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Simultaneous Conditioning in Honeybees (*Apis mellifera*)

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Honeybees (*Apis mellifera*) were classically conditioned with odor as conditioned stimulus (CS), sucrose as unconditioned stimulus (US), and proboscis extension as response. The purpose of Experiment 1 (*N*s = 26 and 27) was to look for facilitation of forward conditioning by CS–US overlap, but rapid conditioning without overlap left little room for improvement. In 2 further experiments, CS and US were simultaneous, and response to odor alone was measured in subsequent tests. In Experiment 2, a Simultaneous group ($N = 25$) responded more to the training odor than did an Unpaired control group ($N = 25$). In Experiment 3, a differentially conditioned Simultaneous group ($N = 29$) responded more to an odor paired with sucrose in training (S+) than to an odor presented alone (S−). The implications of the results for the problem of the role of amount of reward in honeybee learning are considered.

Foraging honeybees trained with two targets different in odor, one of which always contains a 20-μl drop of 50% sucrose solution and the other a 5-μl drop of the same solution, quickly develop a preference for the 20-μl odor, a preference that is most simply explained in terms of a stronger association with sucrose (Couvillon, Lee, & Bitterman, 1991). Because the flying animals seem to detect 20-μl drops more readily than 5-μl drops (Walker, Lee, & Bitterman, 1990), it might be thought that the stronger association is due to closer contiguity between the perception of the 20-μl odor and the initial taste of sucrose (the delay hypothesis), but that possibility can be discounted on the basis that the preference develops even when the locations of the drops are clearly marked (Lee & Bitterman, 1990b). A second possibility, more difficult to test, is that the drops are differentially reinforcing by virtue of their visual appearance or of some physical property that is detected—as the concentration of sucrose is detected—on initial contact of the proboscis (the immediate-evaluation hypothesis). A third possibility, the focus of interest here, is that strength of association increases with the duration of concurrent odor–taste stimulation, which is greater for the larger drop than for the smaller because the time required for ingestion is greater (the concurrent-stimulation hypothesis). In a suggestive experiment on simultaneous conditioning in rats (Burkhardt & Ayres, 1978), suppression of drinking by a noise previously paired with shock was found to increase with the duration of concurrent noise–shock stimulation.

The assumption of concurrent odor–taste association in honeybees might seem insupportable in the light of some experiments by Opfinger (1949) that were designed to determine when in the course of a visit to a feeding place foraging honeybees learn about its odor. Opfinger's method was to wait until her animals had landed at an odor source and begun to feed then lift them briefly, and substitute a second odor source for the first. Tested subsequently, the animals preferred the landing odor to the feeding odor, which led Opfinger to the questionable conclusion that they had learned nothing about the feeding odor. In many instances, in fact, the feeding odor was preferred to no odor, although that preference in itself is not sufficient evidence of an association between the feeding odor and sucrose.

One of the many techniques used to demonstrate simultaneous conditioning in vertebrates is the within-compound conditioning technique (e.g., Rescorla & Cunningham, 1978), which has been used also to look for evidence of association between concurrent odors and colors in free-flying honeybees (Couvillon & Bitterman, 1982). The procedure was, first, to reinforce each of two color–odor compounds (orange–jasmine and yellow–lemon targets with sucrose solution were presented on successive visits to the laboratory), then to differentially reinforce either the odors or the colors alone (e.g., jasmine reinforced vs. lemon unreinforced), and finally to look for differential response to the remaining components (e.g., orange vs. yellow) in a choice test. Because the colors of the targets probably were detected before their odors in the first stage of training (see von Frisch, 1920), color–odor associations might have been expected on the basis of sequential stimulation alone. The effectiveness of concurrent stimulation can be inferred, however, from the symmetry of the results for color and odor; in the example given, orange was preferred in the third stage after jasmine had been differentially reinforced in the second, and jasmine was preferred in the third stage after orange had been differentially reinforced in the second.

In these experiments we look for evidence of concurrent odor–taste association with a classical conditioning technique that affords somewhat better control of stimulation than is possible in work with free-flying foragers (Frings, 1944; Kuwabara, 1957; Takeda, 1961). The animals are not depended on to expose themselves to the training stimuli but are trained while they are harnessed in small tubes. The conditioned

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stimulus or CS (a distinctive odor) is paired with the unconditioned stimulus or US (a small drop of sucrose solution) and soon comes in consequence to elicit extension of the proboscis. However inappropriate it may seem to restrain and isolate such active and social animals as honeybees, the results thus far obtained with the technique are not only orderly and meaningful, but similar to those of analogous experiments with free-flying foragers (Menzel & Bitterman, 1983). They are similar also to the results of classical conditioning experiments with vertebrates in showing a variety of phenomena, such as spontaneous recovery, second-order conditioning, rapid acquisition in omission training, and conditioned inhibition (Bitterman, Menzel, Fietz, & Schäfer, 1983).

Experiment 1

Our purpose in this experiment was to look for a facilitating effect of concurrent stimulation on forward conditioning. Two groups of harnessed subjects were trained with the same 3-s interval between the onset of the CS and the presentation of the US, a drop of sucrose that took about 2 s to consume. For one group, the CS terminated just before presentation of the US, and for the other the CS overlapped the US (i.e., continued while the sucrose was being consumed). In the amount-of-reward experiments with free-flying foragers that prompted these, duration of concurrent stimulation was confounded with amount of sucrose, but here there was no such confounding; US magnitude was constant throughout. CS duration was confounded with duration of concurrent stimulation, but we thought it reasonable to postpone the troublesome task of separating those variables until facilitation could be demonstrated.

Method

Subjects. The subjects were foraging honeybees (*Apis mellifera*), all experimentally naive. They were collected in match boxes on departure from their hives, which were situated near the laboratory, cooled briefly to reduce their activity, and then harnessed in brass tubes. The harnessing technique, illustrated in Figure 1, was like that used previously (Bitterman et al., 1983), except for the application of a second piece of tape behind the subject, which is not shown. About 10–15 min after completion of the harnessing, each of the animals was given 1 μl of 50% sucrose solution, and any that did not take it readily were discarded. Then the training was begun. It may be well to note that there are substantial differences from laboratory to laboratory in the length of the interval between harnessing and training and in the treatment of the animals during the interval. Our own practice, adopted after a certain amount of intuitive exploration, was designed to maximize the survival of the animals and the reliability of the results.

Procedure. There were four replications of the experiment on separate days with four squads of animals. The animals in each squad, randomly assigned in approximately equal numbers to the two experimental groups, were trained in a balanced sequence. The first animal was moved in its tube from an adjacent holding area to the training situation, set down near the opening of an exhaust system that carried ambient odors to the outside, and given a trial. After the trial the first animal was replaced by the second animal in the squad, and so forth; the first animal was brought back for its second trial only after the last animal in the squad had been given its first trial.

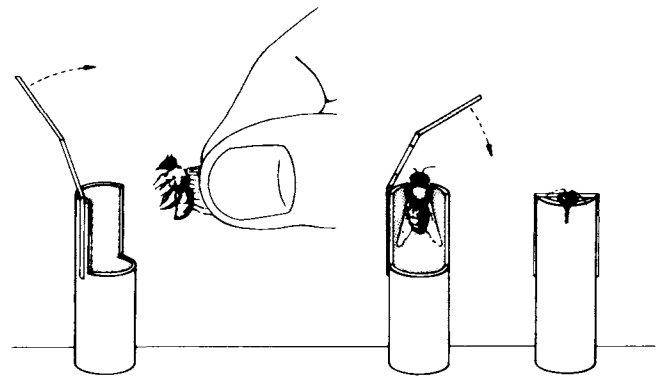

Figure 1. Harnessing technique. (A second piece of tape, not shown, runs horizontally back of the animal.)

The intertrial interval—that is, the interval between each trial for a given animal and the next trial for the same animal—was 10 min. Any animal that responded to the CS on the first conditioning trial was discarded, as was any animal that failed on any trial to respond to the US, although such occurrences were rare. In all of these experiments combined, only 3 animals had to be discarded for responding to the CS on the first conditioning trial, and only 3 others for failure to respond to the US.

The first 8 trials were reinforced. The CS, a gentle stream of air (.04 ft^3/min [1133 cm^3/min]) scented with geraniol (Sigma Chemical, St. Louis, MO) delivered through a glass tube to the head of the animal, was turned on 5 s after placement of the animal in the training situation. The CS–US interval was 3 s. The US was a 1-μl drop of 50% sucrose solution at the end of the blunted needle of a microsyringe that was touched first to the antennae of the animal to elicit extension of the proboscis and then to the proboscis itself for a period of 2 s, during which time the drop was almost entirely consumed. Each reinforcement began with antennal stimulation even when the CS elicited anticipatory extension of the proboscis. Then the needle was retracted, and 5 s later, the subject was returned to the holding area. For animals in the No Overlap group (n = 26), the odor terminated immediately before the antennae were stimulated with the sucrose; for animals in the Overlap group (n = 27), the odor continued for 2 s during ingestion of the sucrose. Although the odor was delivered automatically, the sucrose could only be delivered manually. The experimenters were highly practiced and guided by computer-generated auditory timing signals, and yet it may be well to emphasize that the validity of the outcome depends heavily on their skill; various efforts have been made to automate the delivery of sucrose in such experiments (e.g. Vareschi, 1971), but without much success. After the 8 conditioning trials, there were 8 extinction trials, on each of which the CS alone was presented for 3 s and the subject removed from the situation 5 s later. The conditioned response or CR was defined as extension of the proboscis, full or partial, during the 3-s CS–US interval on training trials and during the 3-s presentation of the CS on extinction trials. Typically, the response was unmistakable, but when there was any doubt, a failure was recorded.

Results

In Figure 2, the performance of the two groups is plotted in terms of probability of response to the CS—defined as the proportion of animals that responded—on each conditioning trial. As the curves show, both groups conditioned rapidly and at about the same rate. The number of responses per

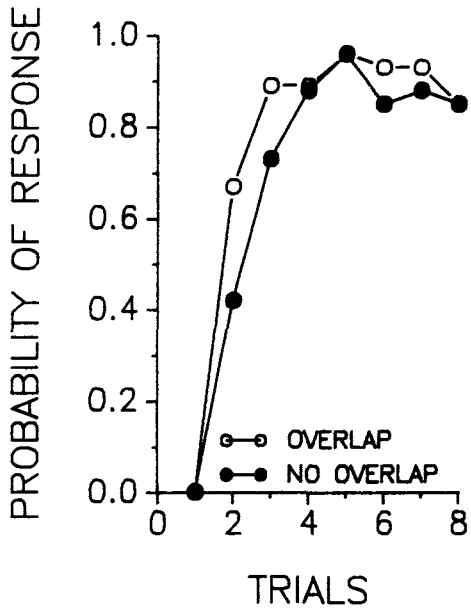

Figure 2. Acquisition in the Overlap and No Overlap groups of Experiment 1.

animal in the 8 conditioning trials was only slightly greater for the Overlap group (M = 6.1) than for the No Overlap group (M = 5.7), and the difference was not statistically significant (median test, Fisher's exact p = .1516).

In Figure 3, the performance of the two groups is plotted in terms of the probability of response to the CS on each extinction trial. Here again, the performance of the two groups was very much the same. The number of responses to the CS in the 8 extinction trials was only slightly greater in the Overlap group (M = 4.2) than in the No Overlap group (M = 3.9), and the difference was not statistically significant (median test, p = .1704).

Experiment 2

It was expected at the outset of Experiment 1 that conditioning might be better in the Overlap group than in the No Overlap group if the odor–taste association were strengthened by concurrent stimulation. The lack of a difference does not, however, contradict the assumption of simultaneous conditioning because there was a possibility of a ceiling effect; that is, the forward-conditioning procedure for the No Overlap group may have been so effective that there was no room for improvement. In this experiment a simultaneous-conditioning procedure was used to look directly for evidence of the effectiveness of concurrent stimulation.

In addition to a Simultaneous group, for which the CS and the US were presented concurrently, two other groups were used. One was an Unpaired group, which served as a control for any sensitizing effects of experience with the CS and the US apart from their contiguity. The other was a Forward group, which was trained like the No Overlap group in Experiment 1 and served as a control for the health of the animals. For reasons that are not understood, an occasional squad of animals will fail to respond very well in experiments of this kind, even when the training procedure is one that typically is highly effective (see also Bitterman et al., 1983). If there were little responding in the Simultaneous group of this experiment, there would be no way to tell—in the absence of the Forward group—whether concurrent stimulation was ineffective or whether the sample of animals was defective.

Method

Subjects. The subjects were collected and prepared for training in the same way as in Experiment 1.

Procedure. There were five squads of animals that were trained on 5 separate days. Each squad contained approximately equal numbers of animals randomly assigned to the three experimental groups. As in Experiment 1, the animals were trained in rotation on each trial and in a balanced sequence. There were 8 reinforced trials followed by 8 extinction trials, with an intertrial interval of 10 min.

The conditioning procedure for the Forward group (n = 24) was exactly the same as for the No Overlap group in Experiment 1: The offset of the 3-s CS (geraniol) was followed immediately by presentation of the US (1 μl of a 50% sucrose solution), first to the antennae and then the proboscis for 2 s. For the Simultaneous group (n = 25), the 3-s CS was turned on immediately after the US made contact with the extended proboscis; because it was possible (given our rather crude manual procedure) that slightly positive intervals might occasionally be generated by accident in efforts at strictly simultaneous presentation, the CS was deliberately withheld until the extended proboscis made contact with the sucrose solution. For the Unpaired group (n = 25), the US was presented first and followed 5 s after its termination by the CS. Although the treatments of the three groups differed, the total time in the training situation was kept the same for all three. In extinction the three groups were treated exactly as in the preceding experiment, the 3-s CS presented alone on each of the 8 trials with an intertrial interval of 10 min.

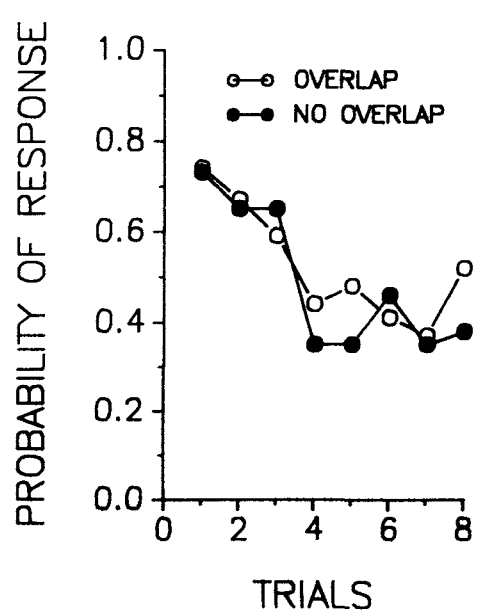

Figure 3. Extinction in the Overlap and No Overlap groups of Experiment 1.

Results

In acquisition the Simultaneous group, of course, had no opportunity to respond to the CS alone, and the Unpaired group hardly responded at all, but the Forward group conditioned rapidly, just as did the No Overlap group of Experiment 1, which was trained in the same way (see Figure 2). In Figure 4, the performance of the three groups is plotted in terms of the probability of response to the CS on each extinction trial, and again the performance of the Forward group was very much the same as that of the No Overlap group in Experiment 1 (see Figure 3). The Simultaneous group also showed substantial responding in extinction, and the Unpaired group showed very little. The Forward group made significantly more responses per animal ($M = 4.5$) than did the Simultaneous group ($M = 2.0$, $p = .0003$), which in turn made significantly more responses than did the Unpaired group ($M = 0.1$, $p = .0004$).

Experiment 3

In this experiment a simultaneous procedure was used again to look for evidence of the effectiveness of concurrent stimulation, but the control for the effects of experience with the CS and US apart from their temporal contiguity was within subjects rather than between subjects. A Simultaneous group was trained with two odors, one (S+) paired with the US and the other (S−) presented alone, a procedure that quickly produces differential responding to the odors when the CS–US interval is positive (Bitterman et al., 1983). There was also a Forward group, the purpose of which, as in Experiment 2, was to check on the health of the animals in each squad—that is, to guard against the possibility that failure of the Simultaneous group to respond to S+ on test trials might be due to poor health. The Forward group was trained exactly like the Simultaneous group, except that there was a 3-s interval between the onset of S+ and the onset of the US.

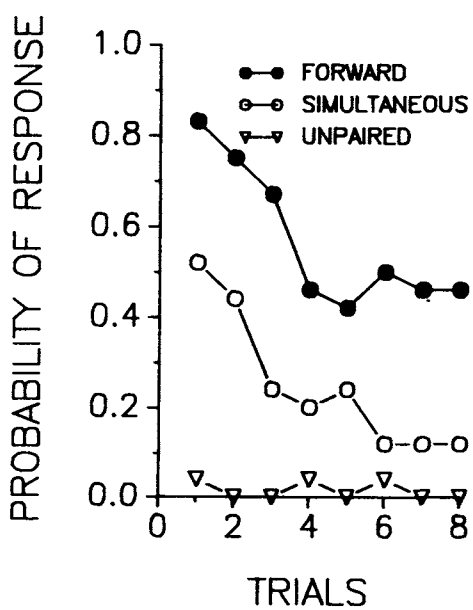

Figure 4. Performance of the Forward, Simultaneous, and Unpaired groups on the test trials in Experiment 2.

Method

Subjects. The subjects were collected and prepared for training in the same way as in the previous experiments.

Procedure. There were four squads of animals that were trained on 4 separate days. Each squad contained approximately equal numbers of animals randomly assigned to the Simultaneous and Forward groups. As in the previous experiments, the animals were trained in rotation on each trial and in a balanced sequence. In all, there were 24 trials for each animal.

The first 16 trials were differential conditioning trials, 8 with geraniol and 8 with oil of peppermint in ABBABAAB order. The intertrial interval was 5 min, with 10 min on the average between reinforcements. For half the animals in each of the two groups, geraniol was S+, and peppermint was S−; for the rest, peppermint was S+, and geraniol was S−. On unreinforced trials for both groups, S− was presented alone for 3 s, but the treatment of the two groups differed on reinforced trials. For the Forward group ($n = 31$), as for the No Overlap group of Experiment 1 and the Forward group of Experiment 2, the offset of the 3-s S+ was followed immediately by the onset of the US—the standard 1-μl drop of 50% sucrose touched first to the antennae and then for 2 s to the proboscis. For the Simultaneous group ($n = 29$), as in Experiment 2, the 3-s S+ was turned on immediately after the sucrose made contact with the extended proboscis. The final 8 trials, 4 with each odor, were scheduled in the same way as the earlier ones, but now all were unreinforced.

Results

At the left of Figure 5, the performance of the Forward group in the differential conditioning phase of the experiment is plotted in terms of the probability of response to S+ and S− on the first 8 trials with each. The curves show good discrimination: Responding to S+ increased fairly rapidly, but there was little response to S− and none at all after the 5th trial. There were significantly more responses on the 8 S+ trials ($M = 4.9$) than on the 8 S− trials ($M = 0.2$, $p < .0001$).

Nothing can be said about the course of acquisition in the Simultaneous group except that, as in the Forward group, there was little response to S−, but clear evidence of differential conditioning in that group appeared in the extinction test. At the right of Figure 5, the performance of the Simultaneous group is plotted along with that of the Forward group in terms of the probability of response on each of the 4 test trials with S+. There was no response at all to S− in either group. The frequency of response on the 4 S+ trials for the Forward group ($M = 2.4$) was significantly greater than zero ($p < .0001$). The frequency of response on the 4 S+ trials for the Simultaneous group ($M = 1.7$) also was significantly greater than zero ($p = .0008$). The difference between the Forward and Simultaneous groups in frequency of response to S+ was not statistically significant ($p = .1569$).

Discussion

In Experiment 1, there was no significant facilitation of forward conditioning by concurrent odor–taste stimulation.

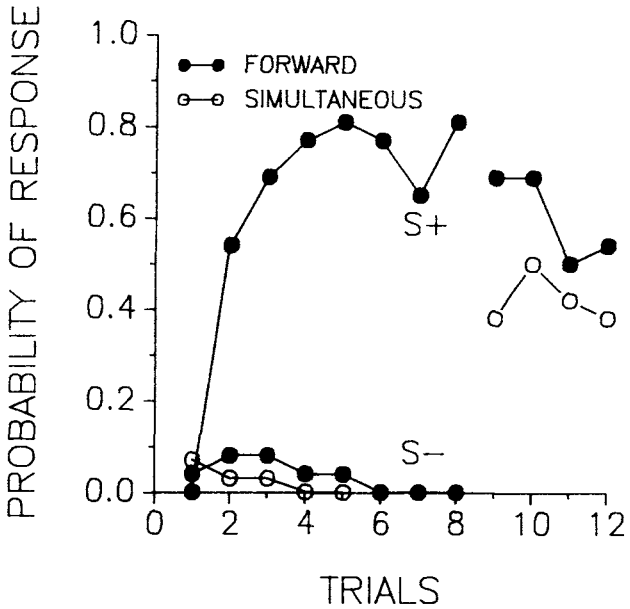

Figure 5. Performance of the Forward group on the 8 S+ trials and on the 8 S− trials during differential conditioning in Experiment 3, performance of the Simultaneous group on the 8 S− trials during differential conditioning, and performance of both groups on the 4 subsequent test trials with S+. (There was no response by the animals of either group on the 4 test trials with S−.)

Evidence of facilitation would have provided direct support for the duration account of the amount-of-reward results for free-flying foragers as compared with the immediate-evaluation account (which gives no reason to expect greater associative strength in the Overlap group than in the No Overlap group). The negative results do not, however, contradict the duration hypothesis, because concurrent stimulation is not assumed to be the sole source of associative strength. Conditioning in the No Overlap group was already so good that there was little room for improvement.

In Experiments 2 and 3, the Forward groups that served as a check on the health of the animals tended to respond more to odors paired with sucrose than did the Simultaneous groups (significantly so only in Experiment 2). It may be well to note in this connection that work with other animals has not always shown better forward than simultaneous conditioning, and on occasion simultaneous conditioning has seemed to be better (e.g., Rescorla, 1980). In any case, the evidence of concurrent odor–taste association required by the duration account of the amount-of-reward results for honeybees is independent of the performance of the Forward groups. That evidence is to be found in the greater response to the CS by the Simultaneous group than by the Unpaired group of Experiment 2 and in the greater response to S+ than to S− by the Simultaneous group of Experiment 3.

The conclusion that simultaneous conditioning has been demonstrated in these experiments might conceivably be questioned, however, on the assumption that the control procedures used actually were inhibitory. If so, response in extinction to the simultaneous training odors might reflect nothing more than a sensitization effect that was counteracted in the case of the unpaired odors by an inhibitory process. The control problem is, of course, a perfectly general one. Although the "truly random" procedure once was widely believed to be associatively neutral—that is, to have neither excitatory nor inhibitory consequences—the belief is without foundation (Papini & Bitterman, 1990), and there is no other control procedure for which the same claim can be made with greater confidence.

What can be said of the Simultaneous group results at the very least is that they are compatible with the assumption of concurrent odor–taste association and provide some warrant for further tests of the duration account of the amount-of-reward results. A reasonable next step may be to study the relation between strength of association and duration of concurrent stimulation in simultaneous conditioning, although our preliminary efforts suggest that such experiments will not be easy to implement. To control for the nutritive condition of the animals requires compensatory intertrial feeding in a different context, which, of course, is perfectly feasible. For example, the animals of a 2-s group are given 8-s intertrial feedings in the holding area, whereas the animals of an 8-s group are given 2-s intertrial feedings in the holding area. The problem is that the reactivity of the harnessed animals tends to decline rather rapidly as the volume of ingested sucrose increases unless the intertrial intervals are very long, but then the length of the experiment increases, with the disadvantage that the health of the animals tends to deteriorate in the course of prolonged captivity. The appeal of free-flying foragers is that they continue to perform well indefinitely, and any decline in motivation in the course of a visit to the laboratory—as indexed, for example, by increased latency of responding after the ingestion of 20 μl of sucrose solution (Lee & Bitterman, 1990a)—is quickly reversed by a visit to the hive. A parallel strategy is to develop some critical tests of the immediate-evaluation hypothesis (the only viable alternative to the duration hypothesis) that may well be feasible in work with free-flying foragers.

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