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THE HOMING OF ANTS

AN EXPERIMENTAL STUDY OF ANT BEHAVIOR

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THE HOMING OF ANTS: AN EXPERIMENTAL STUDY OF ANT BEHAVIOR.

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WITH PLATES II-IV, AND ONE FIGURE IN THE TEXT.

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INTRODUCTION.

Technique.—In the following experiments on ants the attempt has been made to have the conditions so simple that disturbance of the normal activities is reduced to a minimum, and yet to present in each experiment a definite problem which the ants must solve. Excepting where it is otherwise stated, each experiment recorded represents one of several similar experiments.

The apparatus used consisted chiefly of stages, inclined planes and dark chambers. All of these were constructed of cardboard. Occasionally a LUBBOCK or a FIELDE nest was used, but for most experiments I used a modification of the JANET nest. These nests were 39 x 15 x 2.5 to 3 cm. Each contained a well 10 x 5 x 1.5 cm., two living chambers, each 10 x 7 cm. and from a few mm. to a cm. or more in depth and a food-chamber of the same dimensions as the living chambers. The edges of the top of the nest, as far back as the beginning of the well, and the partitions between the cham-

bers and between the last chamber and the well were covered with Turkish toweling one layer thick.

With a fine camel's hair pencil, the upper surface of the abdomen of any ant used for individual experiments was marked with water-color paint. If more than one ant was used simultaneously for such experiments, each was given a distinctive hue. In all experiments with marked ants, any unmarked ant that visited the stage was immediately imprisoned.

The stage used consisted of a piece of white bristol board 15 cm. square; in the edges of two opposite sides perpendicular slits were made 2 cm. from each corner, for the purpose of attaching inclines to the stage. The center of this platform was attached, by means of a pin, to the cork of a bottle about 12 cm. high. Unless otherwise stated, a new stage was used for each series of experiments.

All the inclines were made of the same bristol board as the stage and were about 3 cm. wide and usually 30 cm. long. For special purposes inclines were made by pasting two of these end to end. They were also modified in other ways. When an incline led from a stage downward, it was always attached so as to project 2 cm. above the stage except when a dark chamber was used. When the incline led from the stage upward it was always attached so as to project 2 cm. below the stage. The dark chamber consisted of an inverted pasteboard box 8 x 4 x 1 cm. A flap about one centimeter wide and attached above was cut out of one end, and was pressed inwards to furnish a door through which the ants could enter the dark chamber. In order to observe what was happening on the under side of the stage and incline, a small mirror, inclined at the proper angle, was placed on the island, at one side of the stage.

Unless otherwise stated, preparatory to each series of experiments, the nest with its entrance open was placed on a LUBBOCK island for one or two days in order to familiarize the ants with the island.

Historical Résumé.—Students of ant behavior may be conveniently grouped into four schools: first, those who claim that ants lead a purely reflex life; second, those who hold that ants lead a purely instinctive life; third, those who grant that ants possess a limited amount of intelligence; fourth, those who insist that ants are endowed with anthropomorphic intelligence.

The first school, of which BETHE ('98, '00, '02) is the most noted modern member, claims that these animals are mere machines which respond to certain stimuli, always with the same fixed action or set of actions. Some of these machines are, indeed, quite complex; but so is the linotype. And as the linotype, in mechanical response to a variety of definite stimuli, turns out line after line, no two of which are exactly alike, just so the most complex activities of the invertebrates are but unconscious mechanical responses to diverse stimuli. In other words, the life of these creatures is a life of mechanical responses or tropisms. For them there is no content of consciousness. Heliotropism, galvanotropism, stereotropism, polarized trails, etc., explain all their behavior. They do not learn. All reflexes may not be possible at birth, because the physical mechanism is not yet perfected; but once the mechanism has responded, thereafter under the same conditions, it always responds to the same stimulus in the same way.

The second school, to which I, hesitatingly, assign PIERON ('04, '05), admits that reflex actions, some of which are connate and some of which are deferred, do not fully explain the habits of ants. According to them, the so-called instincts of these creatures are decidedly plastic. They profit by experience; but not by associating present sensations with revived sensations, nor by inference, nor by any of the higher forms of rational thought, but by what MORGAN ('00), THORNDIKE ('98), and others have called the method of trial and error.

The third school, to which belong EMERY, FOREL, LUBBOCK ('81), WASMANN ('98, '00, '02) and others, holds that ants have elementary feelings, ideas, and even what the English have called a simple association of ideas, but that they do not have rational thoughts and emotions.

The fourth school, including L. BÜCHNER ('80), HUBER ('10), MACCOCK, ROMANES ('92) and others, insists that there is difference only in degree between human consciousness and the consciousness of lower animals.

To separate the third from the fourth school is to make a distinction which savors more of convenience than of scientific accuracy; for it is probably true that an idea differs from a product of rational thought, not in kind, but in degree.

Acknowledgments.—The studies on the behavior of ants, of which this contribution is the first fruit, were begun about five

years ago, while I was connected with Clark University of Atlanta, Georgia. They were continued at the University of Chicago during the summer and autumn of 1906 and the winter of 1907. I take this opportunity to express my gratitude to the University of Chicago for the scholarship privileges granted me, without which the publication of this contribution would have been much delayed. I also wish to acknowledge my indebtedness to the members of the Zoölogical and Psychological Departments for their encouragement, and especially to Dr. C. M. CHILD for his sustained interest in my work and for suggestive criticisms, and to Dr. F. R. LILLIE for his assistance in revising the manuscript.

I. EXPERIMENTS ON TROPISMS.

BETHE'S insistence ('98, '02), in spite of the opposition of WASMANN ('98, '99, '01), BUTTEL-REEPEN ('00) and FOREL ('01), that ants are merely reflex machines, led me to plan the series of experiments discussed in this section. The purpose of the experiments was to see what rôle, if any, tropisms play in the homing of ants. These homing activities were selected for study because they could easily be investigated under controlled conditions sufficiently simple to yield reliable results. Only such forms of stimuli were investigated as might possibly influence the normal activities of the ants.

Heliotropism.—"The essential feature of heliotropic reaction" says LOEB ('06, p. 124), "consists in the fact that the light automatically puts the plant or animal (*Eudendrium*, *Spirographis*) into such a position that the axis of symmetry of the body or organ, falls in the direction of the rays of light." Light may play an important rôle in the life of an organism without that creature being heliotropic. "Heliotropism (LOEB '06, p. 135) covers only those cases where the turning to the light is compulsory and irresistible, and is brought about automatically or mechanically by the light itself."

A large number of experiments were made to see what part heliotropism as defined by LOEB plays in the home-going of ants. In each experiment one or more cardboard stages and inclines were used. Illumination was furnished, in some cases by diffuse daylight through a window, and in others by a 16 c. p. incandescent light. For each experiment a new cardboard stage and inclines

were used. Pupæ and ants were placed on the stage and the ants allowed to find their way home.

These experiments fall into the following groups:

1. Those in which the ants in passing home must pass obliquely towards the source of light, then parallel to the rays but away from the source.

2. Those in which the ants must pass obliquely away from the source, then parallel to the rays and towards the source.

3. Those in which the ants must pass obliquely away from the source and then at right angles to the rays.

4. Those in which the ants must pass obliquely towards the source of light and then at right angles to the rays.

5. Those in which the path was practically equally illuminated on all sides.

6. Those in which the ants must pass obliquely towards the source of light, then parallel with the rays and towards the source, then at right angles to the rays, then parallel with the rays and away from the source.

7. Those in which the ants must pass obliquely away from the source, then parallel with the rays and away from the source, then at right angles to the rays, then parallel with the rays and towards the source.

In the sixth and seventh cases two inclines and two stages were used. The stages were connected by an incline and one incline led from stage number two to the ground. The pupæ and ants were placed on stage number one.

All of the above experiments were performed with each of the following species: *Cremastogaster lineolata* Say, *Forelius maccooki* McC., *Lasius niger* L., *Myrmica punctiventris* Rog., *Pheidole* sp.?, *Prenolepis imparis* Say, *Tapinoma sessilis* Say, *Formica pallide-fulva* Latrl., *Formica fusca* var. *subsericea* Say, *Dorymyrmex pyramicus* Rog., *Aphænogaster lamellatus* Mayr, *Monomorium minutum*, Mayr. In most of these cases experiments were performed with several different colonies of the same species.

If ants are heliotropic in the sense of LOEB, they should move from or to the light, in the direction of the rays, until the edge of the stage is reached; then they should pass to the under (shaded) side of the stage, or else remain on its margin until the direction of the rays of light is changed.

But under each of the seven conditions mentioned above, and

with each of the species observed, the neuter (worker) ants when first put on the stage made random movements in every possible direction. After a time in almost every case (over 95 per cent), some one or more ants would find the way from the stage to the nest and back. Such ants then began to convey pupæ to the nest regularly. Gradually they were joined by others. The time required for ants to find the way home varied greatly; not only for different species, and for different colonies of the same species, but for the same colony at different times. That, however, is an irrelevant matter. The essential thing is, not how long did it take them, but which way did they go? In the few exceptional cases mentioned above, after a number of random movements, the ants ceased to search for an outlet and settled down quietly upon the stage. In such cases they usually collected the pupæ in the center of the stage and huddled over them. This getting lost was not confined to any particular species and it was only an occasional thing; no species got lost each time it was used.

It is thought that the above experiments prove conclusively that heliotropism does not influence the home-going of neuter ants. This is in harmony with LOEB's conclusions, for he says ('02, p. 196), "I have never found true heliotropism in the workers."

When winged females were placed on the stage with the pupæ, they would pass sometimes to the under side of the stage, sometimes they would roam about until they found the way home, and in some cases they actually assisted in carrying the pupæ home.

In a very few cases (less than 1 per cent) males placed on the stage with the pupæ flew away; but in almost every case they rushed to the under (shaded) side of the stage. Sometimes these males again returned to the top of the stage; but in no case observed by me, did any of these males reach the nest again until carried there by the workers.

Geotropism.—Any animal moving under the influence of geotropism is automatically forced to orient its body so that its axis of symmetry is at right angles to the horizon; or, if that be impossible, with that axis parallel with the component of gravitation which lies in the plane along which the animal is moving.

In the majority of experiments on heliotropism, the apparatus was so arranged that the ants were forced to go down hill to reach the nest. To determine whether geotropism led them downward, the apparatus was so adjusted that the ants had to go up-hill to reach the nest. The neuter ants readily learned the way home.

Ants that never had been trained to go down-hill to the nest, learned to go up-hill to the nest about as quickly as ants of the same kind had learned to go down-hill. Ants, however, that had previously been trained to go down-hill, often took an unusually long time to learn the way home up-hill. This delay was due to the fact that such ants would over and over again attempt to go home the way they had previously learned. Repeatedly they would partly ascend the incline and then return to its foot and reach down as though seeking something that they could not find. About the same number failed as in the experiments on heliotropism.

To test this point further, two stages were used. Stage number two was four inches higher than stage number one and was connected with it by an incline twelve inches long; an inclined plane twenty inches long connected stage number two with the LUBBOCK island. Thus, in order to get home, the workers, which (with the pupæ) were placed on stage number one, had to pass first up-hill; then across a horizontal plane and then down-hill. It took all of the ants a much longer time to learn this way than the more simple route of the other experiment and the percentage of total failures was almost doubled; but a very large majority (fully 90 per cent) of the ants found the way home. In these experiments I used the same species that were used in the experiments on heliotropism.

These experiments, it seems to me, prove conclusively that geotropism does not guide the worker ants home.

Chemotropism.—The results of numerous investigators demonstrate the presence of well developed olfactory organs in ants. It is also well established that the organ of that sense is the flagellum of the antenna.¹ This possession of well developed olfactory organs makes it possible for ants to be chemotropic. BETHE ('98, '02) has gone so far as to assert emphatically that the home-going of ants is the result of chemotropism. According to him, ants leave behind a polarized odor-trail which mechanically leads them to and from the nest. He thinks that this trail is double, the outgoing ants being guided by one line and the ingoing ants by the other. He also believes that burdened and unburdened ants are affected in different ways by the same trail, burdened ants being

¹ MISS FIELDER ('03) goes further than this. She claims to have proved that the eleventh segment of the antennæ is for detecting the nest aura, the tenth for detecting the colony odor, the ninth for detecting the individual track, the seventh and eighth for detecting the inert young, and the fifth and sixth for detecting the odor of enemies.

driven toward and unburdened ants away from the nest. He further states that burdened ants so scent the trail that ants which come in contact with it can tell whether the ants that passed that way were burdened or unburdened.

WASMANN ('99) raises the following objections to BETHE's polarized odor-track hypothesis: (1) An ant leaving the nest for the first time could not be led home by its own trail. (2) If it did so return the two superimposed trails would so confuse the outgoing ants that they could not find their way. (3) There would be much confusion along the narrow paths of some ants. (4) Many ants in going home do not adhere slavishly to the common path. (He even cites a case of a whole colony moving from one nest to another across an unscented path.) (5) Ants frequently straighten their trails. (6) Unburdened ants find their way home as readily as burdened ants. (7) Ants conveying burdens from the nest pass outward as well as unburdened ants. My observations on ants in the field and in the laboratory support all of the above contentions of WASMANN.

Although WASMANN opposes BETHE's polarized odor-track hypothesis, yet, practically, his view is not very different from that of BETHE. In attempting to explain how ants know which way to go, WASMANN ('01) expresses the belief that their "footprints" have an odor-shape which, combined with the relative intensities of the odor-tracks, enables the ant to tell in which direction the nest lies. On a trail leading from the nest, the nearer the nest the more intense would be the nest-odor of the footprints; on an ingoing trail the reverse would be the case.

Time and again, in the field and in the laboratory, I have noticed ants straighten their trails. This militates against the idea of their home-going being an olfactory tropism, but not against WASMANN's hypothesis nor against the idea that it is a non-tropic reflex caused by odors.

Over a hundred experiments were performed by me to test BETHE's and WASMANN's hypotheses. Although they are unlike, there is a similarity about them which makes it possible to use the same kind of experiments in testing each. The experiments used were of two kinds. In the first, a cardboard stage with one incline leading down to the island was used. On the stage were placed a great many pupæ, larvæ or eggs and several worker ants. After the ants had conveyed all of the pupæ, larvæ or eggs into the nest,

both ants and pupæ, larvæ or eggs were replaced on the stage. After this had been repeated several times, so as to make sure that the ants were thoroughly acquainted with the trail, the incline was reversed, so as to place the original nest-end at the stage, and the stage-end near the nest. Although this was tried several dozen times, and with all the species used in the experiments on heliotropism, the ants continued as though nothing had happened. At first I was inclined to think that these experiments disprove BETHE's contention, but a little reflection showed that they do not; for, if there is a double polarized trail one path of which leads the ants to the nest and the other from it, reversing the incline would still leave a double polarized trail of the same functional type.

This failure to reach a solution led to a different type of experiment. As in the first series, a cardboard stage from which an incline led down to the island was used. A great many pupæ, larvæ or eggs, and workers were placed on this stage. After these burdens had all been carried to the nest, they, with several workers, were replaced on the stage. In a shorter time than before the pupæ were all carried by the workers down the incline to the nest. This was repeated until I thought the ants were thoroughly acquainted with the stage and incline; then a second incline was so placed as to lead from the opposite side of the stage to the LUBBOCK island. If, after the lapse of a few minutes, no worker descended this second incline, I concluded that the ants were thoroughly acquainted with the path down the first incline to the nest. If they proved to be acquainted with the path, I then placed the first incline, which had become scented by the passing to and fro of the ants, where the unscented one had been and placed the unscented incline in the place formerly occupied by the scented one. Thus there was an unscented path in the place of the old trail and the old scented path was in a new position. Now if ants are guided home solely by the sense of smell, then one of two things should happen: they should spend approximately as much time learning the way down the new incline as they did learning the way down the former; or else, in their random movements, they should happen upon the scented incline and go down it. In reality they did neither of these things. They almost immediately went down the unscented incline which occupied the former position of the scented incline. About a hundred experiments of this sort were

performed with *Myrmica punctiventris* Rog., *Pheidole* sp.?, *Prenolepis imparis* Say, *Tapinoma sessilis* Say and *Formica fusca* var. *subsericea* Say. In each case the result was practically the same as stated above. In many cases, on first reaching the unscented incline there would be a momentary hesitation as though they had met an unfamiliar stimulus; but there was no prolonged disturbance. In addition to these experiments with ants acting in concert, similar experiments were tried with marked individuals of *Myrmica punctiventris* Rog., and *Formica fusca* var. *subsericea* Say. The results were the same.

A slight variation of the above experiment was tried with the same species of ants. Instead of substituting a new incline for the old, the stage was revolved through an angle of 180 degrees and the same incline retained in its original position. This gave an unscented path from the pupæ to the incline. With no, or, in some cases, little hesitation the ants found the way to the incline. Rarely would an ant go along the scented path instead of the unscented one that led to the incline. In these experiments where ants worked in concert, two or three large spatulas of ants were placed on the stage. Thus, where the colony was large, it was highly improbable that all the ants would be conveying pupæ at the same time. Even after the experiment had been repeated several times, the chances are that there would still be some ants that had never made the trip. The ants that went along the path that led away from the incline may have been ants that had not yet learned the way. I also tried substituting a new stage for the old. The results were the same as above.

Now both BETHE's and WASMANN's hypotheses demand a scented path over which ants must pass. The unscented path down which these ants passed was twelve inches long. These experiments do not prove that ants are unaffected by odors, nor do they indicate that odors are not utilized by ants in finding their way home; but they do demonstrate that the home-going of ants is not controlled solely by the olfactory sense. They militate against both BETHE's double polarized trail hypothesis and WASMANN's assumption that the footprints have an odor-shape which guides the ants home. The results of these carefully planned experiments harmonize with observations made by myself and others in the laboratory and field.

MISS FIELDE ('03) watched some specimens of *Stenamma* ful-

vum pass back and forth across a trench of water in order to convey their pupæ into their nest. They traveled back and forth across the water for thirty hours until all of the pupæ had been removed. She performed two such experiments with the same colony. To see if the ants left a scented trail on the water, she experimented as follows: (1) She removed a few drops of water from in front of an ant which was returning to the island. Out of thirty-one ants thus treated, twenty-one continued across and ten turned back. (2) She passed a knife-blade through the water and around an ant returning to the island. Out of ten ants experimented on none turned back. (3) She covered the surface of the water with dust, and after the ants had been passing for some time, removed the dust. The ants were not in the least affected. These results led her to conclude that in crossing the water the ants were depending upon something more than mere footprints.

Frequently I have noticed individual ants of most of our common species cross the water ditch that surrounds the LUBBOCK island. Occasionally I have had whole colonies escape in that way, but it has always happened when I was absent. On one occasion I had a colony of *Forelius maccooki* MacCook escape in that way. In this colony there were at least twice as many eggs, larvæ and pupæ as workers and winged females. Since no pupæ, larvæ or eggs were left behind, and since all of the workers do not usually take part in carrying pupæ, some of these ants must have crossed the water several times.

WASMANN ('01) states that if the surface-sand be removed from the vicinity of the nest of busy *Formica sanguineas*, the ants continue to pass back and forth without noticing the change. In the same paper WASMANN relates that he noticed another set of ants, laden with cocoons, travel eighteen meters from one nest to a former nest. On this occasion the ants neither used their antennæ to smell the way nor followed in each other's tracks. Each ant marched along independently as though it knew the way.

These observations of FIELDE and WASMANN serve to emphasize the statement made above, that the home-going of ants is not controlled solely by the olfactory sense.

PIERON ('04) from experiments² of a different kind came to the

² PIERON's experiments bearing on this point may be epitomized as follows: (1) He passed his finger across the path. The ants on each side halted and usually spread out along the line of disturbance,

conclusion that odors play a part in the life of ants, but that it is not by them that ants are guided on their journeys.³ This is a much broader statement than that made above; indeed, it seems much broader than either his or my experiments warrant. Even though ants, favored by the muscular and tactile impressions furnished by the mandibles and feet, can still move with much precision when deprived of the use of eyes and antennæ, yet we have no more right to say that light and odors play no part in the home-going of normal ants than we have to say that, because blind men can move with much precision to and from home, vision plays no part in the home-journey of the normal man. What his and my experiments demonstrate is that odors do not play the sole rôle in the home-going of ants.

II. EXPERIMENTS ON THE HOMING INSTINCT.

Most educated people once believed and many untrained people still think that there is a mysterious power, the homing instinct, which unerringly guides certain animals on their journeys. This "power" differs from a tropism in being guided by an inner rather than an outer stimulus. It was my purpose in the experiments of this chapter to discover whether ants possess a homing instinct.

The fact that ants lose their way militates against the idea that they have a homing instinct. Many a time after a rain, I have caused ants to lose their way by placing them and their pupæ on a stone situated within a few feet of their nest. At times the whole lot would roam aimlessly about; more often a portion would roam at random while the rest would busy themselves placing the pupæ under the stone on which I had placed them, or else under any other cover that they happened across; at yet other times a portion would finally reach the nest, while the rest would wander off.

finally some would strike the trail and the line of march would be renewed. (2) He moistened the path with a decoction of ants from an alien colony. The ants retreated precipitately. (3) He moistened the path with pure water. It had no effect on the ants. (4) He brushed odoriferous herbs across the path. The ants hesitated a moment then passed on. (5) He displaced the dust of their path with a twig. They were not disturbed. (6) He placed a piece of paper across the path of home-going ants. On this paper he scattered bits of turf and other detritus. When an ant had mounted this trap, PIERON gently transported the whole to a new situation in a place similar to the path along which the ants had been moving. In each case the ant continued in the direction it was going for a distance about equal to that between the trap in its original position and the nest opening.

³ According to my understanding, PIERON's conclusion is so out of harmony with what his experiments warrant, that I have thought it wise to give, in this footnote, his exact words: "On en peut conclure que l'odorat doit jouer un rôle dans la vie de ses fourmis, mais ce n'est pas sur lui qu'elles se guidant dans leur passage." *Loc. cit.*, p. 176.

Not only have I caused ants to lose their way in the woods, but I have seen them lose their way on my LUBBOCK islands, which lack two inches each way of being two feet wide by two and a half feet long. Often, when I had disturbed a nest to remove the pupæ, the ants would rush out upon the island in all directions. After the excitement was over, many, sometimes all, of these ants would find their way back to the nest. In a large number of cases, however, instead of going home, a large number would congregate in groups on different parts of the island. These groups would usually be located on the peripheral ditch. There the ants would remain huddled together until discovered by ants that had spontaneously left the nest to seek what was to be found. Then they would be carried back to the nest.⁴

In my numerous experiments with individual, marked ants, I have incidentally obtained abundant evidence of the ease with which ants can be caused to lose their way. It was not an uncommon thing for an individual to fail completely to find its way home from one of my stages on the LUBBOCK island. After numerous random movements such an ant would usually settle down on some part of the stage or else busy itself rearranging the pupæ in the center of the stage. In almost all such cases, individuals from the same colony would learn the way to the nest and pass and re-pass the lost one, which seemed to have given up all attempts to reach the nest. In many cases the lost ant was finally carried to the nest by some other ant. This has happened in almost all the species examined; but it happened more frequently with *Myrmica punctiventris* Rog. than with any other. I have seen individuals lost within a foot of the nest on a piece of cardboard only six inches by six inches, and connected with the LUBBOCK island by an incline only twelve inches long!

To test this matter further the following experiment was devised. *Myrmica punctiventris* Rog. was selected, partly because of the slowness of its movements and partly because experience had taught me that individuals of that species were easily lost. The

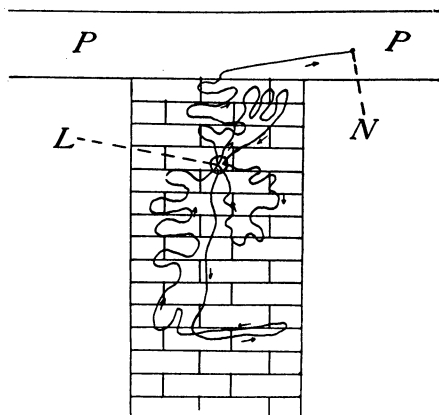
⁴ If, as many claim, ants can communicate by means of their antennæ and say at least "Follow me," it might be asked parenthetically why did not these ants use their antennæ and tell those lost ants to follow them, instead of laboriously carrying them home one by one? For over two years I have had colonies of many of our common ants in the laboratory, and so far as my observation goes, whenever an ant wants another ant to go to a particular place, it picks it up and carries it there. Not only have I seen them thus carry workers, males, and even young females into the nest, but I have seen them thus carry workers and lay them down on a pile of pupæ. In no case have I seen any certain evidence of an antennal language. However, this is a problem that I intend to investigate more carefully in the near future.

nest containing the colony was placed on a new island. At the end opposite to that near which the nest was located was placed a new stage from which a new incline led to the island. On this stage I placed a large number of pupæ and workers. At once the workers began to move about the stage with pupæ in their mouths. Many fell off the stage. Many of these gathered in groups near the ditch; a few went to the nest. This experiment was begun at a quarter past nine in the morning. Occasionally a worker would partly descend the stage and then reascend. Up to ten o'clock, when I was called away, no worker had passed from the stage, down the incline to the nest. When I returned at half past two o'clock, the pupæ had been gathered into the center of the stage and the ants were resting on them. From this time until 4:40 o'clock the stage was watched continuously but no change occurred. When I returned at a few minutes before eight in the evening, everything was as I had left it at twenty minutes to five. I kept watch over these ants until ten minutes of ten without noticing any change excepting an occasional movement by one of them. Thus these ants were lost and remained so for at least thirteen hours, although their home was less than two feet away. When I returned next morning both ants and pupæ were in the nest, but how they got there I do not know. This result cannot be attributed to timidity or fright, for previously the same colony had been successfully used in seven experiments and each time the pupæ were taken home; but in each of those cases the ants had been given an opportunity to become familiar with the island.

But the facility with which ants lose themselves is not the only thing that fails to harmonize with the idea of a homing instinct; for the windings and twistings of the paths of many ants militate against that idea. Two summers ago, while in Elberton, Georgia, I noticed a sinuous line of ants leading from a nest of *Forelius mac-cooki* MacC. to a piece of honey-soaked paper and back. The paper was only three feet from the nest and situated in a level yard which was free from grass and weeds. The tortuous path the ants were following was at least fifteen feet long; it went all the way around the steps of the schoolhouse, although there were no topographical reasons why it should not have passed under the steps direct to the nest. At that place the steps were high enough for a boy to pass beneath them. Now had those ants possessed a

homing instinct, they would have gone in a practically straight line from the paper to the nest and back again.

To test this matter further many experiments similar to the following one were tried in the field. I am uncertain of the species of the ant used in this experiment, but it was one of the small southern camponotids. The ant had its home in the baseboard of our front porch. At the time this experiment was begun, many of them were busy moving to and from some aphids that were feeding on the leaves of a vine that shaded the portico. By searching, I soon found a leaf upon which there was only one ant. This leaf was removed and inserted, by the petiole, in a notch in one of the brick supports of the veranda. The hole in which I had



TEXT-FIG. 1. Path of ant in finding its way home; see text. *L*, leaf; *N*, entrance to nest; *P P*, porch. The arrows indicate the direction in which the ant moved.

placed the leaf was only two feet from the nest opening. The ant acted as though dead for a while and then it thoroughly explored the leaf. From the leaf it mounted the pillar and went downwards (away from the nest) almost to the ground. It then went first to the right and then to the left and then zigzagged upwards again to the leaf. After again exploring the leaf it returned to the pillar and, after passing up and down several times, returned to the leaf. After another exploration of the leaf it returned to the wall and after a little meandering returned to the leaf. After another exploration it returned and zigzagged slowly upwards until it reached the baseboard. Then it at once increased its speed and hastened to the nest (Text Fig. 1). The leaf was placed

in the hole at half past two o'clock. When the ant entered the nest the clock struck three. A half hour to find a nest that was only two feet away!

It is believed that these experiments show conclusively that ants do not possess a homing instinct.

III. EXPERIMENTS ON THE POWER OF ANTS TO PROFIT BY EXPERIENCE.

If ants are guided in their home-goings neither by tropisms nor other forms of reflexes nor by a homing instinct, the probability is that they learn the way home. To test this two classes of experiments were performed. In the first class ants were allowed to work in concert (which is the normal way); in the other class, marked individual ants were induced to work alone or else in company with only one or two marked fellows. The cases where the ants worked in concert will be discussed first.

On the LUBBOCK island, which contained the nest of the colony to be tested, was placed a new cardboard stage from which a new cardboard incline led to the island. Ants and pupæ were placed on top of the stage. As a rule, the workers immediately began to move about at random. Some species moved slowly others more rapidly, and yet others so impetuously that many would fall off the stage. Some carried pupæ and others did not.

After a lapse of time varying with the species examined (for there is a marked contrast in the time it takes different species to solve the problem) usually at least one of the ants would find the way to the nest and back to the stage. As a rule it would carry a pupa the first trip, but sometimes it would go to the nest unburdened. The initial trip having been made, this ant would busy itself conveying pupæ to the nest; in this task it would soon be joined by several or many workers. These recruits were made partly from the ants on the stage and partly from ants roaming from the nest. During the first few trips most species moved slowly and cautiously as though they were feeling every step of the way. Later, they moved much more rapidly. Sooner or later (according to the activity of the species and the number of ants at work) all of the pupæ would be removed. In over a hundred experiments no live pupæ were left on the stage, excepting in cases where the ants failed to find the way home (which happened occasionally),

or where I had added to their pupæ the pupæ of some other colony or species. In the latter case the alien pupæ were sometimes carried in and sometimes not. After the pupæ had all been removed, the ants would explore thoroughly both the stage and the incline. In some of these cases, after they had learned the way down one incline, I would add to the stage two or more inclines. In this case, when the pupæ had been removed, although no pupæ had been carried down these additional inclines, yet they would usually be thoroughly explored by the ants. After the exploration had been completed the ants gradually withdrew from the stage. It may not be out of place to state that if any of the ants originally placed on the stage failed to find their way home, they were carried there by the others.

After the workers had quieted down in the nest, the experiment was repeated; it was repeated not only once but over and over again, the series of experiments on the same colony often extending through several days. In the second experiment, in each of the several dozen series tried, the first ant usually reached the nest with a pupa in a much shorter time than did the first ant in the initial experiment of the series (Figs. 1, 3, 6).

In some experiments there was not much difference in the time of the two cases (Fig. 2) and in a few rare cases the time in the second case was even greater than at first (Fig. 4).

Frequently, in the midst of a series, the ants would act as though they had forgotten the way and had to relearn it (Fig. 5). This usually required much less time than at first. If any complications were introduced in the midst of a series the ants were sure to be delayed until they had mastered the situation (Figs. 3, 6). Sometimes they would fail. All of these points are brought out in Figs. 1 to 6, where the abscissas represent the number of each experiment in the series, and the ordinates the time in minutes that elapsed from the beginning of the series until the first pupa was carried into the nest. No one could watch the random movements made by the ants when first placed on the stage without being convinced that the finding of the nest the first time was merely a matter of chance; indeed, they sometimes failed completely to find it. The slow and exploring gait with which most species make the first few trips of the initial experiment of any series, when contrasted with the rapidity of the later movements, indicates that the ants learn the way home. The short period of time usually required

for the first pupæ to reach the nest in the second or third and most of the subsequent experiments of a series, as contrasted with the long time required in the opening experiment of that series, suggests that the ants retain, for a while at least, what they have acquired. Indeed, there is hardly an experiment recorded in this paper, which does not indicate that ants profit by experience.

That ants can be trained is further evidence that they retain for a time what they acquire by experience. ERNST ('05) succeeded in training a *Formica fusca* to feed from his moving finger. He took a member of a colony of this species which had become somewhat familiar with man and confined it in a test-tube. In three hours after being confined to the tube it would feel with its antennæ the finger of the operator when presented to the open end of the test-tube. In order to tame it, food (honey, sugar) was offered it on the tip of the operator's finger, and in no other way. At the close of a month the test-tube was left open. With keen attention and with that tense attitude which would permit of immediate flight, the ant approached the opening and felt exploringly with its antennæ. On the second day its conduct was similar; but on the third day the ant wandered out for a distance of two centimeters. At the close of the second month the ant would feed from ERNST's finger, even when it was moving and the ant had to stretch half-way out of the tube in order to do so.

I have been able to train several ants to get to and from the stage used in my experiments in extraordinary ways. Two of these were trained to drop down; it might be nearer the truth to say that they trained themselves to jump down. One of these ants was a *Myrmica punctiventris* Rog. and the other was a *Formica fusca* var. *subsericea* Say. In each case the trick was learned in about the same way. A marked ant had been placed on the stage with the pupæ. Picking up a pupa it moved about at random and accidentally fell off the stage. Its impetuous dash was what carried *Formica* overboard; it is not possible to say what caused the fall of the more slowly moving *Myrmica*. Although the vertical distance from the stage to the island was four inches, the ant neither dropped the pupa nor seemed the least disturbed by the jar. It went at once to the nest, deposited the pupa and returned to the island, where it meandered from place to place, evidently not knowing how to return to the stage. With a pair of small forceps I picked it up gently and replaced it on the stage. It picked

up a pupa, moved about the stage for a few moments, then dropped to the island and hastened to the nest with the pupa. Once more the ant was replaced on the stage, once more it picked up a pupa and dropped to the island. This was repeated over and over again.

In the case of *Myrmica*, I was careful always to pick it up at about the same place on the island. After I had picked it up about a dozen times, it would go from the nest direct to that place and wander about in a curve of short radii. When the forceps were presented the ant would mount them of its own accord and rest quietly thereon until transferred to the stage. Then it would pick up a pupa, drop off the stage and hasten to the nest. The ant always dropped off from the same side of the stage; but not from the same spot. Whenever it dropped, it was amusing to note the reflex tendency of its legs to cling to the support. Each time *Formica* would make several false starts before the successful drop was made. It would make a dash and perhaps the front part of the body would clear the edge, but the two hinder pairs of legs would hold fast to the stage. Recovering, it would make another start, and this time in all probability one or both hinder pairs of legs would retain the ant on the stage. But persisting in its efforts, it would finally make the drop through ten centimeters of vertical space—an enormous drop for a creature so small. Towards the latter part of the experiment the ant took much less time to overcome the reflex tendency of its legs to cling to the support. *Formica* continued this dropping until, by accident, I pinched its body with the forceps, and after that, not only would it not mount the forceps; but, when they were brought near, it would dash about in such a lively manner that it was impossible to capture it without injuring it.

Myrmica never dropped off in this headlong manner; on the contrary it usually dropped off sidewise, but like *Formica* it had much trouble in overcoming the reflex tendency of its legs to cling to the support.

In addition to proving that ants retain what they learn, this experiment lends credence to those anecdotes in which ants are reported to have voluntarily dropped from ceiling to table and from leaves to the ground (ROMANES '92, pp. 134, 135).

On another occasion I trained an ant to use a section-lifter as an elevator on which to pass to and from the stage. This time it was

a specimen of *Formica fusca* var. *subsericea* Say. On this occasion two marked workers, A and B, were being experimented upon at the same time. The one I have called A readily learned the way down and up the incline; but to B this was an insoluble problem. It continued for a long time to move at random over the stage, reaching down over first one edge and then over another, as though it were reaching for a support that was not to be found; but nothing prompted it to pass down the incline. In experiments where the time required to learn the trick was not the point to be investigated, I had sometimes helped ants to learn the way by forcing them with forceps or spatula, to move in the right direction. I thought I would thus help B to learn. So with my forceps I pushed it along. Several times I succeeded in getting it to the incline, but nothing that I did would induce it to go down. I had failed, but this was not the first time that I had failed in similar attempts with other ants.

Prompted by another thought, I shoved the section-lifter under the ant and transferred it to the island. The ant then stepped off and carried the pupa into the nest. As soon as B returned to the island, I shoved the section-lifter under it and transferred it to the stage. B stepped off and picked up another pupa. With the section-lifter I again transferred it to the island. After this had been repeated several times, the moment I presented the section-lifter, whether on the island or on the stage, the ant immediately mounted it and rested quietly thereon until it had been removed to the stage or to the island; then it stepped off and picked up a pupa or else went into the nest. I usually held the section-lifter from two to four millimeters above the surface of the island or stage. In this manner the industrious creature passed to and from the stage about fifty times in something less than two hours.

Whenever I presented the section-lifter to other ants of the same colony, they would attack it, or avoid it, or else mount it and roam over blade and handle and sometimes even my hand. When the same section-lifter was presented to A (the one that all this time had been conveying pupæ down the incline) it would avoid it and pass on.

Thus I had two individuals of the same colony, at the same time and under identical external conditions, responding to the same stimulus in quite different ways. To the one the incline had no psychic value, to the other it was a stimulus to pass to and from

the stage. To one the section-lifter was a repellent stimulus, to the other an attractive stimulus. Each had acquired a different way of accomplishing the same purpose and each had retained and utilized what it had gained by experience.

Not only do ants retain, for at least a few hours, what they have learned; but a habit once formed is hard to break. From time to time I have performed experiments for the purpose of breaking up habits. Often I have failed, my patience not being a match for the persistence of the ant; in other cases, by patient persistence, I have succeeded. I desire to relate one such case.

A minute before ten on the morning of September 23, I placed a *Formica fusca* var. *subsericea* Say, together with some pupæ, on a new cardboard stage, from which an incline led to the island. For my purpose, it was necessary for the ant to learn the way down and up the incline, but down the incline it would not go. After passing by the incline several times, the ant passed underneath the stage and down the bottle, which formed the central support of the stage, to the island and thence to the nest. Hoping that it would even now learn the way down the incline, I replaced the ant on the stage. Six times it was replaced on the stage, six times it went down the bottle. To those who believe that the movements of ants are tropic responses to odors, it may be of interest to state that each time the ant went down the bottle by a different path, usually more or less spiral. Now the experiment contemplated demanded that that ant learn the way either down or up the incline. Knowing by experience that ants sometimes go out by one path and return by another, I thought that possibly this ant might learn the way up the incline. So when the ant came out this time I let it alone. It made no attempt to ascend the incline, but after a little meandering, it ascended the bottle to the stage and descended the same way, with a pupa, to the island.

In order to prevent further use of this path, I painted the neck of the bottle with cedar oil and then replaced the ant on the stage.

This was at half past ten in the morning. In a very short time it learned to carry the pupæ down the incline, but at first the ant always went first to the bottle and then to the incline. It was not until two o'clock in the afternoon that it learned to go down the incline without first going to the bottle. And even after that it would occasionally go to the bottle. To learn the way up was even more difficult. Whenever the ant returned from the island

to the nest, it would go almost everywhere except to the foot of the incline and roam about until replaced on the stage or incline. If placed on the incline at its foot, it would ascend; but it was not until six minutes to three that the ant, of its own accord, went to the incline and ascended it to the top. Then it returned to the island and meandered. At three o'clock it ascended the incline to the stage. Thus it took it several hours to unlearn the old way and learn the new.

Although the new adjustment was slowly formed, once formed, it persisted. At a quarter past three the ant was imprisoned. At one minute to seven, when the experiment was resumed, it still retained the new adjustment. At eight o'clock it was imprisoned for the night. At twenty minutes to nine the next morning the experiment was resumed. The ant still retained the new adjustment, for in seven minutes it was busy carrying pupæ up and down the incline. And all of this seven minutes was not consumed in searching for the nest, for fully half of it was spent by the ant in stretching itself and cleaning its antennæ. Contrasting this three minutes with the several hours it took to learn the trick furnishes convincing evidence that ants retain what they acquire. It is unnecessary to describe any more special experiments along this line, for almost every experiment recorded in this paper proves that ants profit by experience.

In profiting by experience and retaining for a time what it has thus acquired, the ant resembles the fish (SANFORD '03), the frog (YERKES '03), the sparrow (PORTER '04), the chick (THORNDIKE '98, MORGAN '00), the rat (WATSON '03), the otter (HOBHOUSE '01, p. 155-184), the elephant (HOBHOUSE '01 pp. 164, 165, 169, etc.), and the monkey (THORNDIKE '98, HOBHOUSE, '01, pp. 167, 182, etc.). It thus appears that the ant is no more guided in its journeys by tropisms, other reflexes, or a homing instinct, than are vertebrates.

TABULATED EXPERIMENTAL EVIDENCE.

To give detailed reports of each of the several hundred experiments upon which the above statements are based would require quite a volume. For the benefit of those who desire a more detailed statement than is given above, I close this section with the tabulated results of four series of experiments conducted with *Prenolepis imparis* Say, two with *Formica fusca* var. *subsericea* Say, and one with *Myrmica punctiventris* Rog. *Prenolepis* and *Formica* are fair representatives of the Camponotidæ, while *Myrmica* is a good representative of the Myrmicidæ. The shortest of these series extended over a little more than two days, the longest over a little less than nine days. Some of the series used extended over several times the longest time recorded here; but these serve as typical series. All of the experiments in each series were conducted upon the same colony; but each series represents a different colony.

EXPLANATION OF ABBREVIATIONS IN TABLES I TO VII.

- Column A. The number of the experiment in the series.
 Column B. Minutes that have elapsed since the close of the last experiment.
 Column C. Minutes that have elapsed from the beginning of the experiment up to the time the first ant reaches the nest (either burdened or unburdened).
 Column D. Ditto. Second ant.
 Column E. Ditto. Third ant.
 Column F. Ditto. Until a line of ants is moving to and from the nest.
 Column G. Ditto. Until all of the pupæ have been carried to the nest.

TABLE I.

Prenolepis imparis Say. Series 1.

A Exp. no.	B Time since last exp.	C Time of 1st ant	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		12			22	202	Stage with one incline.
2	226	9	9.5	9.5	13	14	Do.
3	10	0			1	6	Do.
4	4	0			0	9	Do.
5	11	1			1		Do.
6	17	0			0	11	Do.
7	0	1	2		3	9	New incline substituted for old.
8	0	0			0	10	Same apparatus as above.
9	26	0			0	17	Do.
10	2269	0			0	18	Do.
11	2	1	2		3	27	Used new stage but old incline.
12	2	10*			34	54	Removed old incline and put new incline in new place.
13	37	0*			8	25	Same apparatus as used in 12.
14	2	1			1	21	Do.
15	0	0			0	28	Do.
16	4	0			8	31†	Besides the old incline a second is put on opposite side of stage.
17	9	0			0	11‡	Same conditions as above.
18	443	0			0	21	Do.
19	3	1	6	6	8	28°	Substitute a new incline for the one down which they had been going; left other incline on opposite side of stage.

Any time less than one-fourth minute is called 0.

* Many of the workers passed at once to where the incline had formerly been attached, and up to the end of the experiment some would always go to that place first and then from there to the new incline.

† Two pupæ were carried down the new incline, the rest down the old.

‡ Three pupæ were carried down the new incline, the rest down the old.

° Three pupæ were carried down the old incline, the remainder down the new incline which occupied the position of the incline down which they had learned to convey pupæ to the nest.

TABLE II.
Prenolepis imparis Say. Series 2.

A Exp. no.	B Time since last exp.	C Time of 1st ant	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		34	36	69	93	194*	Stage with incline <i>A</i> on left. Daylight.
2	I	0			0		Do. Daylight.
3	540	15†			60		Do. Night.
4	590	0			0	15	Do. Daylight.
5	1440	0			0	40‡	Do. Daylight.
6	0	2	9	10	12	47°	Same stage, incline <i>A</i> on right, new incline <i>B</i> placed on left.

* This experiment furnishes a good example of the impossibility of predicting what an ant will do when presented with a new problem. A worker spent several minutes wedging a pupa into the space between the underside of the stage and the incline. Having succeeded it moved off; but in a few moments returned, pulled out the pupa and carried it back to the stage. In less than two minutes it returned and replaced the pupa in the crevice between the incline and stage.

While this was going on, worker number two carried a pupa and laid it on the incline near the bottom. One hundred and fifty mm. higher up the incline it placed another pupa. Then, after carrying pupa number two up and down the incline twice, it laid it on the incline thirty mm. higher than the first. Likewise it placed a fourth pupa twenty mm. below the second. While doing so, it accidentally knocked pupa number three off of the incline. It carried the fifth pupa down the stage to the nest, but in doing so knocked another pupa off of the incline. This was the second pupa carried to the nest from the stage. The pupæ that fell to the island were carried to the nest by stragglers from the nest.

† These were working by incandescent light and at night; the two previous experiments had been performed during the daytime.

‡ While the ants were passing to and fro, the incline was so adjusted as to form a vertical gap about five mm. high between the base of the incline and the LUBBOCK island. This did not disturb the ants in the least.

° One worker carried a pupa down incline *A* to the nest, all of the other pupæ were carried down the new incline *B*, which occupied the same position that incline *A* occupied at the time the ants learned the way down it. One worker ascended incline *A* from the island and descended incline *B* with a pupa which it carried to the nest.

TABLE III.
Prenolepis imparis Say. Series 3.

A Exp. no.	B Time since last exp.	C Time of 1st ant.	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		12			21	71*	Stage with incline <i>A</i> on the left.
2	73	0			10	14	Do.
3	1	0			0		Do.
4	35	0			0	11†	Same stage, incline <i>A</i> on right, new incline <i>B</i> on left.
5	4	0			0	35‡	Same as above only incline <i>B</i> has vertical gap, 1 mm., between it and island.
6	40	0			0	42	Do, but with vertical gap 4 mm.
7	47	0			0	30	Do.
8	1490	2°			3		Do.
9	17598	10§			12	28**	Nest higher than stage; incline <i>A</i> on left of stage.
10	1	0			0	39	Do. except that stage was re- volved 180°, inc. <i>A</i> on the left.
11	5	1	2	3	16††		Do. but incline <i>A</i> on the right 'and incline <i>B</i> on the left.
12	21465	4	5	6	54‡‡		Nest lower than stage; incline <i>A</i> on left; 16 c. p. lamp near <i>A</i> .
13	0	3	5	6	∞	135	Do. but the light was placed near incline <i>B</i> .

* In four minutes a worker had passed down the incline and laid a pupa upon the top of the nest. For some time it continued to store pupæ in that place and was soon joined in the occupation by a few other workers. Later stragglers from the nest carried these pupæ into the nest.

† All of the pupæ were carried down incline *B*. A worker ascended incline *A* to the stage and carried a pupa down incline *B* to the nest.

‡ Two of the pupæ were conveyed down incline *A* to the nest, the remainder were carried down incline *B*.

° Immediately several workers picked up pupæ and started down incline *B*, but when they reached the gap, they turned around and returned to the stage.

§ While some were seeking a way home, others were storing pupæ under the foot of the incline plane. These pupæ were finally taken to the nest.

** The ants went practically direct from the pile of pupæ to the incline. No pupæ were stored under the incline.

†† The workers, one by one, passed unburdened to the nest and left the pupæ alone on the stage. Fully eleven minutes elapsed before they returned to the stage and began to carry the pupæ home. One worker passed down incline *A* to the stage and then carried a pupa up incline *B* to the nest. All of the pupæ were carried up incline *B*, which occupied the same position that had been occupied by the incline along which they had learned the way to the nest.

‡‡ All of the workers passed, unburdened, to the nest and over thirty minutes elapsed before any worker returned to the stage for pupæ. All the pupæ were carried down incline *A*.

∞ The pupæ were carried down incline *A*. All of the work seems to have been done by one worker; the others, after once reaching the nest, remained therein.

TABLE IV.
Prenolepis imparis Say. Series 4.

A Exp. no.	B Time since last exp.	C Time of 1st ant.	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		8	10	12	16	69	Stage with incline <i>A</i> on left side.
2	1	2	4	6		100	Do.
3	1	0			0	60*	Incline <i>A</i> on right, inc. <i>B</i> on left.
4	6	0			0	†	Do. revolved the stage through an angle of 180°.
5	1085	0			0	150†	Do.
6	8	0	4	13	20		Do.
7	1260	0			0		Do.
8	51	1	2	4			A vertical gap of 3 mm. between base of incline <i>B</i> and island.
9	2880	4			9	‡	Do. but 16 c.p. lamp near incline <i>A</i> , incline <i>B</i> on opposite side.
10	0	2	8	8	8	40°	Do. but 16 c.p. light placed near incline <i>B</i> .
11	3	0			0	60	Incline <i>B</i> removed, light placed where incline <i>B</i> had been.
12	1271	0			0	§	Incline <i>A</i> on right, incline <i>B</i> on left, 16 c.p. light near <i>B</i> .
13	0	4			4	26¶	Do. but 16 c.p. light is placed near <i>A</i> .
14	4260	12	14	16	91	155**	Do. but placed dark chamber on stage.

* Over 100 pupæ were used. Eight were carried down incline *A*, probably all by the same worker. The remainder were carried down incline *B*.

† All were carried down incline *B*.

‡ The pupæ were all carried down incline *A*.

° The workers were, at the beginning, much disturbed. The first three pupæ were carried down incline *B*. By that time a line of workers had begun to pass down incline *A*. After that occasionally a pupa was carried down incline *B*.

§ All of the pupæ were carried down incline *B*.

¶ At first an occasional worker went down incline *A*, while a line of workers was passing down incline *B*. Gradually the number going down incline *A* increased until there were lines of workers moving down both inclines.

** The majority of the workers began almost at once to store pupæ in the dark chamber. One worker soon found the way to the nest with a pupa, and after that made regular trips. It was not until all of the pupæ had been removed from the open and placed in the dark room that a line of workers began to convey pupæ to the nest.

TABLE V.
Formica fusca var. *subsericea* Say. Series I.

A Exp. no.	B Time since last exp.	C Time of 1st ant.	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		1	2	2	3	23	Incline <i>A</i> on left side.
2	5	5			5	10	Do.
3	0	3			4		Do.
4	0	0			0	13	Do.
5	3	0			0	27	Do.
6	0	0			0	30	Do.
7	240	1			1	17*	Incline <i>A</i> on the right, incline <i>B</i> on the left.
8	53	5			10	33	Do. but both stage and incline new.
9	6661	11	13	15	18	65	Incline <i>A</i> on the right, no other incline used.
10	1	6					Do.
11	5	2					Do.
12	33	5				30†	Incline <i>A</i> on the left, incline <i>B</i> on the right.
13	2400	14				54	Incline <i>A</i> on the right, incline <i>B</i> not used.
14	4	16					Do.

* Three pupæ were carried down incline *A*, the rest down incline *B*. The workers moving down incline *B* rushed along, the ones that went down incline *A* moved very slowly.

† The pupæ were all carried down incline *B*.

TABLE VI.

Formica fusca var. *subsericea* Say. Series 2.

A Exp. no.	B Time since last exp.	C Time of 1st ant.	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		4	5	7	17	43	Incline <i>A</i> on the left.
2	4	1	2	2	2	28	Do.
3	1	0			0		Do.
4	3444	1			10	28	Do.
6	5760	17	42	43	67		2 stages, one higher than other; incline <i>A</i> leads from 1 to 2, incline <i>B</i> from 2 to the island.
7	427	1	4	35			Do.
8	620	21*	29	31	50	95	Do.
9	145	1	3	4	5	69	Do.
10	59	1	2	2	4		Do.
11	194	18†	24	26			Do.
12	720	1	2	4			Do.
13	120	1	3	4			Do.
14	244	2			3	‡	Do. but incline <i>C</i> substituted for <i>A</i> and incline <i>A</i> placed to lead from stage 1 to island.

* At first the ants stored all of the pupæ in the crevice between incline *A* and stage number one. After that had been accomplished, they began carrying them to the nest.

† This was conducted at night, by incandescent electric light; all of the other experiments of the series were conducted by daylight.

‡ The pupæ were carried up incline *C* to stage number two, across stage number two to incline *B*, down incline *B* to the nest. No pupæ were carried down incline *A*.

TABLE VII.

Myrmica punctiventris Rog. Series I.

A Exp. no.	B Time since last exp.	C Time of 1st ant.	D Time of 2d ant.	E Time of 3d ant.	F Time of ant col.	G Total time of exp.	Remarks.
1		35	120	122	152	192	Inc. <i>A</i> on right side.
2	214	8	9	10	40	105	Do.
3	818	2	2	2	5	100	Do.
4	155	0			0	35*	Incline <i>A</i> on the right; incline <i>B</i> on the left.
5	26	0			0	39†	Do.
6	13	1			6	30‡	Incline <i>A</i> on the left; incline <i>B</i> on the right.
7	3142	5	6		7	75°	Do.
8	25820					§	New stage, inc. <i>A</i> on left; placed on new island.
9	1440	5					Same apparatus as in ex. 8.
10	1521	1364**				1395	Same stage; incline <i>A</i> on right; dark chamber on top of stage.

* One pupa was conveyed down incline *B*, all the others down incline *A*. One worker ascended incline *B* to the stage and carried a pupa down incline *A*.

† One pupa was conveyed down incline *B*, the remainder down incline *A*.

‡ All of the pupæ were conveyed down incline *B*.

° A very large majority of the pupæ were carried down incline *B* to the nest. One pupa was carried down incline *A* to the nest and several were carried down incline *A* and stored under the base of the incline.

§ Up to bedtime the pupæ had not been carried to the nest. Thus the ants were lost for over 12 hours.

** In the course of half an hour all of the pupæ had been stored in the dark chamber. There they were left, while the workers, one by one, straggled back to the nest. After the lapse of 21 hours and thirty minutes, the pupæ were still in the dark chamber. I then removed the dark chamber and placed workers from the nest on the stage.

IV. IMPRESSIONS THAT INFLUENCE HOME-GOING ANTS.

I have endeavored to show that ants find their way home by virtue of something which they acquire by experience and retain; in other words, that they acquire from their environment impressions which influence their home-going. I now propose to examine the nature of these impressions.

Most recent students of ants write as though these impressions were composed solely of olfactory elements. One group of writers, represented by BETHE, claims that the home-going of ants is the result of olfactory reflexes; another, represented by WASMANN, claims that olfactory percepts are important.

Scattered through the literature are passages which indicate that some authors are not fully satisfied with this view. LUBBOCK

('81, p. 262) showed that, under certain conditions, *Lasius niger* will move a short distance along an unscented path. WASMANN ('01), although believing that the footprints possess an odor-shape which enables ants to tell which way to go, gives several examples of ants going a short distance along paths that have not been scented with their trail. VIELMEYER ('00), in his study of *Leptothorax unifasciatus*, claims that, when near the nest, light and shadows assist the ants in finding their way, and more than twenty years before that LUBBOCK had stated that "In determining their courses ants are greatly influenced by the direction of the light." PIERON ('04), although admitting that odors play an important rôle in the life of ants, was influenced by his discovery that ants sometimes move along paths that have not been scented by trails to conclude that odors play no part in guiding them home. According to him, their home-going is controlled by a tactile sense and muscular memory.

As far as I can understand PIERON, his hypothesis is as follows. On the outgoing trip the muscular movements made induce in the nervous mechanism a condition which enables the ant to return to the nest, in a reverse order, over the same pathway by which it journeyed forth. That tactile impressions are, and that muscular impressions may be, factors in the impression that guides ants harmonizes with my experiments; but that the muscular movements play any such rôle as is here indicated seems improbable. PIERON's hypothesis implies that an ant returns to its home in practically the path by which it went out. I have conducted a large number of experiments which show conclusively that this is not always the case.

1. I have already mentioned the case of the ant which would drop, with a pupa in its jaws, from the stage to the island; but which, on returning from the nest, would wander about the island until I presented a pair of forceps. It would then mount the forceps and rest quietly thereon until I had placed the tip of the forceps on the stage. It would then step off and pick up a pupa and take a flying leap from the stage to the nest.

2. I had a specimen of *Formica fusca* var. *subsericea* Say, which regularly descended from the stage to the island on the under side of the incline, but on returning to the stage this ant always moved along the upper side.

3. Another specimen regularly descended to the island by way

of the incline and returned to the stage up the bottle by which the stage was supported at its center. This it did until half the pupæ had been conveyed to the nest.

4. On several different occasions, where I had attached a second incline to a stage from which ants had been conveying pupæ down another incline to the nest, I have noticed that an ant would occasionally ascend to the stage by the second incline, pick up a pupa and then pass down the other incline to the nest.

5. During the first part of my experiments I was not looking for data along this line, but towards the close I devoted five hours an evening for two weeks to an investigation of the problem. *Formica fusca* var. *subsericea* served as a subject. I placed a number of pupæ and a marked worker on a stage from which an incline led to the island. I found that in each case the ant had to learn the way, not only from the pupæ to the incline and down it to the island and thence to the nest, but that it had also to learn the way from the nest to and up the incline. And it usually took a much longer time to learn the way from the nest to the stage than it did to learn the way from the stage to the nest. Now if PIERON's hypothesis were true, the muscular memory of the ant should have carried it back to the stage in practically the same path by which it had passed from the stage to the nest. But such was not the case. On leaving the nest, the ant would wander first in one direction and then in another, often returning to the nest. It acted as though hunting for something it could not find. At times it would fail entirely to find its way back.

6. In my experiments on the rôle light plays in the home-going of ants, I gathered some data on this point. With the light in a certain position, the marked ant was allowed to learn thoroughly the way to and from the stage to the nest. Then the light was placed on the opposite side of the stage. The ant was always much disturbed by the change and it always took it a long time to find the way to the nest. But, having reached the nest, if PIERON's hypothesis be correct, its muscular memory should have guided it immediately back along the path by which it reached the nest. The ant, however, always had a hard time finding the way back to the stage and often it failed completely.

Experiments with Odors.—Having observed that ants can find their way about without eyes and without antennæ, PIERON concludes that odors play no part in the home-going of ants; but, as

I have already stated, this no more proves that normal ants do not utilize odors in their home-going than does the fact that blind men are able to find their way about demonstrate that normal men do not use visual sensations in their journeys.

Most writers lay great stress upon the odor of the trail, and FIELDE claims that a special organ (the ninth joint of the flagellum) exists for the detection of the track-odor. If I interpret my experiments aright, it is not the scent of the trail merely, but the odor-peculiarities of the pathway as such, that form a part of the impression which enables ants to pass home. The readiness with which ants react to any strange odor that is added to their pathway lends support to the view that the odors of the pathway itself form a part of the psychic impression of home-going ants. PIERON himself says that ants traveling in a common road are arrested by unexpected odors; they flee from odors of their enemies and cross with little difficulty scents of vegetable origin. To my mind, this statement of PIERON's supports the view just presented.

To test this matter in the laboratory, several experiments like the following were tried. A colony of *Formica fusca* var. *subsericea* Say was divided and each nest placed in the same relative position on different LUBBOCK islands. On each island was placed a cardboard stage from which an incline led to the island. Each of these inclines led from the same relative position on the stage and in the same direction. On each stage was placed a large number of pupæ and a marked worker. After each worker had thoroughly learned the way to and from the stage to the nest, the experiment proper was performed. The ant that was carrying pupæ from stage number one was the subject of the experiment proper. The ant on stage number two being used, in the manner hereafter mentioned, as a control.

Special inclines were made by placing across the middle of the white slip used for ordinary inclines a transverse band, three-fourths of an inch wide, of some odoriferous substance. The chemicals used for this purpose were xylol, oil of cedar and oil of cloves. When the ant on stage number one had become so well acquainted with the way home as not to be disturbed by the substitution of a new incline of the same kind for the old, the old incline was replaced by one of these special inclines. In each case the ant was very much disturbed, but in the case of both the xylol and cedar oil, after a while, the ant began to go back and forth across the band

conveying pupæ to the nest. In a short time after the first few trips had been made across the band, the ant would be making its journeys to and from the nest as rapidly and regularly as down the old incline. Then a new special incline or a plain incline of the ordinary kind was substituted for the one just used and that one transferred to the control stage. In each case the animal used for control was much disturbed, which demonstrated that, from the ant's standpoint, the transverse band of volatile substance was still on the incline. Evidently that odor or better that volatile substance had become for ant number one a familiar element of the homeward path. This experiment then shows that the volatile chemical peculiarities of the path form a portion of the impression experienced by ants on their journeys (Figs. 9, 18).

Experiments with Tactile Stimuli.—That tremors affect the home-going of ants is evidenced by the fact that a comparatively slight tap on the stage will cause an ant to halt and a severe jar will so disturb it as often to make it necessary for the ants to relearn the way home (Fig. 12, D).

A number of experiments were performed for the purpose of discovering whether ants are affected by the surface character of the pathway. In this case a worker was trained to go down and up a smooth black incline. After it had reached the condition where it was not disturbed by the substitution of another smooth black incline for the old one, a black incline with a velvety surface was substituted for the smooth black one. *Myrmica punctiventris* Rog. was much disturbed by the change (Fig. 10, g), but *Formica fusca* was not (Fig. 18, M; 14, P).

It seems legitimate to assume that tremors and jars probably give kinesthetic stimuli and that the velvety surface gives a tactile stimulus. Such being the case, kinesthetic impressions probably form part of the mental furniture of all ants examined by me and at least some ants have tactile impressions.

Experiments with Optic Stimuli.—To see if optical impressions are received by ants two kinds of tests were conducted: experiments with ants working in concert, and with marked individuals.

In experiments of the first type a cardboard stage from which a cardboard incline led to the island was used. A 16 c.p. incandescent electric lamp was placed, sometimes near the side to which the inclined plane was attached, and sometimes near the opposite side. After the ants had thoroughly learned the way

home, a new incline was attached to the side of the stage which was opposite the one to which the old incline was attached. If after a lapse of five minutes no ants went down this second incline, conditions were considered right for the test. The light was now transferred to the opposite side of the stage. In each case the halting movements of the ants showed that they were disturbed (Fig. 6). In most cases, some of the ants would finally go down the new incline and in a few cases, after the lapse of several minutes, all of them would go down the new incline. These experiments were tried on all of the ants used in the experiments on heliotropism (p. 371).

Similar experiments were conducted with marked individuals of the species, *Formica fusca* var. *subsericea* Say, *Myrmica punctiventris* Rog. The results harmonized with those derived from experiments conducted with ants working in concert (Fig. 14, *B*; Fig. 17, *B, H, M*); only, in almost every case, after a greater or less lapse of time, the ant would usually find its way down the old incline to the nest; and after a still greater lapse of time find its way back to the stage.

Fig. 16 illustrates how ants are disturbed by altering the position of the light better than a multitude of words. From the beginning to *B* the ants had been working by daylight, the light coming from two windows, one on the south and one on the west. From *B* to *C* the ants were working at night, the illumination being furnished by electric lights and coming from the northeast. From *C* to the end, the conditions were the same as from *A* to *B*.

To determine whether this effect was due to the intensity of the light, to the direction of the rays or to heat, the following series of experiments were conducted with *Formica fusca* var. *subsericea* Say.

That the effect described above was not due to heat, was proved in the following manner. A cardboard stage was arranged with its left side connected to the table by a cardboard incline. At the right and left of this stage was placed a heat-filter, consisting of a tall museum jar 34 cm. x 16 cm. x 7 cm., filled with cold distilled water. At the beginning of the experiment, a 32 c.p. incandescent lamp was placed behind one of these filters (usually behind the one near the incline). After the ants had traveled the path long enough to make the trips regularly and rapidly, the lamp was transferred to a point behind the opposite filter. In every case

the workers were much disturbed in the manner stated above. Since the heat had been excluded, it is evident that the disturbance was the result of some form of light stimulus. This was repeated with seven different colonies of *Formica fusca*.

To determine whether the intensity or the direction of light was the determining factor, a different kind of experiment was used. The stage and incline were arranged as before. Sometimes the heat-filters were used, but more often they were not. To furnish illumination, four different candle powers (4, 8, 16 and 32) of incandescent electric lamps were used, one at a time, in a darkened room. At the beginning of the experiment a lamp of a certain candle power was placed near the side of the stage to which the incline was attached. After the ants had thoroughly learned the way home, a different candle power was substituted for the first. After the lapse of a few more minutes this lamp was transferred to the opposite side of the stage. Shortly it was returned to its former position. A few minutes later a different candle power was substituted for this. This performance was repeated over and over again until each lamp had thus been used one or more times. It was found (Fig. 17) that substituting a lamp of one candle power for one of a different power had no disturbing effect on the actions of the ants; but that by any marked change in the angular position of the light, no matter what the candle power, the ants were very much disturbed. This warrants the conclusion that when light is present the direction of its rays plays a prominent rôle in the home-going of ants whose eyes are normal.

LUBBOCK over twenty-five years ago stated this fact, but his observation has been either overlooked or ignored by recent continental writers.

Experiments with Colored Pathways.—The purpose of the experiments now to be described was not to determine whether ants have color vision, but simply to ascertain whether the color of the path plays a part in the home-going of ants. In these experiments the usual stage was employed; but the inclines were composed of colored papers of practically the same texture. Each incline was composed of one color. Of the color series I used, red, yellow, green, blue, purple; of the brightness series, white and black. When an ant had learned the way down a certain colored incline so well that it was not disturbed by the substitution of another of the same color, an incline of a different color was

substituted for the old one. This was repeated until all of the colors had been used at least once. All ants were not affected in the same way by these changes. *Myrmica punctiventris* was slightly affected each time a change in color was made (Fig. 15); another ant (sp. ?) was disturbed by a change from black to white, but not by changes from one member of the color series to another. *Formica fusca* was not usually disturbed by any changes made but occasionally (Fig. 14) it was slightly disturbed. This shows that changes in color of the pathway do not disturb some ants at all⁵ whereas other ants seem to be slightly affected by such changes,⁶ while yet others are affected by changes in brightness but not by changes in hue.

Experiments with Auditory Stimuli.—This section is not intended to be an exhaustive discussion of the auditory sense of ants. It is, however, an attempt to collate our knowledge on the subject, to give additional experimental data and to harmonize the conflicting views.

About a century ago ST. FARGEAU, in his *Hist. Nat. des Hymenopteres*, asserted positively that ants hear (LUBBOCK '81, p. 221). But HUBER (*Nat. Hist. of Ants*), FOREL (*Fourmis de la Suisse*) and LUBBOCK ('81) conducted experiments to test the power of ants to hear and each decided that they were deaf to sounds that fall within the human auditory range.

Sir JOHN LUBBOCK's experiments were especially well planned. He used sounds produced by a dog whistle, a violin, the human voice, a shrill penny pipe, and a full set of tuning forks. These experiments were tried both upon ants that were carrying pupæ home and upon ants confined to paper bridges. In no case did he get the slightest response to any of the sounds made. Since, however, he had discovered in ants what he thought was an auditory organ, he presumed that it was probable that ants both heard and produced sounds; but that they were tones that fell outside of the human auditory range.

The negative results of the experiments of these three authorities have caused most people to believe that ants cannot hear.

⁵ LUBBOCK (*loc. cit.*, p. 198) performed an experiment which showed that the ants studied by him did not notice the color of the path. He placed some ants on a narrow bridge, which was supported by pins with their bases in the water. On this bridge he projected a spectrum and noticed that the ants acted as they did on the plain bridge.

⁶ It is not improbable that these disturbances may have been due to a slight difference in the texture or odor of the different papers.

Yet, if they cannot hear, it is hard to understand why so many ants are provided with organs for producing sound. DAVID SHARP ('93) has proved conclusively that the Dorylidæ, the Pon-
eridæ and the Myrmicidæ possess stridulating organs, each consisting of a file on the anterior portion of the tergum of the third abdominal somite, which file is rubbed against the roughened underside of the second abdominal ring. He did not find any such organ in either the Camponotidæ nor the Dolichoderidæ and he was doubtful of its presence in the Cryptoceridæ. LANDOIS ('67) had seen such an organ about fifty years ago in PONERA.

SHARP's work was strictly morphological, but physiological evidence that ants can make audible sounds is furnished by WROUGHTON ('92), FOREL (*Fourmis de la Suisse*), WASMANN ('91) and JANET ('94), each of whom has heard sounds produced by ants. WROUGHTON listened to *Cremastogaster rogenhoferi*, FOREL to *Camponotus ligniperdus*, JANET to *Myrmica rubra* L. and *Tetramorium cæspitum* L. and WASMANN to *Myrmica ruginodis*.

So far as I have been able to ascertain, WASMANN ('91) is the only European who has produced any experimental evidence against the negative results of HUBER, FOREL and LUBBOCK. He experimented with *Formica rufa*, which was confined in a LUBBOCK nest, the floor of which was covered with one mm. of dirt. Whenever he scratched on the glass with a needle, he found that the ants made responsive movements which demonstrated they were affected by the stimulus. Experience has taught me that the slightest touch upon any portion of my JANET nests is almost certain to be responded to by some movement of the ants within. It is to be regretted that WASMANN did not produce his sounds in some other way than by scratching on the nest; for, since there is a possibility that the scratching produced a slight tremor, a fair critic is bound to admit that the positive evidence furnished by this experiment is not of sufficient weight to offset the negative results of the three men mentioned above.

About eight years ago an American, LE ROY D. WELD ('99) performed a carefully planned series of experiments, which seem to prove that *Cremastogaster lineolata*, *Lasius Americanus* and *Aphænogaster* sp. can hear sounds that are audible to man. Some of these experiments were conducted under conditions that apparently precluded the possibility of jars from the sounding body reaching the nest by any other medium than the air. The

sounds used were produced by a steel bar, a tin whistle, a wooden whistle, a middle A tuning fork and a milled disk rotating against the edge of a card. FIELDE and PARKER ('04) claim that ants do not react to aerial sound waves from a piano, violin, or GALTON whistle; but only to vibrations that reach them through some solid body.

Recently I have performed a series of experiments upon *Formica fusca* var. *subsericea* Say, and a variety of *Formica sanguinea* Latr. For these experiments the ants were housed in JANET nests, the covers of which were composed of orange colored glass. During the day, the experiments were never begun until the sun was several hours high; and at night, the experiments were not begun until the electric lights had been shining for at least three hours. These precautions were taken to eliminate the disturbing effects of a change in illumination. To lessen the possibility of jars from the sounding body reaching the nest through any medium other than air, the nests were placed on a layer of cotton batting half an inch thick. For the same reason, the legs of the table on which the nests rested were placed on thick wads of cotton batting.

The sounds used were produced by the Galton whistle, organ pipes and the human voice. Sometimes the whistle or pipe was held near the nest and in other cases a short distance away. The pipes were always held in such a position that the air when expelled from the pipe could not impinge directly upon the nest. These experiments were conducted during the winter and early spring.

They showed conclusively that each of the two species of ants mentioned was sensitive to vibrations of the air which to the human ear would be sounds. I obtained responses to notes as high as 4138 vibrations per second and as low as 256 vibrations per second. The responses, in the form of zigzag movements, were usually slight for pitches higher than 3000 vibrations per second and sometimes slight for other pitches; but, to most pitches under 3000 vibrations per second, the ants usually responded in a pronounced manner, usually darting about as though much excited.

After the ants had been subjected to the sounds for a long time they seemed to become fatigued, failing to respond in the least to pitches which would call forth pronounced responses from fresh ants. The fertile females seemed to be more intensely excited by the tones than the neuters. Several series of experiments were performed. Details of four typical series are recorded in the following table.

TABLE VIII.

Series 1.

VIBRATIONS.	FORMICA FUSCA.	FORMICA FUSCA.	FORMICA SANGUINEA.
3480	Slight	Slight	Response
3906	Marked	Slight	Marked
4138	?	?	Slight
	None	None	None

Series 2.

VIBRATIONS.	FORMICA FUSCA.	FORMICA FUSCA.	FORMICA SANGUINEA.
256	Marked	Slight	Marked
3168	Response	Slight	Slight
3480	Very slight	Very slight	Very slight
512	Marked	Marked	Marked
316	Slight*	Slight ?	Slight ?
880	Response	Response	Response
3906	Slight	Slight ?	Slight ?
4138	Very slight	None	Very slight
4645	?	None	?
256	Slight	None	Marked
512	Slight	Slight	Slight

Series 3.

VIBRATIONS.	FORMICA FUSCA.	FORMICA FUSCA.	FORMICA SANGUINEA.
1760	Marked	Response	Slight
1056	Marked	Slight	?
880	Slight	Slight	None ?
512	Marked	Very slight	Marked
362	None ?	None ?	Slight ?
256	None	None	Slight ?
3168	Response	Response	None
2816	Slight	Slight	Response
2640	Response	Slight	Slight
2280	Marked	Marked	Marked
2112	Response	Response	Response
1980	Response	Response	Very slight
1900	Marked	Slight	Response

Series 4.

VIBRATIONS.	FORMICA FUSCA.	FORMICA FUSCA.	FORMICA SANGUINEA	FORMICA FUSCA.
512	Slight	Slight	Slight	None
880	Very slight	Very slight	Slight ?	None
256	?	?	Marked	None
1056	Marked	Marked	?	None
3168	Slight ?	None ?	Slight ?	None
	Slight	Slight ?	?	None
512	Marked	Response	Marked	None
362	Marked	Slight ?	Slight	None
256	Marked	Slight	Marked	None

* The fertile females gave a marked response.

EXPLANATION OF TABLE VIII.

- Column 1. The number of vibrations per second.
- Column 2. A colony of *Formica fusca* var. *subsericea* Say, containing three fertile females and about two hundred neuters.
- Column 3. A colony of *Formica fusca* var. *subsericea* Say, containing about two hundred neuters and no fertile females.
- Column 4. A mixed colony of *Formica sanguinea* Latr. and *Formica fusca*. This colony contained about two hundred neuters, over two-thirds of which were *fusca*. No females were present.
- Column 5. A few workers of *Formica fusca* var. *subsericea* Say, the antennæ of which had been removed two days before.

Some may think the response of these ants was the result of tactile stimuli caused by shaking of the nest by the sound wave. To me it does not seem possible for the nests to have vibrated in response to each of so wide a range of pitches. However, to meet that objection, the following experiment was devised. I obtained some felt cloth two mm. thick and placed two layers of it in the bottom of each of the living chambers of a JANET nest. This nest rested on cotton placed on the table the legs of which rested on wads of cotton. After the ants had become accustomed to their carpeted floor, various sounds were made. This experiment was tried upon both *Formica fusca* var. *subsericea* Say and *Formica sanguinea* Latr. It is important to note that even with the false felt bottom to stand on, the ants could not reach the top of the nest with their antennæ. In each case the ants responded to the sound in the same manner as has been described above. Since the felt would prevent nest tremors reaching the ants, the response, it seems to me, must have been to air vibrations which the human ear would sense as sounds.

At present I have housed in a JANET nest a small colony of *Camponus herculeano-ligniperdus*. This colony consists of eight winged females and about twice as many neuters. Usually one of the neuters mounts guard in the outer doorway. Whenever sounds similar to those mentioned above are made, this guard shows marked evidence of being disturbed. Under such conditions it makes agitated movements with its antennæ and often snaps with its jaws right and left. If the noise is continued, the guard is apt to rush back into the nest.

Undoubtedly, artificial colonies of each of these species of ants respond in a pronounced manner to atmospheric vibrations which to the human ear would be sounds.

When, however, I tested ants that were moving about outside the nest, I obtained no such marked reactions. Often I could

detect no response whatever. But usually there would be a slight movement of the antennæ, or a slight but sudden acceleration of speed, or else a halting movement. Sometimes the ant would stop still. All of these movements were slight, usually so slight that they might easily be overlooked by an observer who was not expecting a response of some kind.

Even with single individuals confined to a test-tube which was suspended by a string (a method much used by WELD), I sometimes obtained no response. Indeed, I seldom received more pronounced responses than a slight movement of an antennæ, or a twitch of one or more legs, or a more tense attitude of the body. In most cases, however, I did get these slight movements, and, occasionally, I observed wide sweeping movements of the antennæ or other easily observed bodily movements.

The pronounced positive results obtained by WELD and myself do not seem to harmonize with the equally pronounced negative results obtained by HUBER, FOREL and LUBBOCK. One cannot believe that the American ants are physiologically as much unlike the European as these antagonistic results would seem to indicate. It seems to me that these contradictory results can be harmonized in the following manner.

LUBBOCK's experiments were made either upon ants that were carrying pupæ home, or else upon ants that were confined to paper bridges. As has been stated above, my experiments show that under such conditions the ants usually do not respond at all to sounds, or else react with movements so slight that they might easily be overlooked by one not expecting movements of the kind made. I am fully convinced that experiments conducted upon European ants colonized in JANET nests, would yield the same positive results obtained by WELD and myself.

To harmonize FIELDE and PARKER's ('04) work with mine is not an easy task. We agree that, up to about 4000 vibrations per second, ants respond to a long range of vibrations which a human ear would sense as sounds. They claim that these vibrations are responded to only when received through a solid medium; while my experiments seem to show that they are responded to when received through the air. Yet two of the species used by me (*F. sanguinea* and *F. fusca* var. *subsericea*) were also used by them. They used the piano, the violin and the Galton-whistle; I used organ pipes and the Galton-whistle. It seems to me that

I have taken even more precautions to preclude the possibility of the vibrations reaching the ants through a solid medium than they did. The only precaution they took was to rest the nest upon a thick layer of paper. I carpeted my nests with two layers of thick felt, placed a thick layer of cotton between the nest and the LUBBOCK island and thicker wads of cotton beneath the legs of the table upon which the island rested. The lowest note of the whistle used by FIELDER and PARKER was 10,000 vibrations per second, which is far above the highest pitch to which ants respond. The whistle I used ranged from 3480 to 51,000 vibrations per second. If the sound of the piano and of the violin were common in the room where the ants were kept they may have become too familiar to arouse responses. My ants were kept in a room facing a paved street. The noises of this street did not disturb them.

The more I meditate on FIELDER and PARKER's paper, the more I am inclined to believe that the lack of harmony between their results and mine is due to the difference in our technique. In their experiments the same note was sounded ten times in slow succession; in mine each note was sounded continuously or else in rapid succession for one minute or longer. I thought that, if ants can hear, the occasional production of a note might simply attract attention, while a continuous rapid repetition of the same would arouse some form of visible motor response. In my own experiments a note repeated a few times in slow succession would often cause no response, yet a prolongation of the sound or a continuous rapid repetition of the same would soon produce marked responses. If this contention be valid, we would expect FIELDER and PARKER's technique to yield nothing more than an occasional response. And this is the result they obtained; for on page 643 (*loc. cit.*) they say, "Now and then an ant would seem to respond to a given note, but in every case repetitions of the experiment gave a negative result."

Responses to light within and without the nest exhibit differences similar to those observed for sound. If light is admitted into a nest, the ants at once are much disturbed and show it by vigorous movements. Yet in the outer world, so long as the direction of the rays remains the same, ants are scarcely, if at all, affected by changes in the intensity of the light. Both light and sound are almost constant factors of the external world, but are

rare phenomena in the confines of the nest. With ants, as with us, it seems that unusual stimuli cause unrest.

Experiments on Direction and Distance.—LUBBOCK ('81, p. 260) devised an experiment which shows that ants have accurate impressions of direction in a horizontal plane. This experiment, a portion of which I shall presently quote, has been repeated by me, with confirmatory results, on most of our southern species of ants. LUBBOCK writes as follows, "I then accustomed some ants (*Lasius niger*) to go to and fro over a wooden bridge, *b, c*, to some food. When they had got quite accustomed to the way, I watched when an ant was on the bridge and then turned it around, so that the end *b* was at *c*, and *c* at *b*. In most cases the ant immediately turned around also; but even if she went on to *b* or *c*, as the case may be, as soon as she came to the end of the bridge she turned around. I then modified the arrangement, placing between the nest and the food three similar pieces of wood. Then when the ant was on the middle piece, I transposed the other two. To my surprise this did not at all disconcert them."

LUBBOCK next tried a different experiment. By means of a pin through its center, he pivoted a disk of cardboard to the middle of the table. At one corner of the table he placed some food. When the ants had come to know their way so that they passed straight over the paper disk on their way from the nest to the food, he moved the disk around with an ant on it, so that the side that had been towards the nest was now towards the food. As in the above experiment, the ants turned round with the paper. He also repeated it with a table arranged to revolve in three concentric sections. The result was the same as above.

I think some of my experiments warrant the assertion that ants have an impression of vertical as well as horizontal direction.

In my experiments (excepting those on color and tactile phenomena) the stage and incline were made out of the same material, often being cut from the same piece of cardboard. The apparatus was so adjusted that when the ant reached the union of stage with incline, only two changes in movement were necessary in order to take the next lap of the journey; the ant must turn so as to receive the light rays on a different side than before, and it must move obliquely downward instead of moving in a horizontal plane. The apparatus was also so adjusted that if the ant turned at the parting of the ways and moved horizontally along the stage in

the direction of the nest, it would receive the light rays on the same side of the body as it would in passing down the incline. The only new factor that entered the life of the ant that moved down the incline rather than horizontally along the stage towards the nest was the experience of moving downward. Vertical changes in direction must affect ants differently from horizontal changes in direction, otherwise there is no reason why the ant should pass regularly down the incline rather than horizontally along the stage towards the nest.

Again, after an ant had thoroughly learned the way down and up the incline, it would often not take the trouble to go all the way to the union of stage and incline, but, reaching the edge of the stage at a greater or less distance from its union with the incline, the ant would reach downward over the edge; if it could not touch the incline it would move nearer the junction of stage and incline and again reach downwards. If necessary, it would move nearer still. As soon as the ant could touch the incline, it would step off of the stage and move obliquely downward to the nest.

To test this matter further, the following experiment was devised. Underneath the incline of one of my stages was placed an adjustable support made by sticking a pin vertically into the cork of a small bottle. Since the lower end of the incline was free while the upper was attached to the stage, by moving this adjustable support more or less towards the base of the incline, a vertical gap of any desired size could be formed and maintained between the base of the incline and the island. After the ants had thoroughly learned the way to and from the nest, a small vertical gap, which was gradually increased until the ants on the island could no longer touch the base of the incline with their antennæ, was made between the foot of the incline and the island. Now so long as the ants could touch the incline with their antennæ, they would stretch upward until their forefeet touched the incline, then mount the incline and go to the stage. Ants coming down the stage acted the same way, only they stretched downward rather than upward. When, however, the base of the incline could no longer be touched by their antennæ, the ants would come to the place where the foot of the incline had been, elevate the front part of their bodies as much as possible and reach upwards with their antennæ. Elevating the base of the incline still more, I placed along the side of the path and parallel to it a stack of clean microscopic slides, one

cm. high. This stack of slides was placed near enough to the incline for the ants, by stepping across a narrow horizontal gap, to pass easily from it to the incline. At once the ants mounted the stack of slides and went up the incline.

Does not this indicate that the ants have an impression of vertical direction? Does it not also indicate that they have an impression of distance? Otherwise, what makes them stop at that place and feel upward for the incline? It will not do to say that they stopped because the scented trail terminated there, for, even if it were not true that tracks of those ants cross that place in all directions, it has already been shown that the termination of a scented trail does not impede the progress of ants moving in a direction that is thoroughly known. Nor will it do to say that they halted and acted that way because they sensed the incline above them; for they do not react that way towards bodies held above them on other parts of the stage, nor do untrained ants react that way when they pass underneath the incline. In each of these test cases, ants may reach upward with the antennæ and then pass on; but they do not return to the spot over and over again and reach up as though they were hunting for something that was lost.

This view is supported by yet other experiments. In another connection, I have mentioned the case of a worker ant that learned to come to a certain point on the island, mount my forceps and be conveyed to the stage. After this mode of conduct had been thoroughly learned, the ant, on leaving the nest, would immediately go to this position on the island and meander in a small circle until my forceps were presented.

It was not an uncommon thing for an ant that knew the way up and down a certain incline, occasionally to miss arriving at the foot of the incline. In such cases, the ant would not, as a rule, roam here and yon, but would usually turn quickly and hunt for the incline. If it missed it again, it would go back to some point in its path, often as far as the nest opening itself, and, taking a new start, arrive at the incline without further trouble. This mode of conduct not only indicates that ants use certain landmarks as such, a subject which will be referred to in the next section, but it also seems to harmonize with the views stated in this section.

Another common occurrence which puzzled me not a little may, perhaps, be best explained in this connection. In some

experiments planned to solve a problem not discussed in this paper, two stages were used, from each of which an incline of the same kind led to the island. In one case the incline was attached to the right side of the stage and in the other to the left. Incline number two was nearer the nest opening than was incline number one. An ant that had thoroughly learned the way up and down incline number one, would occasionally start up incline number two. Sometimes it would continue on to the stage, but more frequently, when only part of the way up, it would turn about and return to the island and continue on to incline number one; either directly, or else after having first retreated to some point farther back on the trail. The same thing sometimes happened where two inclines were attached to opposite sides of the same stage.

From a psychological point of view, there were only two differences between incline number one and incline number two; incline number one was scented with the footprints of the ant, while incline number two was not; and incline number one was farther from the nest than incline number two. Since it has been shown that the substitution of an unscented incline for one scented by the tracks of ants is not a disturbing stimulus to ants that are moving in a well known path, the difference in the distance traveled seems the only thing that could have caused the inhibition.

The grouping of all these data in one section does not imply that they are of the same psychic order. Some may be simple and others complex. Some may even be the derivatives of others mentioned here. To discuss such issues is not the purpose of this section. Its sole aim is to show that the psychic impression that confronts the home-going ant is not a simple olfactory stimulus, as most writers seem to suppose, but that it is a complex impression composed of contributions from the olfactory (topochemical), visual, tactile and kinesthetic and auditory senses.

V. HAVE ANTS ASSOCIATIVE MEMORY?

“By associative memory, I mean the two following peculiarities of our central nervous system: First, that processes which occur there leave an impression or trace by which they can be reproduced even under different circumstances than those under which they originated The second peculiarity is, that two processes which occur simultaneously or in quick succession will leave

traces which fuse together, so that if, later, one of the processes is repeated, the other will necessarily be repeated also. By associative memory we mean, therefore, that mechanism by means of which a stimulus produces not only the effect which correspond to its nature and the specific structure of the stimulated organ, but which produces, in addition, such effects of other causes as at some former times may have attacked the organism, almost or quite simultaneously with the given stimulus" (LOEB '02, pp. 213 and 214).

As to the criteria of memory, the same author writes (*ibid*, p. 218): "It will require more observations than we have made at present to give absolutely unequivocal criteria. For the present, we can say that if an animal can learn, that is, if it can be trained to react in a desired way upon certain stimuli (signs), it must possess associative memory. The only fault with this criterion is that an animal may be able to remember (and to associate) and yet not yield to our attempts to train it The fusion or growing together of heterogeneous but by chance simultaneous processes is a sure criterion for the existence of associative memory."

If we consider the experiments herein described in the light of these criteria of LOEB, we must certainly conclude that ants have associative memory; for, as has been shown, ants learn by experience, retain what they learn in a way that can be recalled by the proper stimuli, and they can be trained to do certain things.

Some psychologists do not agree with LOEB that the mere ability to learn predicates memory. There is a method of learning depending on repeated blundering efforts with fortuitous successes that are gradually selected which LLOYD MORGAN calls the method of trial and error. Such a mode of learning, some say, does not indicate the existence of memory. Memory predicates the existence of ideas which are associated. In learning by trial and error, no association of ideas is involved; we have simply assimilation of a sense impression or impressions with an impulse. To use the words of THORNDIKE (*loc. cit.*, p. 71) "The ground work of animal associations is not the association of ideas, but the association of idea or sense-impression with the impulse."

HOBHOUSE ('01), who experimented on the same animals as THORNDIKE, differs from him in his conclusions. He thinks that the average laboratory psychologist has gone to extremes in his

conclusions which the experiments do not warrant. He reminds us that, "A dog may show not merely highly developed hunting instincts, but real cleverness in the adaptation of past experience when it is a question of catching a hare, but may also be an intolerable dullard about opening a box To test an animal's intelligence by mechanisms, seems to be about on a par with gauging the nature of a man's intelligence by certain puzzles, in which, as is well known, many able men are, indeed, dullards What Mr. THORNDIKE's experiments prove so far is, not that cats and dogs are invariably educated by the association process, that is by habituation, but, on the contrary, that at least some cats and dogs conform, in at least one point, to the method of acquisitions by concrete experiences In some cases they not only merely learn to meet a given perception with a given motor reaction, but also to combine and adapt their actions so as to effect physical changes which, as they have learned, aid them in gaining their ends."

HOBHOUSE further reminds us that habits are generally formed gradually by many repetitions and that, where the act is the result of habituation, the time curve should gradually descend. Indeed, THORNDIKE himself lays stress upon this same point; for he says (*loc. cit.*, p. 45): "And if there were in these animals any power of inference, however rudimentary, however sporadic, however dim, there should have appeared among the multitude some cases where an animal, seeing through the situation, knows the proper act and does it, and from then on does it immediately upon being confronted with the situation. There ought then to be a sudden vertical descent of the time curve. Of course, where the act resulting from the impulse is very simple, very obvious, and very clearly defined, a simple experience may make the association perfect and we may have an abrupt descent in the time curve without needing to suppose inference. But if in a complex act, one found such a sudden consummation in the associative process, one might well claim that reason was at work The gradual slope of the time curve, then, shows the absence of reasoning. They represent the wearing smooth of a path in the brain, not the decisions of a rational consciousness."

If a gradual descent of the time curve be a sure test that a creature has learned by the method of trial and error and if an abrupt descent is an indication of perceptual learning, we must conclude

that the ant's mode of learning is not the trial and error but the perceptual mode and that they have memory (Figs. 8, 10, 12, 18). I freely confess, however, that this seems to me a very unsatisfactory criterion. For this criterion to be of any real value, we would need some way to determine, from the animal's standpoint, what is complicated and what is not; and there is no known way.

There are, however, other considerations that lead me to believe that ants have memory. In memory we usually find a complex impression composed of contributions from more than one sense organ. In the section that precedes this, I have tried to show that home-going ants have a complex impression which is composed of contributions from several sense organs. Now the existence of this complex impression does not necessarily prove the existence of memory, but, it does demonstrate the existence of one of the usual physiological accompaniments of memory.

BUTTEL-REEPEN ('00) chloroformed some bees and found that they were no longer able to find their way home. This he considered a proof of memory. How, he asks, could they forget unless they had a psychic content to forget. Is it not reasonable to consider cases of "forgetting" that cannot be attributed to injuries received nor to retardation due to fatigue as evidences of memory? In my experiments, I frequently met cases of what might be called lapses of memory. Sometimes this would happen on the stage, at others on the island. The ant would move about at random as though it had forgotten the way. These lapses would increase the time ordinarily required for the trip, from one to three minutes. The subsequent trips were made as rapidly and as regularly as before. I have also met with cases of what might be called mistaken identity (Fig. 7). Recall the experiment with two stages, from each of which an incline descended to the island—the case when the ant occasionally went up the wrong incline—and you have a case of this kind.

Then, too, I have noticed cases which I think reveal ants as using a thing or things as a means of accomplishing a certain end, rather than responding to it as an end. Take the experiment mentioned in the previous section, where a high vertical gap was present between the foot of the incline and the island. The ants were coming repeatedly to the same point and reaching upward for something beyond their reach. In that place, a stack of clean glass slides was placed a little to one side of the path. At once the

ants climbed the slides and mounted the incline. Similar stacks of slides placed just to one side of the path at other points along the trail were not thus mounted by the ants. The road by which the ants had learned to reach the stage from which the gap now separated them, had no vertical walls that needed to be climbed. This wall of slides was not placed across the path, but a little to one side of it. Immediately, the ants mounted it and thereafter used it as a means of passing from island to incline and from incline to island.

Then, too, it seems to me that ants use light as a means to an end. In a former section, an attempt was made to prove that light is not for ants a tropic stimulus, yet, by a repetition, under control, of one of LUBBOCK's experiments, I have shown that the direction of the rays of light does have a guiding influence.

In each of those experiments, I used a cardboard stage, which was connected with the LUBBOCK island by means of a single incline. In some experiments, I placed the light (a 16 c.p. incandescent electric lamp) near the side to which the incline was attached, in other cases the light was placed on the opposite side. There was no other light in the room. After waiting until the ant had thoroughly learned the way down the incline,⁷ I transferred the light to the opposite side. Invariably, as shown by its movements, the ant would be very much disturbed by the change. Now to my mind, this disturbance seems due to the fact that the ants use the direction of the rays of light as reference data. In other words, the light is responded to as a means to an end and not as itself an end. If this contention be valid, then ants learn, not by the method of trial and error, but perceptually, and they have associative memory. As the result of careful observation, I am convinced that ants use such things as irregularities of the surface, edges of flat surfaces, the edges of shadows, etc., as reference data.

On several occasions, after a marked worker had been carrying pupæ for a long time, it was imprisoned from one to several hours and then returned to the stage. In some cases the ant failed completely to find the way to the nest, in a few others it went to the nest immediately; but in most cases, it took some time to find the way to the nest. Usually the time required to re-solve the problem was

⁷ When the ant was not disturbed in its movements by the substitution of a new incline of the same kind for the old, the ant was judged to be thoroughly acquainted with the way. This was the test I always used in such cases.

shorter, often much shorter, than was needed by the ant the first time such a problem was presented. Aside from the differences of time required for different individuals to reach the nest, there were marked individual differences in their conduct. I noted five different modes of response: (1) An ant would take a pupa to the nest and remain therein instead of returning to the stage. (2) An ant would pass unburdened to the nest and remain therein instead of returning to the stage. (3) An ant would carry a pupa to the nest or to some point on the island and then return to the stage and make repeated trips. (4) An ant would pass, unburdened, to the nest, and then immediately return to the stage for a pupa and thereafter make regular trips. (5) Occasionally, a worker would pass, unburdened, to a point near the nest, then return to the stage for a pupa and thereafter make regular trips.

Such marked individual differences in conduct were noted between members of the same colony, under the same external environmental conditions. All of these individuals, at the time of their imprisonment, were thoroughly acquainted with the way between the nest and the stage. The difference cannot be attributed to fatigue, for they had been resting from one to several hours. It seems to me that these facts harmonize rather with the memory hypothesis than with either the "assimilation of idea to impulse" or to the "determination of stimulus" hypothesis.

If either of the two latter hypotheses is true, the following is probably a fair statement of the factors that guided my ants to and from the stage to the nest. The sensing of the pupa on the stage causes the ant to pick it up and move in a certain direction. The direction of the rays of light, etc., cause it to move to the point of union of stage and incline. Contact with that point, etc., cause it to turn and pass down the incline, receiving the light on a different side than before. At the base of the incline, contact with the zinc, etc., cause it to pass to the side of the nest, where other stimuli cause it to go into the nest, where yet other stimuli cause it to lay down its pupa. Now all of these several stimuli act on it in a reverse way and cause it to return to the stage. After the "assimilation of impulse and idea" or the "determination of stimulus" has been made, the animal moves along just as automatically as an animal in a tropic response. Each stimulus is responded to as an end in itself and not as a means to an end. Now, if I interpret my experiments aright, none of the ants examined acted this way.

They acted as though getting the pupæ under some shelter, preferably the nest, was the end in view, and as if all of their responses to stimuli were but means put forth to accomplish that end.

If either of these hypotheses applies to ants, a worker meeting a pupa anywhere in the open air, unless carried on by the momentum of other stimuli, should respond to it in the same way that it would had it encountered the pupa on the stage. Now what are the facts in the case? Whenever I place a pupa in the track of such a worker, as soon as the pupa was sensed it was picked up by the worker and carried to the nest; either back along the path just traveled or first to some reference point and thence to the nest. One might suppose that this is what would have happened had the ant encountered the pupa on the stage, for there is a general belief that the ant picks up the pupa, turns about at once and returns in its own tracks to the nest. With some species of ants, especially when they are working in concert, it is hard to decide whether this is the case or not; but even a casual observation of an individual of *Formica fusca* var. *subsericea* Say, working alone, will convince anyone that such is not the case. With the pupæ scattered here and there over the stage, the ant must hunt for them, and each pupa is approached over a different, more or less sinuous, line. When the pupa is reached, the axis of the ant's body may make almost any angle, from zero to one hundred and eighty degrees, with the line that leads from the pupa to the union of stage and incline. Hardly any two of these positions are alike. Whether or no, on picking up the pupa, the ant turns about at once is a secondary matter, dependent upon the position of the ant's head at the time. The species just mentioned rarely, if ever, returned in its own tracks from the pupæ to the union of stage and incline. What the ant really does is to pick up the pupa and move off in such a direction as to keep the light rays falling on that portion of the body which it has learned from other trips, must receive the rays of light if it is to reach the union of stage and incline. This may not take it direct to the junction but it will take it to some familiar point and from there it will take a bee-line to the junction. In the test experiments, I took especial pains to place the pupæ in such situations that, to get to the nest, the ant must move in such a direction as to receive the rays of light on a different side of the body and at a different angle than would have been the case had the pupa been encountered on the stage. And

yet the ant always went home without a moment's hesitation. To say that the pupa does not give the ant a stimulus to make a certain definite movement, but any movement necessary to take it home, is equivalent to saying that the ant responds to the stimulus as a means to an end.

There is yet another observation which deserves mention in this connection. In all my experiments with ants working in concert, when the pupæ had all been removed from the stage the ants would thoroughly search the stage and incline and then retire to the nest. Why did the ants stop going to the stage? Surely the same stimuli existed in the nest as formerly; the only new factor is that there are no more pupæ on the stage. This cessation of movement cannot be attributed to fatigue, for they act in the same manner after removing a small lot of pupæ as they do after removing a pile many times as great. It would be equally fallacious to assume that the pupæ on the stage influence the ants directly from afar, and that the lack of pupæ to furnish an immediate stimulus is the cause of the cessation; for ants roaming over the island in search of pupæ are not attracted by the pupæ. Many a time I have seen specimens of *Lasius*, and *Formica* pass repeatedly back and forth beneath the stage without being attracted by the pupæ on the stage; I have known *Formica* to ascend the incline and pass to within three centimeters of the pupæ and return to the island without sensing them. To test whether such ants were in a condition to be affected by the sensing of pupæ, I have placed pupæ in front of them as soon as they reached the island. Immediately such pupæ were picked up and carried to the nest. Nor would it be consistent to assert that the stimulus-to-return did not affect ants that returned unburdened to the nest; for after the pupæ were removed, each ant always made from one to a few round trips; and, furthermore, it frequently happened, when the stage was well supplied with pupæ, that an ant would pass, unladen, to the nest, and then immediately, or after a few moments, resume its periodical round trips.

I fail to see how these facts can be harmonized with either the assimilation hypothesis of THORNDIKE or with the determination of stimulus hypothesis, but they do harmonize with the assumption that ants have associative memory. It is not claimed that ants exhibit a high grade of intelligence in finding their way about. In my experiments, the first trip to the nest was always the result

of happening to succeed after making many blunders. So far this accords with the observations made by all students of vertebrate animal behavior. During the first few trips, however, aided by memory, certain associations of ideas are formed which persist and enable the ant to orient itself. To men of THORNDIKE's conviction, this is a discordant note, but it accords perfectly with HOBHOUSE's view concerning vertebrates. Although this does not necessarily make the ant a self-conscious creature, it makes it much more than a mere reflex machine.

It is worth noting that in ascribing associative memory to ants, I am in perfect accord, not only with WASMANN, but also with such a staunch advocate of the tropisms as LOEB. In his chapter on "The distribution of associative memory in the animal kingdom" ('02, p. 224), LOEB says, "Although I heartily sympathize with BETHE's reaction against the anthropomorphic conception of animal instincts, I yet believe that he is mistaken in denying the existence of associative memory in ants and bees."

After the space occupied in attempting to show that the "assimilation" and "determination of stimulus" hypotheses do not adequately account for the conduct of home-going ants, I fear that by "associative memory" I may be misunderstood to mean some high type of rational life. Therefore, I wish to emphasize the fact that I use the term as LOEB uses it in the quotation with which this section opens.

VI. DOES DIVISION OF LABOR AMONG ANTS SIGNIFY MUTUAL COÖPERATION?

In the course of my experiments many examples of division of labor have been noticed. I have known one set of workers to store the pupæ under the incline, or in a dark chamber, or on the stage in the open, while yet other workers conveyed them from these places to the nest. I have seen one set of workers lay pupæ down on the island, while a different set carried them into the nest. I have even seen cases where one set laid the pupæ down in the feed chamber, from which another set carried them into the nest proper. I have noticed similar examples of division of labor in most of the species experimented upon. It was with *Prenolepis imparis*, however, that I took pains to investigate it carefully. Here we have one set of workers bringing pupæ to a certain spot

whence they are carried further by another set of workers. Each set does its share, and between them the work is quickly accomplished. Thus stated, these facts suggest the thought that these coöperating ants must have some kind of mutual understanding.

I am constrained, however, to add a statement which will give a different interpretation to the act. In all of the cases of coöperation observed by me, the pupæ were carried into the nest by workers which, roaming from the nest, by chance discovered them. The workers that stored the pupæ under the incline, those that hid pupæ in the dark chamber, and those that piled them in the open on the stage, were ants which, being unable to find the way home disposed of the pupæ in these special ways. Those that laid them on the island simply brought the pupæ thus far and laid them down. They did not go to the nest, nor did they touch with their antennæ any of the ants that subsequently carried these pupæ to the nest. In all of the cases mentioned, some worker or workers, roaming from the nest, discovered the pupæ and carried them home. The only observations that did not accord completely with the above statement, were those few cases in which the workers from the stage deposited the pupæ in a group of ants that was swarming against one side of the nest. In that case, it was impossible to be sure that some of those did not assist the stragglers from the nest in carrying the pupæ. Even in that case, I could detect no evidences of communication between the ants from the stage and those from the nest. These observations warrant the assertion that each case of division of labor observed by me was the result, not of mutual understanding, but rather of accidental coöperation.

On re-reading MOGGRIDGE's (ROMANES '92, p. 98) account of ants dropping leaves for other ants to pick up, LESPE's (*ibid.*, p. 99) account of "regular depots for their provisions," and BELT's (*ibid.*, p. 99) account of ants casting down burdens for other ants to carry, I cannot help but feel that had these special cases been observed from the beginning, they would have proved to be of the same type as those described above. Any one acquainted with the habits of ants who reads MOGGRIDGE's account of the coöperative dismemberment of a grasshopper by ants, is certain to be reminded that any large insect dropped in the midst of ants is sure to be independently attacked from all sides by ants which, acting as individuals, gnaw and pull away from the object.

MOGGRIDGE (*loc. cit.*, p. 98) tells us that the grasshopper was "too large to pass through the door, so they tried to dismember it. Failing in this, several ants drew the wings and legs as far back as possible, while others gnawed through the muscles where the strain was greatest. They succeeded at last in thus pulling it in." It is a pity this account is so meager. If there were only two ants to each member, one pulling it out and the other gnawing at the place of greatest strain, we would have an undoubted case of intelligent coöperation; whereas, if there were a large number of ants attacking each member, the fact that some happened to gnaw at the point of greatest strain does not prove intelligence. To repeat, there is nothing in the anecdote, as recorded, to show that this was was not a case of accidental rather than of mutual coöperation.

A case cited by ROMANES ('92, p. 99) is so remarkable that I quote it in full. "In Herr GREDLER's monastery, one of the monks had been accustomed for some months to put food regularly on his window sill for ants coming up from the garden. In consequence of 'Herr GREDLER's communications, he took it into his head to put the bait for the ants, pounded sugar, in an old ink stand, and hung this up by a string to a cross piece of the window and left it hanging freely. A few ants were in the bait. They soon found their way out over the string with the grains of sugar and so their way back to their friends. Before long a procession was arranged on the new road from the window sill along the string to the spot where the sugar was, and so things went on for two days, nothing fresh occurring. But one day the procession stopped at the old feeding place on the window-sill and took the food thence without going up to the pendant sugar jar. Closer observation revealed that about a dozen of the rogues in the jar above were busily and unwearyingly carrying the grains of sugar to the edge of the pot and throwing them over to their comrades down below."

Remarkable? Yes; but before passing judgment, let us recall a few results of experiments. It is a common occurrence to have different ants of the same species doing different things at the same time. I have had a portion of the ants of a colony busy conveying pupæ into an artificial nest, while the remainder were industriously excavating holes in the sand. Likewise, in my cardboard stage experiments, I have observed at one and the same time, one set of ants storing pupæ under the incline, another set

conveying pupæ to the nest, and yet another set piling the pupæ in the center of the stage.

Time and again, when ants were busy conveying pupæ from the stage to the nest, I have dropped pupæ in the path of ants returning from the nest. I have tried this experiment with all the species of ants considered in this paper; and, without exception, the pupa was picked up and carried into the nest.

In the light of these facts, let us consider Herr GREDLER's account. In this case the ants had learned the way from the sugar, by way of the string, wall, window-sill and wall to their nest. Now had a small number of these ants begun to pile the sugar on the edge of the bottle, from which most of it would surely have fallen to the window-sill, the case would have been similar to the one where one portion of one of my colonies conveyed pupæ from the stage to the nest, while another portion piled the pupæ at a certain place on the stage. But the falling of a portion of the sugar to the window-sill, which was a portion of the pathway of the ants returning from the nest, would introduce a modifying variation. As soon as a returning ant encountered a grain of sugar, it would pick it up and carry it to the nest. And if the grains fell from the rim of the bottle fast enough, we should soon have no ants taking the trip up the string. Thus would be produced a behavior which simulates mutual coöperation. Since Herr GREDLER failed to observe the stages by which the continuous line of ants was transformed into two distant yet coöperating lines, this anecdote has no value as evidence proving that ants rationally coöperate.

To sum up the results of this section, it is quite probable that division of labor of the type mentioned above is of rather common occurrence among certain ants; but until new data are forthcoming, we must consider all such cases as coincidences, rather than as proofs of rational coöperation.

VII. CONCLUSIONS.

1. In their journeys, the movements of ants are not tropisms.
2. Ants are not as slavishly guided by the scent of their footprints as is usually believed, for all of the species examined by me could be trained to pass over at least twelve inches of an unscented path. This discovery furnishes an easy means of investigating many problems in ant psychology.

3. LUBBOCK was right when he said, "In determining their course ants are greatly influenced by the direction of the light."

4. The color of the pathway has no, or little, effect on the home-going of ants. There are a few doubtful cases where the hue may have had some effect. There are many in which pronounced changes in the brightness of the pathway seem to affect the ants.

5. In their wanderings, ants are influenced by olfactory (*i.e.*, topochemical), optic, auditory, kinesthetic and tactile stimuli.

6. Ants seem to have fairly definite impressions of direction in both horizontal and vertical planes, and also impressions of distance.

7. They are enabled to take long round trips by learning by experience and retaining what they thus learn.

8. They have associative memory.

9. Such cases of division of labor as ROMANES—quoting from MOGGIDGE, LESPES, BELT and Herr GREDLER—describes in his "Animal Intelligence," are to be looked upon as cases of coincidence rather than as examples of mutual coöperation.

10. In their home-goings, ants display marked individual variations.

11. They are not guided by a homing instinct.

12. While conducting these experiments, I have made many observations, unrecorded in the body of the text, which show that WHEELER is right in emphasizing the high development of the female, for the winged females often take part in the regular duties of the nest. I have had them learn the way home from new situations and assist the workers in carrying the pupæ home.

13. The males seem unable to solve even the simplest problems.

14. The major workers of *Pheidole*, which ERNEST ANDRÉ claims function as soldiers and do not take any active part in the ordinary work of the nest, frequently assist the workers in making excavations and, occasionally, assist in conveying pupæ from one place to another. I have never noticed one continue to carry pupæ for any considerable length of time. This statement is based upon numerous observations which were omitted from the body of the text on account of lack of space.

15. Ants are much more than mere reflex machines; they are self-acting creatures guided by memories of past individual (ontogenetic) experience.

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EXPLANATION OF FIGURES.

In all of the figures the successive ordinates represent minutes of time. In Figs. 1 to 6 (see text, p. 382) each abscissa represents an experiment in the series tabulated and each ordinate the time in minutes that elapsed in that case from the beginning of the series until the first pupa was carried to the nest. These experiments were conducted on ants acting in concert, the purpose being to see if ants retain what they gain by experience. In the remainder of the figures the abscissæ represent successive trips to the nest. When a line terminates in an arrowhead, that indicates a failure. In all curves any time less than a quarter of a minute is considered zero.

PLATE II.

FIG. 1. Learning curve of *Myrmica punctiventris* Rog., acting in concert, showing how easily it is affected by even slight changes in the environment, and that it has not a homing instinct.

1. June 21, 7:30 a.m. Apparatus, a cardboard stage connected on the right to the island by means of a cardboard incline (A).

2. Do. 2:45 p.m. Same apparatus as before. The ants have had a rest of two hours and thirty-five minutes.

3. June 22, 11:08 a.m. Same apparatus as before. The ants have had a rest of twenty hours and twenty-three minutes.

4. Do. 2:35 p.m. Same apparatus as before. The ants have had a rest of one minute.

5. 3:56 p.m. Same apparatus as above. The ants have had a rest of twenty-six minutes.

6. Do. 4:48 p.m. Same stage as before, but the scented incline is placed on the left side of the stage and a new unscented incline (B) placed where the scented incline had been. The pupæ were all carried down the new incline. No larvæ were carried down the old incline; one worker started down the old incline and then returned to the stage. Occasionally, a worker would ascend the old incline from the island. The ants had rested one minute.

7. June 23, 10:40 a.m. Same apparatus as before. Workers carry the pupæ down incline B to the nest; other workers convey pupæ down incline A and store them under its foot, thence stragglers from the nest convey them to the nest. The ants had rested twenty-nine hours.

8. July 11, 9:15 a.m. A new cardboard stage, a new incline and all (even the nest) was placed on a new island. The figure indicates a failure but does not indicate how great. Those ants were lost for over twelve hours. At 9:50 p.m. when I left the laboratory, they were resting quietly on the stage. Sometime before 8:30 the next morning they found the way to the nest (see text, p. 379).

9. July 13, 7:54 a.m. Same apparatus as above. The ants had rested a day and had had a chance to become acquainted with the island.

10. July 24, 9:15 a.m. A cardboard stage from which one incline passed to the island. A dark chamber opening upon the stage and also upon the incline, was placed over the top of the incline. All the pupæ were stored under the dark chamber, none were carried to the nest. The workers went to the nest and left the pupæ on the stage. The ants had rested eleven days and seventy-four minutes.

FIG. 2. Learning-curve of *Prenolepis imparis* Say, showing that the homing of ants is not a chemotropism and that ants can learn a new way home when the way they once knew has been removed.

1. June 24, 7:38 a.m. A new cardboard stage with a new incline (A) attached to the left side.

2. Do. 2:46 p.m. Same apparatus as above. The ants had rested three hours and forty-six minutes.

3. Do. 3:10 p.m. Same apparatus as above. The ants had rested ten minutes.

4. Do. 3:20 p.m. Same apparatus as above. The ants had rested four minutes.

5. Do. 3:40 p.m. Same apparatus as above, only I added incline *B* to the right side of stage, so that now incline *A* is on the left and incline *B* on the right. The ants carried the pupæ down *A*, none were carried down *B*.
6. Do. 3:58 p.m. Same apparatus as above. The ants had rested seventeen minutes.
7. Do. 4:20 p.m. Same apparatus as before, only inclines *A* and *B* were made to change places. All the pupæ were carried down *B*, none were carried down the scented incline *A*. The ants had rested one minute.
8. Do. 4:40 p.m. Same apparatus as above. No pupæ carried down *A*. The ants had rested one minute.
9. Do. 5:06 p.m. Same apparatus as above. The ants had rested one minute.
10. June 26, 7:12 a.m. Same apparatus as above. All the pupæ were carried down *B*, a few unburdened workers occasionally promenaded on *A*. The ants had rested one day, thirteen hours and forty-nine minutes.
11. Do. 7:42 a.m. Used the same stage but turned it bottom side up, thus making practically a new stage. The same inclines were used in the same position, *A* on the right and *B* on the left. All the pupæ were carried down *B*, none were carried down *A*. The ants had rested two minutes. (An unburdened worker went down *B* to the nest one minute after the ants were placed on the stage.)
12. June 26, 8:11 a.m. Same stage, but inclines *A* and *B* are both removed and a new incline *C* placed where *A* had been; this left no incline at the place where the ants had been descending and an unscented incline on the other side. The ants pick up pupæ and go immediately to the place where *B* had been. Failing to find *B*, they become much confused. They return over and over again to that point and reach down as though hunting for something. Finally they carry the pupæ down *C* to the nest. The ants had rested twenty-nine minutes.
13. Do. 9:42 a.m. Same apparatus as above. Several workers convey pupæ to where *B* had been. The ants had rested two minutes.
14. Do. 10:09 a.m. Same apparatus as above. The ants had rested two minutes.
15. Do. 10:30 a.m. Same apparatus as above. The ants had rested one minute.
16. Do. 11:02 a.m. Same apparatus as above, only I added a new incline *D* to the left side of the stage. The majority of the pupæ were carried down *C*; only two pupæ were carried down *D*. The ants had rested four minutes.
17. Do. 11:24 a.m. Same apparatus as before, only *C* and *D* were interchanged, so that we now had the unscented path *D* in the path the ants had been traversing. The majority of the pupæ were carried down *D*, only three were carried down *C*. The ants had rested nine minutes.
18. Do. 6:55 p.m. Same apparatus as above. The ants had rested one hour and two minutes.
19. Do. 7:18 p.m. Same stage, but I replaced *C* by *D* and placed a new incline *E* where *D* had been. The majority of the pupæ were carried down *D*. The ants had rested two minutes.

FIG. 3. Learning-curve of *Prenolepis imparis* acting in concert, showing lapse of memory, the effect of light rays, interruptions of the path, etc.

1. June 27, 9:42 a.m. A new cardboard stage with new incline *A* descending from its left side to the island.
2. Do. 10:55 a.m. Same apparatus as above. The ants had rested two minutes.
3. Do. 11:20 a.m. Same apparatus as above. The ants had rested one minute.
4. Do. 12:15 a.m. Same apparatus as above. The ants had rested thirty-five minutes.
5. Do. 12:30 p.m. Same apparatus as before, only there is a vertical gap of 1 mm. between the foot of the incline and the island. The ants had rested four minutes.
6. Do. 1:15 p.m. Same apparatus as before, but the vertical gap is increased to 4 mm. The ants had rested ten minutes (see text, p. 410).
7. Do. 2:35 p.m. Same apparatus as before, only the 4 mm. gap was horizontal instead of vertical. The ants had rested forty-two minutes.
8. June 28, 10:55 a.m. Same apparatus as before only the ants must cross a horizontal gap of 4 mm. to a pile of slides and down them to the island. The delay was caused by the gap. They went down to the gap and there hesitated, many returning to the stage. This was unexpected, since only yesterday they had been trained to cross a horizontal gap of that kind. The ants had rested twenty-two hours and twenty minutes.
9. July 10, 7:16 a.m. A cardboard stage from which an incline ascends to the nest. The ants had rested thirteen days, twenty hours and eleven minutes.
10. Do. 7:55 a.m. Same as above. The pupæ had rested four minutes.
11. Do. 8:46 a.m. Used same stage and incline but rotated the stage through 180°. Incline in same position. This gave an unscented path from pupæ to the incline. The ants went direct to the incline. The ants had rested one minute.

12. Do. 9:30 a.m. Same stage, substituted incline *B* for *A* and placed incline *A* on the opposite side of the nest. The ants had rested five minutes. (At the beginning a worker went, unburdened, up incline *B* to the nest, but did not return to the stage.)

13. July 25, 7:30 a.m. A stage from which incline *A* descends from the left side to the nest. It was illuminated by a 16 c.p. incandescent lamp placed near to the off-side of the incline. The ants had rested fifteen minutes.

FIG. 4. Learning-curve of *Formica fusca* var. *subsericea* Say, acting in concert; showing the effect of frequent changes of environment.

1. July 1, 8:30 a.m. A cardboard stage with an incline attached to the left side.
2. Do. 9:00 a.m. Same as above. The ants had rested ten minutes.
3. Do. 9:10 a.m. Same as above. The ants had rested one minute.
4. Do. 9:33 a.m. Same as above. The ants had rested one minute.
5. Do. 10:33 a.m. Same as above. The ants had rested three minutes.
6. Do. 11:00 a.m. Same as above. The ants had rested one minute.
7. Do. 3:30 p.m. The same stage used in the above, but a new incline *B* is substituted for incline *A*. *A* is then attached to the opposite side of the stage. The majority of the pupæ were carried down incline *B*. At first, occasionally, a worker would carry a pupa down *A*, but in each case that worker moved much slower than those moving down *B*. The ants had rested four hours.
8. Do. 4:40 p.m. A new stage and a new incline. The ants had rested one hour.
9. July 6, 11:24 a.m. A new stage with a new incline on the right side (the other inclines had been on the left side). The ants had rested four days, fourteen hours and thirty-four minutes.
10. Do. 12:28 p.m. Same apparatus as above. The ants had rested one minute.
11. July 6, 2:25 p.m. Same apparatus as above. The ants had rested five minutes.
12. Do. 3:00 p.m. Same stage, but incline *A* was placed on the opposite side of the stage and a new incline *B* placed where *A* had been. The pupæ were all carried down *B* to the nest, occasionally a worker would carry a pupa partly down *A* and then return to the stage. The ants had rested thirteen minutes.
13. July 10, 7:55 a.m. A new stage with a new incline attached to the right side of the stage. The ants had rested four hours and twenty-five minutes.

FIG. 5. Learning-curve of *Prenolepis imparis* Say acting in concert, showing unexpected variations in the mode of response.

1. July 9, 7:31 a.m. A cardboard stage with an incline *A* attached to the left side.
2. Do. 10:46 a.m. Same apparatus as above. The ants had rested one minute.
3. Do. 8:05 p.m. Same apparatus as above. The workers had rested over nine hours.
4. July 10, 6:30 a.m. Same apparatus as above. The ants had rested eight hours and ten minutes.
5. Do. 7:55 a.m. Same apparatus as above. The ants had rested ten minutes.
6. Do. 9:35 a.m. Same stage, a new incline *B* is substituted for *A* and *A* is placed on the opposite side of the stage. The ants had rested ten minutes.

FIG. 6. Learning-curve of *Prenolepis imparis* Say acting in concert, showing the effect of the direction of the rays of light and the result of placing a dark chamber over the top of the incline.

1. July 9, 7:06 a.m. A cardboard stage with incline *A* on left side.
2. Do. 8:16 a.m. Same apparatus as above. The ants had rested one minute.
3. Do. 9:55 a.m. Same apparatus as before. The ants had rested one minute.
4. Do. 10:45 a.m. Same apparatus only the stage was revolved through an angle of 180°, but the incline was left in the same position. Thus there was an unscented path from the pupæ to the incline. The ants had rested six minutes.
5. July 10, 6:30 a.m. Same apparatus as before. The ants had rested twenty hours.
6. Do. 9:08 a.m. Same as above only the stage was revolved through 180°, *A* was left in the old place. Thus there was an unscented path from the pupæ to the incline.
7. July 11, 6:28 a.m. Same apparatus as above. The ants had rested twenty-one hours.
8. Do. 7:21 a.m. Same apparatus as above. The ants had rested fifty minutes.
9. July 12, 7:46 a.m. A new cardboard stage with a new incline leading down to the island. A 19 c.p. incandescent lamp was placed near the incline. The ants had rested one day and twenty-five minutes.
10. Do. 8:53 a.m. Same apparatus as before. The ants had rested three minutes.
11. July 13, 7:11 a.m. Stage with incline *B* on the right. 16 c.p. lamp on the same side as *B*. The ants had rested forty-nine minutes.

12. Do. 8:05 a.m. Same apparatus as above, only a dark chamber opening upon stage and incline was placed over the top of the incline. One set of workers conveyed pupæ to the dark chamber; another set, stragglers from the nest, conveyed them from the dark chamber to the nest. The delay represents the time that elapsed before a straggler from the nest discovered the pupæ in the dark chamber. The ants had rested nine minutes.

13. July 16, 7:39 a.m. Same as above. The workers had rested two days, twenty-one hours and fifty-nine minutes.

14. Do. 2:07 p.m. Same apparatus as above. The delay was caused because they stored all of the pupæ in the dark chamber before any were carried into the nest. The ants had rested four hours and a half.

FIG. 7. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing lapse of memory, etc.

Apparatus. Two cardboard stages, 1 and 2; inclines *D* and *E* leading to the island from each, respectively. The feet of the inclines were side by side. Each was attached to the right side of the stage. The marked worker was placed on stage 2 (see p. 412).

A. On trips 6 and 7 the pupa was taken from stage 1 to the nest.

B. On trip 12, do.

C. The worker ascends and descends incline *D*, then ascends and descends incline *E*, then ascends to stage 2 and carries a pupa to the nest.

D. On trip 36 the pupa was taken from stage 1.

E. On trips 43-45, do.

F. On trip 50, do.

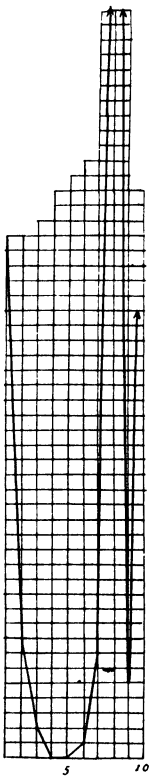


Fig. 1

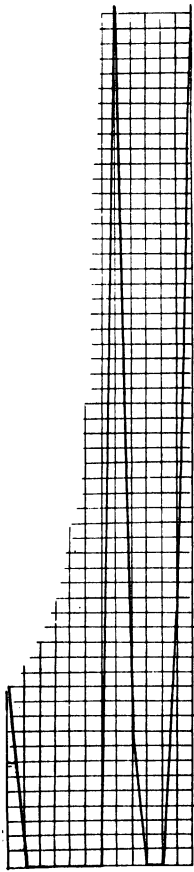


Fig. 3

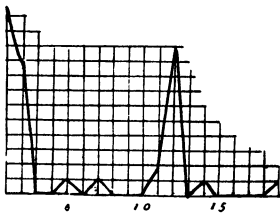


Fig. 2

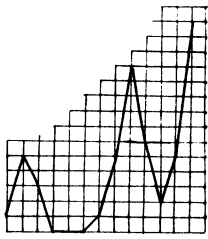


Fig. 4

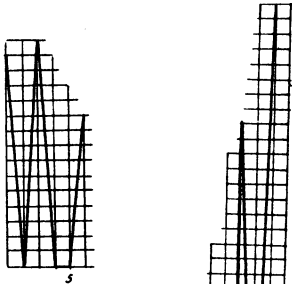


Fig. 5

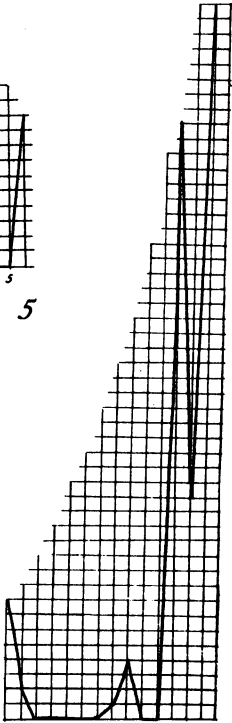


Fig. 6

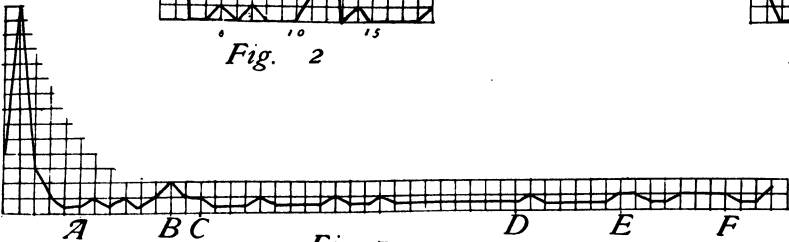


Fig. 7

PLATE III.

FIG. 8. Learning-curve of an individual *Myrmica punctiventris*, showing its reactions to colored pathways.

Apparatus, cardboard stage with a red incline leading down to the island; illuminated by diffuse daylight.

- a. While the worker was on the stage a new red incline was substituted for the old.
- b. Do. Green for red.
- c. Do. Purple for green.
- d. Do. Blue for purple.
- e. Do. Yellow for blue.
- f. Do. White for yellow.
- g. Do. Red for white.
- h. Do. White for red.
- i. Do. Smooth black for white.
- k. Do. Black with velvety feel for smooth black.

FIG. 9. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing its reactions to odors encountered in its path.

Apparatus, a cardboard stage with an incline passing down to the island. On this stage the pupæ and a marked worker were placed. The worker had made several trips before the first trip plotted here.

A. While the worker was on the stage, I substituted for the incline one with a transverse band of xylol across its middle.

B. I replaced the old incline.

C. While the worker was on the stage I substituted the incline with the transverse band of xylol.

D. While the worker was on the stage the incline with the xylol band was transferred to the control stage and allowed to remain there eight minutes. The ant used for control was much disturbed. During the eight minutes it mounted the incline several times, but would not cross the band.

E. The incline with the xylol band is reattached to stage 1. During the eight minutes that have elapsed the marked ant has made several trips down an unscented incline which was attached to the stage when the incline scented with xylol was removed.

F. The incline with the xylol band is transferred to the control stage and causes the same disturbance as before.

FIG. 10. Learning-curve of a *Myrmica punctiventris*, showing its reactions to light rays and to tactile stimuli.

Apparatus, a cardboard stage with an incline *A* passing from left side to the island. Near the left side of the stage was placed a 16 c.p. incandescent lamp. The room was darkened.

a. While the worker was on the stage the 16 c.p. lamp was transferred to the right side of the stage.

b. While the worker was on the stage, the incandescent lamp was extinguished and the curtain of a window thrown up so as to illuminate strongly the left side with daylight.

c-d. Experiment was interrupted for six minutes.

d. The same stage, but illuminated uniformly by diffuse daylight instead of by an incandescent lamp in a special position. A smooth black incline leads from the stage to the island.

e. While the worker was on the stage the white incline was substituted for the black.

f. Do. Smooth black incline for white.

g. Do. Black incline with velvety feel for the smooth black.

FIG. 11. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing its reaction to a colored pathway.

Apparatus, a cardboard stage with red incline leading down to island, illuminated with diffuse daylight.

a. While the worker was on the stage a new red incline was substituted for the old. The paper on this incline was somewhat wrinkled.

b. Do. Green for red.

FIG. 12. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing effect of a jar upon its behavior, etc.

Apparatus, a cardboard stage with a white incline leading from its right side to the island. A heat-filter composed of a tall rectangular museum jar filled with water was placed near both the right and

left sides of the stage. Behind the heat-filter on the right was placed a 32 c.p. incandescent lamp. Excepting for this light the room was dark.

A. Placed a new white incline on the opposite side from the first incline.

B. While the worker was on the stage the 32 c.p. lamp was placed behind the heat-filter on the side where the second incline was.

C. While the worker was in the nest the light was replaced on the same side as the first incline.

D. While the worker was on the stage I substituted a new white incline for the old. In doing so the stage was jarred considerably.

E. Do. White for black.

F. Replaced the worker on the stage.

G. While the worker was on the island, I substituted a white incline for the black.

H. Do. New white for the old.

FIG. 13. Learning-curve of an individual *Myrica punctiventris*, illustrating one of those occasional cases in which it took the ant much longer to make the second trip to the nest than it did to make the first.

Apparatus, two cardboard stages, each with an incline leading down to the island. Pupæ are placed on both stages. The marked worker is placed on stage number one.

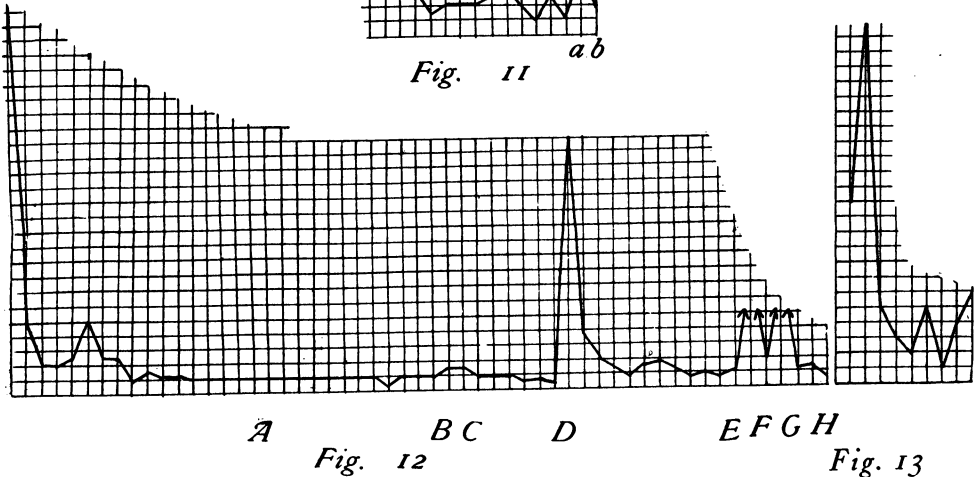
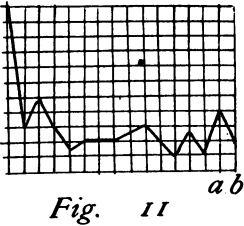
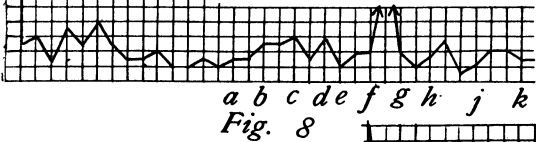
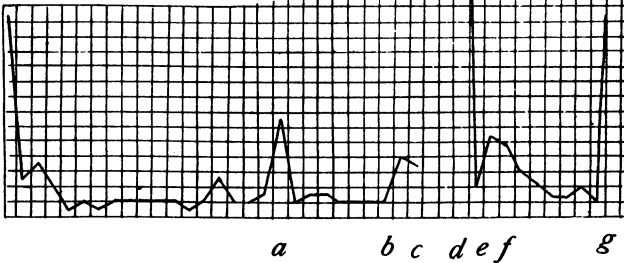
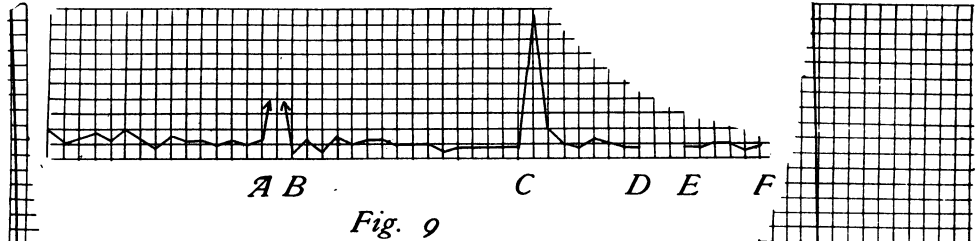


Fig. 13

PLATE IV.

FIG. 14. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, illustrating its reaction to changes in the direction of light, to colored pathways, and to tactile stimuli.

Apparatus, a cardboard stage with a white incline leading from the right side to the island. A 16 c.p. lamp is placed on the same side of the stage as the incline. Throughout the whole of this part of the experiment the worker ascended to the stage on the top side of the incline, and descended to the island on the lower side.

- A. Placed a new white incline on the side opposite the old incline.
- B. While the worker was on the stage, the 16 c.p. was transferred to the opposite side of the stage.
- C. Replaced the light on the same side as the incline.
- D. While the worker was on the stage, I transferred the light to the opposite side of the stage.
- E. I replaced the light in former location.
- F. While the worker was on the stage, I substituted a smooth black for the white incline.
- G-H. The experiment was interrupted from 7:41 p.m. to 8:41 a.m.

H. The same stage, but a red incline is substituted for the white and no artificial light is used. In this section of the experiment the worker goes in almost a straight line from the foot of the incline to the side of the nest and then to either the right or the left (for it does not always follow the same line) to the nest; but in returning to the incline it meanders a great deal.

- I. While the worker was on the stage, I substituted a new red incline for the old red one.
- K. While the worker was in the nest, a green incline was substituted for the red.
- L. While the worker was on the stage, a purple incline was substituted for the green.
- M. While the worker was on the stage, I substituted a yellow for the purple incline.
- N. While the worker was on the stage, a blue incline was substituted for the yellow.
- O. While the worker was on the stage, a smooth black incline was substituted for the yellow.
- P. While the worker was on the stage, a black incline with velvety feel was substituted for the smooth black.

FIG. 15. Learning-curve of an individual *Myrmica punctiventris*, showing its reactions to colored pathways, etc.

Apparatus, a cardboard stage with an inclined plane leading down to the island. Illumination, diffuse daylight. During the first twenty-three trips the pupæ were carried only so far as the base of the incline; from there other workers conveyed them to the nest.

- A. While the worker was on the stage a new white incline was substituted for the old.
- B. Do. Smooth black for white.
- C. Do. Black with velvety feel for smooth black.
- D. Do. Red for black.
- E. Do. Green for red.
- F. Do. Purple for green.
- G. Do. Yellow for purple.
- H. Do. Blue for yellow.
- J. Do. White for blue; placed a 16 c.p. incandescent lamp on the same side of stage as the incline and darkened the room.

FIG. 16. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing the effect upon its behavior of a change in the direction of the light rays.

Apparatus, cardboard stage with incline descending to the island.

A. Between 24 and 25 the experiment was suspended for one hour.

B. Between 49 and 50 the experiment was suspended for four hours and twenty-six minutes.

From B to C the ant was working at night by lamplight and the direction of the rays was from the northeast. The rest of the work was done by daylight and the direction of the rays of light was from the south and west (see p. 400).

C. Between 66 and 67 the experiment was suspended for eleven hours and twenty-six minutes.

FIG. 17. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, showing its reactions to changes in the direction of the rays of light.

Apparatus, a cardboard stage with a white incline leading from the right side to the island. A 4 c.p. incandescent lamp was placed near the right side of the stage; otherwise the room was dark.

- A. While the worker was on the stage, I substituted a 32 c.p. lamp for the 4 c.p.
- B. While the worker was on the stage, I transferred the 32 c.p. to the left side of the stage.

- C. Do. The 32 c.p. to the right side.
- D. While the worker was on the stage, I substituted an 8 c.p. lamp for the 32 c.p.
- E. While the worker was on the stage, I transferred the 8 c.p. lamp to the left side.
- F. Do. 8 c.p. lamp to the right side.
- G. While the worker was on the stage, I substituted a 4 c.p. for the 8 c.p.
- H. While the worker was on the stage, I transferred the 4 c.p. to the left side.
- I. Do. 4 c.p. lamp on the right side.
- K. While the worker was on the stage, I substituted a 32 c.p. lamp for the 4 c.p.
- L. While the worker was on the stage, I placed the 32 c.p. at the back of the stage.
- M. Do. 32 c.p. at the front of the stage.

FIG. 18. Learning-curve of an individual *Formica fusca* var. *subsericea* Say, illustrating its reactions to odors of the pathway and to tactile stimuli.

Apparatus, cardboard stage with white incline on the left. Illumination by incandescent lamps; practically uniformly illuminated.

- A. While the ant was in the nest, a new white incline was substituted for the old.
- B. The old incline was substituted for the new.
- C. While the worker was on the stage, a new white incline was substituted for the old.
- D. Do. an incline with a three-fourths inch transverse band of oil of cloves across its middle was substituted for the other.
- E. Replaced the old incline.
- F. Do. an incline with middle three-fourths inch band of xylol for the other.
- G. Do. with fresh xylol band.
- H. Do. with fresh band of cedar oil.
- I. Do. with fresh band of oil of cloves.
- K. Do. with unscented white incline.
- L. Do. with smooth black incline.
- M. Do. with black incline with velvety surface.

