (Gerber & Ulrich, 1999; Smith & Cobey, 1994), present the same difficulty. In general, any experiment with a formally satisfactory control treatment—one that equates exposure to the stimuli as well as that to reinforcement and nonreinforcement—reduces to an experiment on what Wagner (1969) termed “stimulus validity”. Experiments 3–8 are immediately reminiscent of some of Wagner’s early experiments with rats, improving on his I/II control procedure (–/+/AB+, in our notation) by equating experience with A. Although the traditional blocking terminology is convenient, our broader concern in this work is with the sufficiency for honeybees of the parsimonious independence assumption of traditional continuity theory (Hull, 1929; Spence, 1936)—the assumption that the components of a compound stimulus gain or lose associative strength independently with reinforcement or nonreinforcement of the compound—which is challenged by a difference in responding to B whatever its source. Widely rejected in the vertebrate literature, the independence assumption is compatible with a rather substantial set of data on compound conditioning in honeybees (Couvillon & Bitterman, 1991), and its validity for honeybees has only recently begun to be questioned (Couvillon et al., 1996; Shapiro & Bitterman, 1998; Smith & Cobey, 1994). Experiments such as the present ones may help to decide what should be put in its place.

FURTHER LANDMARK EXPERIMENTS (1–2)

Couvillon et al. (1997) looked for blocking of colour and of odour by an adjacent landmark, with results that were positive for colour and negative for odour. Here we looked for blocking of the landmark by the same colours and odours, which now served as prospective blockers of the landmark rather than as objects of blocking by the landmark. For simplicity, we use the
notation colour $\rightarrow$ odour to refer, for example, to an experiment designed to look for blocking of odour by colour (colour the prospective blocker and odour the object). In this notation, the experiments by Couvillon et al. (1997) were landmark $\rightarrow$ colour and landmark $\rightarrow$ odour experiments, whereas those now to be described were colour $\rightarrow$ landmark and odour $\rightarrow$ landmark experiments. Bidirectional blocking was not necessarily to be expected, as it seemed reasonable to suppose that relative salience might be critical (Mackintosh, 1975, 1976), and there already was some indication of asymmetry in the vertebrate literature (Williams & LoLordo, 1995). We anticipated, in fact, that the landmark might be blocked, not only by colour, but also by odour, and thus provide the first evidence of intermodal blocking in honeybees.

Method

Subjects

The subjects were 48 honeybees (*Apis mellifera*), all experimentally naive, from our own hives situated near the laboratory. They were assigned to four groups of 12 animals, two in each experiment.

Procedure

The subjects of these (and all following) experiments were trained individually, each in a single session lasting several hours. In the pretraining, a forager was selected at random from a group of foragers at a feeding station providing 10–12% sucrose solution, picked up in a match box, carried to a laboratory window, and set down at a 100-μl drop of 50% sucrose solution on a grey, unscented, pretraining target centred on the deep sill of the window. The animal was marked with a spot of coloured lacquer as it fed to repletion, after which it left for the hive to deposit the sucrose. Typically, the animal would return after a few minutes, continuing to fly back and forth between the hive and the window as long as sucrose was available there. If the marked animal did not return after its first placement, it was taken again from the feeding station (where it usually could be found) to the pretraining target and permitted again to feed to repletion. More than two placements were rarely required. The pretraining ended with the first return of the animal to the window of its own accord, and discriminative training began: A+/C−/AB+ training for the blocking group of each experiment and A−/C+/AB+ training for the control group.

The targets were plastic petri dishes, 5.5 cm in diameter, with grey covers. In Experiment 1 (colour $\rightarrow$ landmark), the targets were labelled with yellow or blue plastic discs (2.5 cm in diameter) affixed to the covers. For half the animals in each group, A was yellow and C was blue, whereas the opposite was true for the rest. In Experiment 2 (odour $\rightarrow$ landmark), all covers were plain grey, but drilled in each cover, 6 mm from its outer circumference, was a circle of eight equally spaced holes, 5 mm in diameter, and the labelling was with the scent of geraniol or peppermint emanating from impregnated cotton batting inside the targets. For half the animals in each group, A was geraniol and C was peppermint, whereas the opposite was true for the rest. (The colours and odours of the present experiments were the same as those of the previous blocking experiments.) Each target used on any visit in each experiment was drawn at random from a large set of identical targets to which it was returned, after washing of its cover, at the end of the visit; the purpose of the procedure (used routinely in this laboratory) is to randomize irrelevant stimuli. The landmark used in the present experiments, as in the previous ones, was a white wooden block that was 11 cm long and 4 cm in each of its other dimensions.

On 8 of 16 training visits in each experiment, there was an AB+ trial. Centred on the window sill was a target labelled with the A colour or odour. Directly behind the target, at a distance of 1 cm, was the landmark (B) lying on its long side, parallel to the outer edge of the window sill. Centred on the cover of the
target was a 100-μl drop of 50% sucrose solution from which there was feeding to repletion. On the remaining eight visits, intermixed with the eight AB+ visits in balanced quasi-random order, the subjects were trained to discriminate between A and C (the colours in Experiment 1 and the odours in Experiment 2) by a method used in the earlier work, which was designed to ensure substantial experience with the negative alternative. Each visit began with the presentation of C− for the blocking (A+/C−/AB+) group and A− for the control (A−/C+/AB+) group. The target contained a 100-μl drop of water, unacceptable to the animal and distinguishable from the sucrose solution only by taste, its purpose being to prevent discrimination between positive and negative targets on the basis of the presence or absence of a drop of sucrose. Then, after a set period (1 min on the first visit, 1.5 min on the second, and 2 min on the rest) during which the animal was free to land on it repeatedly, the negative target was replaced by the positive target (A for the blocking group and C for the control group) containing a 100-μl drop of 50% sucrose solution from which there was feeding to repletion. On the visit following the last training visit, there was for each subject an extinction test with the landmark (B) set behind an unlabelled grey target. The target contained a 100-μl drop of water, and all contacts with the target in a 10-min period were recorded. The familiar behaviour of a forager in such a test is to land on the target, taste the water, fly up from the target, land again, fly up again with or without tasting the water, and so forth, the interval between successive contacts with the target increasing progressively during the 10-min test period (the animal being free, of course, to leave the situation entirely before the end of that period).

Results and discussion

In Figure 1 (left panel), the performance of the blocking and control groups of Experiment 1 (colour → landmark) in the extinction test with B is plotted (as is conventional in our experiments) in terms of the mean cumulative number of responses in successive 30-s intervals. The curves show less responding in the blocking group than in the control group. Analysis of variance (ANOVA) based on the uncumulated data yields a significant group effect, $F(1, 22) = 6.17 (p < .05$, the $\alpha$-level used throughout), a significant change in responding over 2.5-min blocks, $F(3, 66) = 55.06$, and a significant Group × Block interaction, $F(3, 66) = 11.72$. It seems, then, that there is not only the blocking of colour by landmark previously demonstrated by Couvillon et al. (1997), but blocking of landmark by colour as well; the blocking is bidirectional.

The performance of the blocking and control groups of Experiment 2 (odour → landmark) also is plotted in Figure 1 (right panel). Here again the curves show less responding in the blocking group than in the control group. ANOVA yields a significant group effect, $F(1, 22) = 8.95$, a significant change in responding over 2.5-min blocks, $F(3, 66) = 35.16$, and a significant Group × Block interaction $F(3, 66) = 3.64$. These results for odour provide the first indication of intermodal blocking—blocking of landmark by odour—in honeybees. Interesting, too, is the implication that the blocking is not bidirectional, Couvillon et al. (1997) having previously failed to find blocking of odour by the landmark, although their procedure was somewhat different than that employed here. (In both of their landmark experiments—the landmark → colour experiment, which gave positive results, and the landmark → odour experiment, which did not—the blocking animals were trained AC+/C−/AB+, and the control animals were trained AC−/C+/AB+.) In the following set of four experiments—all identical in design—unidirectionality was found again, together with further evidence of intermodal blocking.
In these experiments, we extended our work on blocking in compounds with visual and olfactory components to another modality, substituting for the landmark a localized anomaly in the ambient geomagnetic field; honeybees are known to be quite sensitive to such anomalies (Walker & Bitterman, 1989). In Experiment 3 (colour → anomaly), we looked for blocking of the anomaly by colour, in Experiment 4 (odour → anomaly) for blocking of the anomaly by odour, in Experiment 5 (anomaly → colour) for blocking of colour by the anomaly, and in Experiment 6 (anomaly → odour) for blocking of odour by the anomaly. The blocking group of each experiment was trained A+/−/AB+, and the control group was trained A−/+/AB+. The anomaly served as B in Experiments 3 and 4 and as A in Experiments 5 and 6.

Method

Subjects

The subjects were 64 honeybees, all experimentally naive, from our own hives situated near the laboratory. They were assigned to two groups of eight animals in each experiment.

Procedure

The targets used in these experiments were like those used previously—some unlabelled, others labelled with discs of yellow and blue (in Experiments 3 and 5, the colour used was yellow for half the animals and blue for the rest) or with odours of peppermint and geraniol (in Experiments 4 and 6, the odour was peppermint for half the animals and geraniol for the rest). Some of the dishes in each category contained ceramic permanent magnets (surface field 27.6 mT, 282.7 emu), generating at the location of the dish a strong anomaly in the ambient geomagnetic field. We knew from previous experiments in which honeybees were trained with such dishes in much the same way as in these experiments that the anomaly was readily discriminable, and more immediate evidence of discriminability is provided by Experiments 7–8 described later.
Pretraining in the present experiments consisted of two rewarded visits (a placement and a return) to A for animals of the blocking group and to an unlabelled target for animals of the control group. In the training of the blocking group, there were six visits to AB+, of which (in quasi-random order) three began with a nonreinforced 1-min exposure to an unlabelled target, and six visits to A+, of which three began with a nonreinforced 1-min exposure to an unlabelled target. For the control group, there were six visits to AB+, of which three began with a nonreinforced 1-min exposure to A, and six reinforced visits to an unlabelled target, of which three began with a nonreinforced 1-min exposure to A. On the visit following the last training visit, there was for each animal a 10-min extinction test with a target labelled with B alone.

Results and discussion

In Figure 2, the test performance of the blocking and control groups in each of the experiments is plotted in terms of the mean cumulative number of responses in successive 30-s intervals. Both in Experiment 3 (colour → anomaly, upper left quadrant) and in Experiment 4 (odour →
anomaly, lower left quadrant), there was less responding in the blocking group than in the control group. For Experiment 3, ANOVA yields a significant group effect, $F(1, 14) = 8.24$, a significant change in responding over 2.5-min blocks, $F(3, 42) = 14.38$, and a significant Group × Block interaction, $F(3, 42) = 3.12$. For Experiment 4, ANOVA yields a significant group effect, $F(1, 14) = 32.96$, a significant change in responding over 2.5-min blocks, $F(3, 42) = 12.47$, and a significant Group × Block interaction, $F(3, 42) = 16.18$. In both cases, then, the results for the magnetic anomaly mirror those of Experiments 1 (colour → landmark) and 2 (odour → landmark); that is, the anomaly, like the landmark, was blocked both by colour and by odour. A special feature of these new results is that they provide two further instances of intermodal blocking.

Neither in Experiment 5 (anomaly → colour, upper right quadrant of Figure 2) nor in Experiment 6 (anomaly → odour, lower right quadrant) was there evidence of blocking. In each case there was a significant change in responding over 2.5-min blocks, $F(3, 42) = 19.63$ and 21.38, for Experiment 5 and 6 respectively, but in neither case was there a significant group effect ($F < 1$) or a significant Group × Block interaction, $F(3, 42) < 1$, for Experiment 5, and $F(3, 42) = 1.79$ for Experiment 6. These results differ from those of Couvillon et al. (1997) for the landmark, which showed blocking of colour but not of odour by the landmark; the magnetic anomaly blocked neither colour nor odour, although it was itself blocked by both.

CONTROL BY THE MAGNETIC ANOMALY (EXPERIMENTS 7–8)

A question suggested by the negative results of Experiments 5 (anomaly → colour) and 6 (anomaly → odour) is whether the prospective blocker simply failed to acquire substantial associative strength under the training conditions employed or whether it was without effect on the conditioning of colour and odour despite having acquired such strength. Experiments 7 (anomaly → colour) and 8 (anomaly → odour), which were designed to answer the question, were like Experiments 5 and 6, but with two main differences. One is that there now was opportunity for sequential blocking; before the concurrent training began (as well as after it began), there were differentially reinforced choice trials, which provided data on control by the anomaly in advance of the AB+ training. Another difference is that, instead of a small number of training trials with feeding to repletion as reward, there were more frequent trials with a smaller (10–40 μl) reward, the purpose being to obtain a refined measure of the course of discrimination. The extinction test with B was the same as before.

Method

Subjects

The subjects were 32 honeybees, all experimentally naive, from our own hives situated near the laboratory. They were assigned to four groups of eight animals, two groups in each experiment.

Procedure

The design of the two experiments was the same, with colour (yellow or blue) as B in Experiment 7 (anomaly → colour) and odour (peppermint or geraniol) as B in Experiment 8 (anomaly → odour). In the
pretraining, the blocking (A+/−/AB+) animals fed to repletion on A and the control (A−/+/AB+) animals on an unlabelled target. In the first stage of training, there were 20 differentially reinforced choice trials with A versus the unlabelled target, A being rewarded for the blocking animals and nonrewarded for the control animals. On each of those trials, the targets were presented 10-cm apart on the window sill, their lateral arrangement balanced quasi-randomly over trials, with the positive target containing a 10-μl drop of 50% sucrose solution and the negative target a 10-μl drop of water. If the animal went first to the water, it was free at once to correct its choice, and both targets were removed after the animal ingested the sucrose and flew up from the depleted target. Quasi-randomly interspersed among the 20 choice trials were 20 nonreinforced trials with the unlabelled target for the blocking animals and with A for the control animals; on each of these trials, the target was presented for 30 s. In the second stage of training, there were 12 more differentially reinforced choice trials and 12 more nonreinforced trials, exactly as were given in the first stage. Interspersed in addition for both blocking and control animals were 12 AB+ trials (the AB target containing a 10-μl drop of sucrose solution). On each visit in each stage of training, the prearranged schedule of trials continued (with an intertrial interval of about 10 s) until the animal was replete and left of its own accord for the hive to deposit the sucrose. The training of each animal continued until it had at least the scheduled number of trials of each kind; in no case did the mean number of trials exceed the scheduled number by more than one in an average total of 10.3 visits. On each animal’s return from the hive after its last training visit, there was the usual 10-min extinction test with B.

Results and discussion

As may be seen from Figure 3, the magnetic anomaly was clearly discriminated in both experiments. The curves are plotted in terms of the proportion of choice trials on which the first actual contact was with the anomalous target. In each case, the blocking group, for which the anomaly was positive, came to prefer it, whereas the control group, for which the anomaly was negative, came to avoid it. In each case, too, the preference appeared in the first stage of training and persisted in the second. ANOVA yields, for Experiment 7, a significant group effect, \( F(1, 14) = 102.3 \), with a significant interaction between group and four-trial block, \( F(7, 98) = \)

![Figure 3](image-url)

Figure 3. Mean probability of choosing the magnetic anomaly on choice trials in the two stages of training in Experiments 7 and 8. The anomaly was reinforced for the blocking groups and nonreinforced for the control groups.
3.51, and, also for Experiment 8, a significant group effect, $F(1, 14) = 262.7$, with a significant Group × Block interaction, $F(7, 98) = 3.35$.

In Figure 4, the test performance of the blocking and control groups in each of the experiments (Experiment 7, anomaly → colour, left panel; Experiment 8, anomaly → odour, right panel) is plotted in terms of the mean cumulative number of responses to B in successive 30-s intervals. In each case, there was a significant change in responding over 2.5-min blocks, $F(3, 42) = 26.22$ and 15.93 for Experiments 7 and 8, respectively, but in neither experiment was there a significant group effect or a significant Group × Block interaction ($F < 1$ in each case). Again, then, there was failure of the anomaly to block colour or odour, but here this cannot be attributed to the failure of the anomaly to acquire any considerable associative strength when reinforced outside the compound.

**GENERAL DISCUSSION**

We now have a substantial number of blocking experiments (those of Couvillon et al., 1997; Funayama et al., 1995, and the present ones) in which free-flying honeybees were trained and tested under similar conditions with a defined set of stimuli that served both as prospective blockers and as objects (colours, odours, a landmark, and an anomaly in the ambient geomagnetic field). In experiments with two odours and two colours, there was bidirectional blocking; each colour blocked the other colour, and each odour blocked the other odour. There was bidirectional blocking also in experiments with colour and the proximal white landmark, which seemed to function in the same way as a coloured label on the cover of a target; colour blocked landmark and landmark blocked colour. For intermodal compounds, the results were not bidirectional; odour blocked both landmark and anomaly, but landmark and anomaly did not block odour, nor did colour block odour. It is clear from the present experiments that heteromodality is not a bar to blocking in honeybees as suggested by the earlier work that showed only intramodal blocking, although modal relationships may still seem to have some importance because the only failures of blocking thus far have been intermodal.
The possibility has been considered that intramodal and intermodal compounds may function differently because afferent interaction is more pronounced in intramodal compounds than in intermodal compounds (Couvillon et al., 1997; Kehoe et al., 1994; Rescorla & Coldwell, 1995), and it might be argued on that assumption that intramodal blocking would be less likely. Loss in the identity of A or B stemming from interaction in the compound, although conducive to overshadowing (in the prototypical design, AB+ vs. B+ training followed by testing with B), should contravene blocking; to the extent that A and B in the compound, or the compound as a whole (Pearce & Wilson, 1990), are different from A and B alone, independent treatment of A should have little effect on subsequent response to B. With a compound–unique component assumed to be generated by the interaction of A and B, the theory of Rescorla and Wagner (1972) suggests that the blocking effect will tend to decrease rather than to increase as the salience of the compound–unique component increases.

It is evident, too—in given that free-flying honeybees must be depended upon to expose themselves to the stimuli—that intramodal and intermodal compounds may differ substantially in their temporal properties. Two colours or two odours labelling a target are more likely to be detected simultaneously by an arriving animal than, say, a colour and an odour, and there is also some learning on departure from the target (Couvillon, Leiato, & Bitterman, 1991; Lehrer, 1991) in which asynchrony may play a role. How asynchrony would contravene blocking is not, however, very clear; serving to minimize interaction of the components and so protect against loss of identity, it might well have the opposite effect. Much better control of stimulation is provided by the technique of proboscis extension conditioning, which has been used to study odour → odour blocking in harnessed honeybees; unfortunately, the results of that work are subject to considerable controversy (Gerber & Ullrich, 1999; Hosler & Smith, 2000; Smith & Cobey, 1994). A limitation of the technique for our purposes is that the proboscis response is elicited only by a narrow range of stimuli (olfactory and mechanical), although there is some indication that it can at least be modulated by light (Gerber & Smith, 1998).

Another possibility worth considering is that failures of blocking are to be understood, not in terms of modal relationships, but on the assumption that blocking, like overshadowing, is a function of the relative salience of the stimuli employed (cf., Feldman, 1975; Hall, Mackintosh, Goodall, & dal Martello, 1977; Kamin, 1969; Pearce, 1987). If the salience of B is much greater to begin with than that of A, what is learned about B on AB+ trials may be little influenced by the independent treatment of A. The failure of the magnetic anomaly to block odour or colour may be attributed to their greater salience, and the failure of colour and landmark to block odour to its greater salience. On the scale of salience, the results suggest: odour > colour = landmark > anomaly. Independent evidence that odours of the intensities routinely employed in our experiments—not necessarily odours in general (Bitterman & Couvillon, 1991)—are more salient than the colours comes from other experiments. In some of our earliest work with honeybees, odour overshadowed colour but was not overshadowed by colour, and response to odour alone was much greater than to colour alone in a choice test given after training with the compound (Couvillon & Bitterman, 1980, 1982). In more recent overshadowing experiments, learning about the colour but not the odour of a target was impaired by a white dot used to mark the location of a small drop of sucrose solution on its surface (Couvillon et al., 1996). Further blocking experiments with colours and odours obviously are called for, among them experiments in which the intensity of the odours is varied systematically, as Pelz, Gerber, and Menzel (1997) have done in proboscis extension experiments on overshadowing.
In the vertebrate literature, failure of blocking has sometimes been attributed to absolute properties of the stimulus to be blocked apart from those of the blocker—“preferential access to associative mechanisms” (Williams & LoLordo, 1995, p. 114), or “high biological significance” that makes a stimulus “immune to cue competition” (Miller & Matute, 1996, p. 384). However satisfying such explanations may seem, our results for honeybees are clearly more amenable to interpretation in terms of relative than of absolute properties; failure of the magnetic anomaly to block colour cannot, for example, be attributed to properties of colour per se, as colour can itself be blocked by another colour or by odour.

Although the mechanisms of blocking in honeybees and vertebrates need not, of course, be the same, it is interesting to ask how well the various theories of blocking in vertebrates fit the results for honeybees, which are brought into closer correspondence with the vertebrate results by the intermodal blocking found in Experiments 2–4. Evident from the outset is that theories that make no provision for the modification of salience by training are not tenable. The comparator assumption that blocking is a performance effect (Miller, Barnet, & Grahame, 1995)—that response to B is determined by its excitatory strength relative to the excitatory strength of A, which (having been paired with B in the AB+ training) is associatively reinstated in the test—does not explain the failure of blocking where the control acquired by A is demonstrably substantial. The central tenet of comparator theory is challenged in any case by the results of experiments on within–compound association in honeybees (Couvillon & Bitterman, 1982); after reinforced training with two colour–odour compounds (AX+/BY+) followed by differential conditioning with X and Y (X+/Y–), the animals respond more to A than to B, although the excitatory strength of B relative to that of Y should be greater than the strength of A relative to that of X. The interpretation of blocking by Rescorla and Wagner (1972) in terms of competition for associative strength also is challenged by failure of blocking where substantial associative strength is acquired by A; the Rescorla–Wagner theory does predict that the magnitude of the blocking effect will increase with the salience of A, but simulation of A+/−/AB+ vs. A−/+/AB+ training shows (perhaps surprisingly) hardly any variation at all with increase in the relative salience of B. Other results not easily accommodated by the Rescorla–Wagner theory have been obtained in experiments on overshadowing in honeybees (Couvillon et al., 1996). The clever experiments with rats and pigeons recently reported by Rescorla (2000) suggest, in fact, that the principle of shared associative strength might well be abandoned altogether.

The several variations of traditional attention theory (Sutherland & Mackintosh, 1971), although with modification of salience at their core, fail on at least two counts to deal with our blocking results. Colour → colour and odour → odour blocking are not understandable in terms of competition for attention if the competition is dimensional, nor is failure of blocking (even where attention to B is assumed to be high at the outset of training) if attention governs performance as well as learning. A later version of attention theory sketched by Mackintosh (1975) seems more satisfactory in both respects. Given its focus on learned changes in the salience of individual stimuli rather than of dimensions, the theory has no difficulty with colour → colour and odour → odour blocking. On the assumption contemplated by Mackintosh that salience is a determinant of learning but not of performance, failure of blocking is understandable where the initial salience of B is high if the rate of change in associative strength is high relative to the rate of change in salience; associative strength acquired by B early in training will continue to control performance even after attention to it may have waned. The same
purpose is served by Pearce and Hall’s (1980) pivotal distinction between associability and associative strength; a stimulus with substantial associative strength will evoke a response even though it fails, as they say, to engage the mechanisms of associative learning. With satisfactory rules for computing change in salience (or associability) as a function of correlation with reinforcement remaining to be developed, such ideas may provide a useful guide in further work designed to discover how salience affects learning in honeybees and how it is affected by learning.

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