Aversive Conditioning in Honeybees (*Apis mellifera*)

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Learning in honeybees, previously studied by appetitive techniques, was studied here by aversive techniques. In one series of experiments, a shuttle box was used, with the odor of formic acid as the aversive stimulus. A punishment contingency was found to suppress shuttling more in master animals than in yoked controls, whereas escape and unsigned avoidance contingencies facilitated shuttling in master animals compared with yoked controls. In a second series of experiments, the subjects were unrestrained foragers flying back and forth between the hive and the sll of an open laboratory window to take sucrose solution from targets so constructed that shock could be delivered between the proboscis was in contact with the solution. A group of animals trained to discriminate between two differently colored targets, one providing sucrose and the other sucrose plus immediate shock, performed as well as a group trained with sucrose and tap water, and better than a group trained with sucrose and sucrose plus delayed shock. Animals for which a signal was paired with shock while they were feeding from a single target quickly learned to avoid the shock by flying off the target. The effectiveness of the pairing was demonstrated both by an explicitly unpaired procedure (which retarded acquisition when the signal and shock subsequently were paired) and by differential conditioning. This work substantially extends the range of vertebrate learning phenomena found in honeybees.

Recent experiments on appetitive conditioning have revealed some striking similarities between the learning of honeybees and vertebrates, whose nervous systems have evolved independently for the most part and differ substantially both in organization and complexity. The technique used in the majority of these experiments has been to train free-flying foragers to shuttle back and forth from the hive to the laboratory where they take sucrose solution from targets distinguished by color, odor, or position (Couvillon & Bitterman, 1980, 1982, 1984; Couvillon, Klosterhalfen, & Bitterman, 1983; Klosterhalfen, Fischer, & Bitterman, 1978). This simple technique has made possible a variety of sophisticated learning experiments in which an array of vertebrate conditioning phenomena have been demonstrated. Among them are overshadowing, potentiation, and within-compound association in compound conditioning; dimensional shift in choice problems; the overlearning-extinction effect and its dependence on magnitude of reinforcement; and successive negative incentive contrast. With foragers temporarily confined on each visit to permit better control of certain critical variables, Sigurdson (1981a, 1981b) did a variety of fully automated, massed-trials experiments demonstrating such phenomena as behavioral contrast, probability matching, progressive improvement in reversal learning, and the partial reinforcement effect. Work has been done also on the classical conditioning of proboscis extension in harnessed foragers, showing, for example, rapid acquisition with an omission contingency to control for adventitious reinforcement, second-order conditioning, and the inhibitory effect of explicitly unpaired conditioned and unconditioned stimuli (Bitterman, Menzel, Fietz, & Schäfer, 1983; Menzel & Bitterman, 1983).

Nowhere in the substantial set of results obtained in those experiments is there anything at all unfamiliar to students of vertebrate learning.

In the experiments reported here, aversive rather than appetitive reinforcement was used. Because much of what is known about vertebrate learning comes from experiments with aversive reinforcers, the comparative study of learning in honeybees would not be complete if it were restricted to appetitive reinforcers. Work with aversive as well as appetitive reinforcers is important for what it may tell us about the interplay of opposed affective systems in honeybees and about the relation between learning and performance. As Mackintosh (1983) argued from the vertebrate literature, a strong case can be made for the essential similarity of the associative processes in appetitive and aversive conditioning, with different rules only for translating the associations into behavior. Whether the same is true of honeybees can be determined only by systematic study, and the purpose here was simply to explore the adjustment of the animals to a variety of aversive contingencies in preparation for each study.

There have been experiments on escape, punishment, and avoidance in other insects (ants, flies, roaches, and beetles), most of which are inconclusive because of poor design. A common shortcoming is lack of control for the effects of the aversive stimulus independently of the behavioral contingency (see, e.g., Alloway, 1970; Chen, Aranda, & Luco, 1970; Freckleton & Wahlsten, 1968; Leeming & Little, 1977; Morgan, 1981). A widely used punishment technique for fruit flies, intended primarily to provide a target behavior for
Experiments With Formic Acid

In the first series of experiments reported here, bees were trained in a shuttle box, with movement from one compartment to the other monitored by a pair of photodetectors. The aversive stimulus was air impregnated with formic acid which was pumped into the shuttle box, replacing the uncontaminated moist air with which the apparatus normally was ventilated. In this situation, it was possible to do fully automated experiments on escape, punishment, and unsignaled avoidance. Formic acid was used as the aversive stimulus primarily because of difficulties encountered in attempts to shock freely moving confined bees, but there was interest as well in the potential application of the findings to problems in the use of insecticides. The results of experiments with insecticides as aversive stimuli, although lacking essential controls, suggest the possibility that learning may play an important role in the survival of animals treated with insecticides. (Ebeling, Reier-son, & Wagner, 1968; Ebeling, Wagner, & Reier-son, 1966). The shuttle box is ideally suited for such work because it permits better control of critical variables (such as the position of the animal and the intensity of stimulation) than do techniques used previously.

General Method

Subjects

The subjects were honeybees selected at random from a group of foragers at a feeding station equipped with a large jar of 10%-15% sucrose solution. Each animal was carried in a small matchbox to the laboratory and placed on a petri dish, where it was permitted to drink its fill of a 50% sucrose solution before being confined in the training situation. Different sets of subjects were used for the three experiments described.

Apparatus

The training apparatus, a shuttle box adapted from one used in previous work with ants (Abramson, Miler, & Mann, 1982), is diagrammed in Figure 1, which presents a lateral view. It was constructed

![Diagram (lateral view) of the shuttle box used in Experiments 1-3. IN, air or odor intake; OUT, air or odor outflow. The hurdle defines two compartments (left and right) separated by a crawl space through which the animal moves from one to the other.](image)

from a Plexiglas tube (7.5 cm long and 2.5 cm in internal diameter) divided into two equal compartments (left and right in Figure 1) by an inverted hurdle which sloped gradually toward the center of the tube, leaving a 5-mm crawl space between the ceiling and floor. The position of the animal was monitored by a pair of infrared photoemitters (General Electric led 55cf) and detectors (General Electric L14g3) located 10 mm from the center on each side and oriented perpendicularly to the plane of the diagram. A crossing was defined as an interruption of the beam farthest away from the subject at any given time, that is, at the entrance to the compartment opposite to that occupied by the subject. The odor of formic acid entered both compartments of the shuttle box through a screen (replaced after each subject) which served as the floor of the apparatus. Compressed air (7.5 pounds per square inch [psi]) was forced into bottles containing formic acid (Mallinckrodt 88% HCOOH) and out into the apparatus at appropriate times through Asco three-way valves. In Experiment 1, the bottles contained 15 ml of formic acid. In Experiments 2 and 3, out of concern for the health of the animals, the formic acid was diluted to 2/3 strength with distilled water, preliminary trials showing it still to be effective. When no odor delivery was scheduled, the air directed into the chambers came through bottles containing 15 ml of tap water.

Two identical shuttle boxes were used in these experiments, because pairs of subjects (master and yoke) were trained concurrently in each case. The functions of the two shuttle boxes (master and yoke) and their positions in the enclosure that contained them were counterbalanced over pairs of subjects. The airflow through both of the shuttle boxes and the odor delivery were determined by the behavior of the master animal. The purpose of the yoking procedure was to control for the effects of aversive stimulation apart from the behavioral requirements.

Experiment 1

Procedure

In this experiment, an escape contingency was programmed for 10 pairs of subjects. There were 40 trials at a variable intertrial interval averaging 2 min—20 escape trials and 20 blank trials in quasi-random
order. Each escape trial began with the onset of the aversive stimulus and ended with the response of the master animal or after 45 s if it failed to respond in that time. The blank trials were exactly like the escape trials except that there was no aversive stimulus. Because the basal level of crossing was substantial at the outset (as many as 10–12 crossings per minute), a fixed-ratio-of-two schedule was used; that is, response was defined as two crossings (movement from the compartment initially occupied by the animal to the opposite and back again).

Results

Plotted in Figure 2 are the mean natural log latencies of response for the master animals on blank and escape trials in four-trial blocks. The latencies were equal at the outset of training, after which they declined differentially on escape trials. Analysis of variance yielded a significant conditions (escape vs. blank trials) effect, $F(1, 9) = 57.18, p < .0001$, and a significant Conditions $\times$ Blocks interaction, $F(4, 36) = 8.41, p < .0001$. The decline in latency of response on escape trials also is significant, $F(4, 36) = 6.63, p = .0004$. Comparable curves cannot be plotted for the yoked animals, because there are no data for trials on which the masters responded first. The performances of the two groups are shown in Figure 3, which is plotted in terms of the proportion of trials on which yoked animals responded before their masters. The probability of prior response by yoked animals declined progressively from the chance level at the outset to .15 in the last block of four trials. It is this change—statistically significant, $F(4, 36) = 2.92, p = .0346$—that demonstrates the effectiveness of the escape contingency.

Experiment 2

Procedure

The contingency in this experiment was punishment. Each of the 16 pairs of subjects was trained in a single 30-min session during which each crossing of the master animal produced a 0.5-s presenta-
Experiment 3

Procedure

In this experiment, unsignaled avoidance (Sidman avoidance) was studied. Each of 10 pairs of subjects was trained in a 1-hr session. The aversive stimulus, a 3-s exposure to the odor of dilute formic acid, was scheduled by a 20-s cycling clock that was reset by response. Response was defined as two crossings, just as it was in the escape training.

Results

In Figure 5, the performance of the two groups in this experiment is plotted in terms of the mean number of responses per minute in successive 5-min blocks. Here the rate of responding was somewhat higher at the outset in the yoked animals than in the masters (subjects were assigned at random to the two groups). With further training, the frequency of responding in yoked animals declined as did it in the punishment experiment and presumably for the same reason—decrease in the frequency of aversive stimulation contingent upon the behavior of the master animals. In this case, however, an avoidance rather than a punishment contingency was in force, and the frequency of responding in the master animals increased. An overall analysis of variance shows no significant groups effect $F(1, 18) = 2.07, p > .05$, but a significant Groups × Blocks interaction, $F(11, 198) = 5.20, p < .0001$. The increase in responding by the master animals is significant, $F(11, 99) = 1.96, p = .0410$, as is the decrease in responding by the yoked animals, $F(11, 99) = 5.42, p < .0001$. Plotted also in Figure 5 is the number of presentations of the aversive odor in successive 5-min periods, which declined significantly as training continued, $F(11, 99) = 3.59, p = .0003$.

Experiments With Electric Shock

In the second series of experiments, the subjects were unrestrained foragers flying back and forth between the hive and the sill of an open laboratory window every few minutes to take sucrose solution from a target set on the sill. The target was constructed in such a way that shock could be delivered while the proboscis was in contact with the sucrose solution. The advantage of mild shock over aversive odor is that its onset, offset, and intensity can be exactly controlled (as long as the animal is in contact with the electrodes), and there is no suspicion that it may adversely affect the well-being of the animal. There is something to be said also for having a range of aversive stimuli available for the work with honeybees—to be sure that the results obtained are not specific to a given reinforcer.

General Method

Subjects

The subjects were selected at random from a group of foragers at a feeding station providing 10%-15% sucrose solution. A single animal was picked up in a small matchbox and carried to a target containing 50% sucrose presented on the sill of an open laboratory window. While the animal was feeding, it was marked with a spot of colored lacquer, and when it finished feeding, it was free to go to the hive. Typically, the bee returned to the target within a few minutes; if not, it was recaptured at the feeding station (where it usually could be found) and placed again on the target. More than two placements rarely were required. The first time the subject returned to the laboratory window of its own accord was counted as the first training trial. After the experiment, the subject was captured and destroyed. Different sets of subjects were used for the three experiments.

Apparatus

The targets used in these experiments were made of disposable petri dishes, 5.5 cm in diameter. In order to provide a conductive surface, a copper plate (5 cm in diameter) was mounted on the cover of the dish. In the center of the target was an insulating feeding hole (1 cm in diameter and 0.5 cm deep) which could be filled with either sucrose solution or water. When the animal was standing on the copper plate and its proboscis was in contact with the solution, shock could be delivered by connecting the plate to one side of the supply and the cup to the other. For the work on punishment in Experiment 4, the targets could be differentiated by attaching an annulus of colored plastic, nominally either orange or blue, as illustrated in Figure 6. The annulus covered most of the copper plate except for a region in the vicinity of the cup on which the animal rested while drinking. For subsequent experiments on avoidance, in which vibration and airstream were used as conditioned stimuli, the target (without colored annulus) was mounted on a vibrator (Goodman Industries, Wembly, England) set to produce a frequency of 50 Hz and a peak-to-peak amplitude of 0.15 mm. The rod connecting the target to the vibrator, which was below the window shelf, protruded through a small hole in the shelf. Above the target, at a height of 2.5 cm, was a second petri dish with 46 small holes drilled in the bottom through which a stream of compressed air (7.5 psi) could be directed upon the animal below. This apparatus (lateral view) is diagrammed in Figure 7.
Experiment 4

Procedure

In previous work on simultaneous discrimination in free-flying bees (Klosterhalfen et al., 1978), two targets differing in color or odor were used, one containing sucrose solution and the other tap water (distinguishable from the sucrose solution only by taste). The purpose of the present experiment, designed to study punishment, was to compare performance under these conventional conditions with performance under conditions in which both targets contained sucrose solution but response to one was followed by shock. Two targets were presented on each visit, an orange annulus affixed to one and a blue annulus to the other, with a 10-cm separation (center to center) and the right-left arrangement of the colors balanced in quasi-random order from visit to visit. One color was consistently positive (S+) and the other (the one chosen on the first training visit) consistently negative (S–). For 8 subjects in the conventional group, the positive target contained 50% sucrose solution, and the negative target contained tap water. For 8 subjects in the punishment group, both targets contained 50% sucrose solution, but the negative target always was connected to the shock supply (4 V ac). Eight subjects in the delayed punishment group were treated exactly as those in the punishment group except that the shock supply was not connected until 5 s after initiation of drinking on the negative target. The animal was free to correct its errors, and each visit ended with feeding to repletion on the positive target. There were 20 such training visits, followed on the next visit by an extinction test on which both targets (thoroughly cleaned in the intervisit interval) contained water, the shock circuit was disconnected, and all contacts with either target were recorded for a period of 10 min. The positions of the two colors were balanced over subjects. The experimenter was equipped with two hand-held switches (one for each target), which were pressed whenever contact was made, and the data were taken on printing counters programmed to print stored frequencies in successive 30-s periods. The discriminative training was preceded by four pretraining visits, during two of which the animal fed to repletion on the orange target alone and during the remaining two (in balanced orders) on the blue target alone. The purpose of the pretraining was to familiarize the animal with both targets and to produce a relatively strong tendency to respond to each.

Results

In Figure 8, the results of this experiment are plotted in terms of the mean initial errors made by the conventional, punishment, and delayed punishment groups in successive five-visit blocks. At the outset, all three groups (trained against the preference shown on the first trial) tended to choose the incorrect target, but as training continued, errors declined progressively. The decline was less rapid in the delayed punishment group than in the other two, whose performance was almost identical. Analysis of variance showed a significant groups effect, $F(2, 21) = 35.07, p < .0001$, and a significant Groups x Blocks interaction, $F(6, 63) = 2.89, p = .0149$.

In Figure 9, mean cumulative frequency of response to S+ and S– over 20 successive 30-s periods in extinction is plotted for the punishment and the conventional groups. Coming into contact with tap water in extinction, an animal would immediately fly up, return to one of the targets, taste the tap water, fly up, return, and so forth, with the number of target contacts progressively decreasing—a pattern of behavior perfectly familiar from previous experiments (Couvillon & Bitnerman, 1980). Although the performances of the punishment and the conventional animals were much the same in terms of errors made during acquisition, the preference for S+ during extinction was significantly greater in the conventional group. Analysis of variance revealed no significant groups
effect ($F < 1$) but a significant Groups $\times$ Stimuli interaction, $F(1, 14) = 6.08, p = .0272$. On the assumption that resistance to extinction is a more sensitive measure than choice during acquisition, it might be assumed that to pair $S-$ with water produces better discrimination than to pair it with sucrose plus shock, although it is not immediately clear why the differences should show up in terms of response to $S+$ or why the performances of the punished and delayed punishment animals, different in training, were essentially identical in extinction ($F < 1$). A more likely explanation is that the change in conditions from training to extinction was greater for these animals than for the conventional animals.

**Experiment 5**

**Procedure**

In this experiment, signaled avoidance was studied in free-flying foragers, which were conditioned while feeding to repletion on a target in the course of a series of visits. The conditioned stimulus (CS) was a 5-s period of substrate vibration at the end of which a 30-ms pulse of 25-V ac shock—the unconditioned stimulus (US)—was delivered. The animal could avoid shock simply by withdrawing its proboscis during the CS-US interval, although what it actually did in response both to the CS (after conditioning) and to the US (when it did not avoid) was to fly off the target. After the animal had been pretrained to come to the laboratory in the usual way, there were 20 training visits. On each visit for the 16 animals in Group PP, a paired presentation of the CS and US was scheduled either 5 or 30 s after feeding began. For the 16 animals in Group UU, the CS alone was presented after 5 s and the US alone after 30 s on some visits and in the reverse sequence of other visits (again in quasi-random order). This "explicitly unpaired" procedure was used to control for the possibility that changes in the performance of Group PP might be due merely to exposure to the stimuli independently of their temporal relation. For the 16 animals in Group UP, the CS and US were unpaired on the first 10 visits and paired on the next 10. For the 16 animals in Group PU, the stimuli first were paired and then unpaired.

**Results**

In Figure 10, the results of this experiment are plotted in terms of mean probability of response to the CS in successive five-trial blocks. Comparison of the performances of Groups PP and UU clearly shows an effect of pairing, $F(1, 30) = 201.09, p < .0001$. The fact that the probability of response in Group PP remained less than 1 was not due, it should be noted, to the failure of some animals in the group to condition (all did) but presumably to the use of an avoidance contingency—the frequency of reinforcement became low as the frequency of response to the CS increased. A second way to compare the effects of paired and explicitly unpaired presentations is to look at the performance of Groups PP and UP in Trials 11–20, when the CS and US were paired for both. In those trials, the mean probability of response to the CS was significantly higher after paired training than after unpaired training, $F(1, 30) = 77.30, p < .0001$. The poor performance of Group UP in the first block of paired trials suggests that in this signaled avoidance procedure, as in the appetitive proboscis-extension procedure (Bitterman et al., 1983), explicitly unpaired experience impairs subsequent acquisition. This conclusion is supported by analysis of variance based on the performance of Group UP in Trials 11–20 and that of Group PP in Trials 1–10, which reveals both a significant groups effect $F(1, 30) = 32.40, p < .0001$, and a significant Groups $\times$ Trials interaction, $F(9, 270) = 2.13, p = .0273$. A third way to compare the effects of paired and unpaired training is in terms of the performance of the PU and UU animals on Trials 11–20, when the CS and US were unpaired for both. In these trials, the mean probability of response to the CS was significantly greater in the PU than in the UU animals, $F(1, 30) = 67.50, p < .0001$. The performance of Group PU in Trials 11–20 shows the high resistance to extinction that we might be led to expect on the basis of avoidance experiments with vertebrates.

An interesting difference between the effects of paired and unpaired training was evidenced in what may be called return...
time—the time between departure from the laboratory after feeding to repletion on one visit and return from the hive on the next visit—which provides a measure of the aversiveness of the training situation apart from the CS. The results are plotted in Figure 11 in terms of the mean log return times for Groups PP and UU. As the curves show, return times stayed very much the same in the course of paired training but increased progressively in the course of unpaired training: groups, $F(1, 30) = 4.63, p = .0397$, and Groups $\times$ Five-Visit Blocks interaction, $F(3, 90) = 3.51, p = .0185$. This difference is easy to understand in terms of the principle of shared associative strength (Rescorla & Wagner, 1972), which accounts also for the acquisition data. Background cues should be more strongly conditioned in explicitly unpaired training than in paired training and should block acquisition in paired training that follows unpaired training. Aversion to a locus of negatively correlated signal and shock relative to a locus of positively correlated signal and shock is known also in rats (Fanselow, 1980).

**Experiment 6**

**Procedure**

Differential conditioning was studied in this experiment, whose purpose was twofold. One purpose was to provide further support for an associative interpretation of the avoidance data obtained in Experiment 5; differential conditioning is one of several conventional controls for the effects of stimulation per se in conditioning experiments. The second was to set the stage for analytical experiments on compound conditioning, which would require another effective CS that was easily distinguishable from vibration. After a number of pilot experiments with light that gave negative results, airstream was explored. The experiment, which began with the usual pretraining, consisted of 20 visits, on each of which both vibration and airstream were presented. On half of the trials, vibration was presented after the animal had been feeding for 5 s and airstream after 30 s (not counting any interruption of feeding produced by the first stimulus). On the remaining visits (in quasi-random order), airstream was presented before vibration. The duration of each stimulus was 5 s. For 8 animals, vibration was $S^+$ (followed by a 30-ms pulse of 25 V ac shock) and airstream was $S^-$; for 8 other animals, airstream was $S^+$ and vibration was $S^-$. As in Experiment 5, the animal could avoid shock by withdrawal of the proboscis from the sucrose in response to $S^+$, but what it actually did was to fly off the target as it did in response to the shock itself.

**Results**

In Figure 12, the results of the experiment are plotted in terms of the probability of response to $S^+$ and to $S^-$. The curves show that discrimination developed very quickly. Analysis of variance yielded both a significant effect of stimuli ($S^+$ vs. $S^-$), $F(1, 8) = 142.55, p < .0001$, and a significant interaction of Stimuli $\times$ Five-Visit Blocks, $F(3, 24) = 8.78, p = .0004$. It made no difference whether airstream or vibration was $S^+$, $F(1, 8) = 2.91, p < .05$, or whether the training began with an $S^+$ or an $S^-$ trial ($F < 1$).

**Discussion**

Escape, punishment, and avoidance procedures seem to have much the same effects on honeybees as on vertebrates. Evidence for the effectiveness of the contingencies in the series of experiments with formic acid comes from comparisons of the performance of master animals with the performance of yoked controls. Although the yoking technique has received some criticism (Church, 1964), it is difficult to believe that what one is seeing here is nothing but the differential unconditioned influence of the aversive stimulation itself. When shuttling terminated the aversive stimulus, or postponed its occurrence, there was more responding in the masters than in the yokes, but when shuttling produced the aversive stimulus, there was less responding in the masters than in the yokes. In the work with shock, the effectiveness of the punishment contingency was established, not by the use of yoked animals but by the use both of a choice procedure and of delayed punishment.

![Figure 11](image1.png)  
*Figure 11. Mean natural log return time for Groups PP and UU in successive five-visit blocks of Experiment 5. (PP, paired presentation of stimuli; UU, unpaired presentation.)*

![Figure 12](image2.png)  
*Figure 12. Probability of response on $S^+$ and $S^-$ trials during differential conditioning in Experiment 6.*
The processes responsible for the changes in behavior remain, of course, to be analyzed. Corresponding behavioral outcomes in analogous experiments with widely divergent animals do not necessarily imply common processes, although commonality may be defended on grounds of parsimony as a reasonable working hypothesis (Bitterman, 1975). In the case of punishment, it is easy to suppose that local stimuli correlated with formic acid or shock come in consequence to acquire aversive properties for the master animal. Although a parallel interpretation of escape training in the shuttle box might be acceptable—that is, an interpretation in terms of approach to stimuli contiguous with the termination of the aversive odor—it seems more likely that what one is seeing both in escape and in shuttle box avoidance is the direct strengthening of response tendencies by the consequences of response in the sense of traditional reinforcement theory. The two-factor analysis developed to account for avoidance conditioning in rats (Mowrer, 1947), whatever its alleged limitations with respect to rats, readily applies to the shuttle box results for honeybees presented here: “Fear” is conditioned to chamber stimuli, and shuffling is reinforced because it generates stimuli that become conditioned inhibitors of fear (Weisman & Litner, 1969).

What is happening in the signaled avoidance training with shock as the aversive stimulus is difficult to say because no control for the response-shock contingency is possible in free-flying subjects. The unpaired control procedure does show the importance of signal–shock pairing, and it is possible that the results can be interpreted fully in Pavlovian terms. An appetitive analogue of the differential conditioning in Experiment 6 is provided by an experiment on proboscis extension in honeybees with one odor followed by sucrose solution on an omission schedule and a second odor unreinforced (Bitterman et al., 1983). In that experiment, a high level of responding to S+ was maintained despite the fact that an appetitive rather than an aversive stimulus was “avoided.”

What can be said for the present is that these experiments on punishment, escape, and avoidance substantially extend the range of vertebrate learning phenomena found in honeybees. The powerful analytical paradigms developed in the study of vertebrates will help us to determine whether the underlying mechanisms are the same or whether the resemblances are only superficial, although it may be difficult to imagine—given the simplicity of the phenomena—that there will be any functional surprises.

References


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