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MANIPULATORY LEARNING IN ANTS

Jan DOBRZAŃSKI

Department of Neurophysiology, Nencki Institute of Experimental Biology, Warsaw 22, Poland

Initially, the aim of my work was to study hereditary building reactions of ants and effects of great individual variability of these animals' behavior on the social performance of the function of building nests. In the course of the studies, which required observation of particular individuals, it turned out, however, that the differences in the ants' behavior did not resolve themselves only into those between individuals, which more than once have been noted by many investigators. It was also the behavior of various individuals during the performance of a given building function that was subject to changes in the course of time.

The last-named phenomenon was new enaugh to become quite naturally the central subject of my further studies. Thus, the variability in the behavior of worker ants as they performed their building functions, its sources and character have ultimately become the aim of my work.

MATERIAL

The structures of nests of various species of ants have been described by many authors, whereas the process itself of building them and the ants' building activity have been dealt with in only a few investigations. This fact may be explained by the existence of countless equally important and fascinating problems in the life of social insects. In addition, great methodical difficulties are encountered in the course of studies on the construction of the ants' nests. To begin with, the construction of a nest takes place throughout its existence and together with its expansion. Depending on changes in environmental conditions, changes are also constantly introduced into the architecture of a nest. There is no final,

perfect form, the attainment of which might be objectively noted by an investigator.

The course itself of building processes depends on so many external and internal factors (a current biological state of a given community, the age of a nest, the season of the year, the weather, and many accidental factors) that they are almost imperceptible for an observer. For instance, we can never decide whether building work has been stopped at a given moment bacause there was no demand for it (that is, because the current architectonic state of the nest met the requirements), or, on the other hand because it was a symptom of the community's disorganization (caused by, for instance, the lack or barrenness of the female ant). It may also mean that the nest has ceased to suit its purpose and that a removal is being prepared, or that a social demand has arisen for performing other operations more urgent at a given moment. I have mentioned a few exemplary causes of the lack of building activity in a given nest. The heart of the matter resolves itself into the fact that so far we are unable to estimate objectively either an actual demand for, or a purposefulness of the construction of an ant nest.

After a long search, I have found that the easiest thing is an objective estimation of the construction, in particular the repair work, of a mound of ants of the genus *Formica*. My observations have shown that there are possibilities of estimating adequately the repair work done in an anthill.

My fundamental studies have been conducted on the species *Formica rufa* L. and *Formica exsecta* Nyl.

METHODS

1. Objective estimation of the quality of work done by the ants

My studies were in principle conducted by recording the behavior of worker ants, which carried and deposited building materials on the mound. However, it is difficult to estimate objectively a usual arrangement of this material on the surface of the mound. Although I succeeded in observing certain regularities governing the construction of the mound, they were insufficient as a *comparable* criterion of purposefulness of one or another arrangement of building materials.

On the other hand, on the basis of many observations, I succeeded in finding certain constant principles which ruled the repair operations on the nest done by workers of the genus *Formica*, such as, putting right the defects, stopping openings and smoothing the surface of the mound. Finding these rules allowed me for an objective estimation of the activities of particular individuals.

The method consisted, therefore, in making artificial, stereotyped

breaches in a mound and, afterwards, observing the repair activity and quality of work done by particular workers. This had also the additional advantage of evoking to a certain extent an artificial building activity.

2. Individual marking of the builders

The studies of individual differences observed during the performance of building operations required an individual marking of building workers, which was done by means of leather dyes.

3. Recognition and marking of beginner builders

A very difficult methodological problem arose as a result of focusing my main studies on changes in the behavior of particular workers. To study the changes in the behavior of an individual as it performed a building function, a method had to be developed of recognizing workers which were *beginners* in such a work.

A building function is frequently the first activity of a young worker outside its nest. Thus, the problem was reduced to an apparently easy task of marking and observing young workers as they came out of the nest for the first time. As a matter of fact, this was not so easy as it seemed. It is a well-known fact that young workers only reluctantly leave their nest. In the genus *Formica,* under normal conditions, they come out of it only after hardening and darkening of their chitin and, therefore, when getting out of the nest they are practically indistinguishable by appearance from those which already frequently saw the light of day.

Quite young, still light-colored individuals might have been taken out of the nest, marked, and observed when some of them would have left the nest after some time. This method, relatively the easiest to apply, had to be rejected for the following reasons:

1. It causes a considerable damage to the nest and disturbs the normal mode of life.

2. It increases to a considerable extent the demand for the building activity and, consequently, attracts to it workers whose history is unknown to the investigator.

3. It causes panic and attracts masses of very restless and agitated workers which, coming to the surface of the nest, disturb the observation of a relatively small number of those busy with construction.

4. And, what is most important, it prematurely stimulates very young individuals, which might be still too immature physiologically to perform outdoor functions, to come out of the nest (Goetsch 1953, Dobrzańska 1959); their behavior may, therefore, be nontypical and mislead an investigator.

After many trials, the most effective method turned out to be marking workers which were carrying out pupae from the nest to expose them to the sun after a night chill or rains. Some of these ants are permanent caretakers who will return to their functions inside the nest, but some others are young individuals who, owing to the necessity of carrying the pupae out of the nest, for the first time overcome their reluctance to meet the outside world (it may be supposed that, since the life of the offspring is at stake, the stimuli coming from the chilled or moist pupae, are stronger than this reluctance). Some of them have matured sufficiently for coming out of the nest and this compulsory overcoming of the reluctant attitude causes their permanent switch-over to the performance of outside functions.

The marking with dye of all individuals carrying out pupae, allows the investigator to distinguish the ants which, after carrying the pupae back to the nest, reappear on the surface and for the first time undertake outward functions. Such workers are then permanently marked by wire rings (Dobrzański 1966). The ring becomes a common mark of an entire group of beginner workers which start their activity outside the nest, while the dye is their individual badge, enabling the identification of particular specimens.

After these preliminary operations, the investigator may finally start his detailed studies.

Unfortunately, as is clear from the description of the method, the very slow selection procedure provides the investigator with only a few workers which may serve as material for further investigation. Besides, it should be borne in mind that by far not all workers with our marks will subsequently undertake their building activities and that yet fewer of them may be observed many times during these activities, which is necessary for studying possible changes in their behavior that take place during the performance of these operations. This is the reason my studies took many years and why, of the vast number of notes and records, only those have been selected which deal with a small number of individuals which could be observed sufficiently frequently to enable conclusions about the changes in their behavior.

RESULTS

I. The search after hereditary building reactions

Experiment 1

Observing workers as they seize sticks, laying about on the nest, we may easily distinguish two absolutely different types of behavior (not mentioning transitional forms of behavior):

Type 1. The ant seizes a stick by the end and, if it is light enough, carries it in front of itself so that the other end does not touch the ground; if the stick gets stuck in some obstacle, the ant moves back, disentangles it and, afterwards, continues walking in the previous direction. If, on the other hand, the stick is heavy, the ant drags it by the end, walking backwards; if it gets stuck, the animal seizes it by some other part or, instead of dragging, pushes the stick, thus loosening it from the obstacle. In both cases, the sticks are deposited on top of the dome or in the place of repair. In the case in which the stick offers a strong resistance, the ant promptly abandons it and grabs another one.

Type 2. The ant steps on the stick with all its limbs and, not changing this position, jerks it sometimes for as long as five minutes without any observable effect.

These two types of behavior may be concisely described as follows:

Type 1. The ants efficiently carry the sticks and repair their mound.

Type 2. The ants pull at the sticks which do not move at all.

The individual marking of all ants which seize the building material, has revealed that there are *two groups of workers* who correspond to *the two types of behavior*. In other words, each of the ants observed could be assigned to a definite type of behavior. This was in complete conformity with the existing opinion on the individual variability in the behavior of ants.

Experiment 2

It remained to determine whether the behavior of the second group of workers was concealing the same tendency as that in the first group (that is, to carry the sticks onto the summit of the mound and to repair it), but were only thwarted by their inefficient performance, or some different tendency, imperceptible to the observer. For this purpose, using pincers I took 1 cm long sticks, easy for ants to carry and too short to be seized with jaws when standing on them, and threw them to the workers of the second group. They seized them and carried them uphill (not always to the very top), much in the same manner as the workers of the first group.

Thus, the tendency to seize building materials and carry them onto the top of the nest is common to all workers, who only differ in the degree of efficiency with which they follow this tendency.

Experiment 3

At the moment when a worker of the second, inefficient group seized a small stick offered to it, I held back the other end of the stick with

pincers. Then, a similar situation arose as that described in experiment 1, that is, the ant jerked at the stick for several minutes, while similar sticks which I had scattered beforehand were loosely lying around the insect.

In the case of an ant of the first group, it promptly abandoned the stick withheld by me and seized another one.

Experiment 4

Instead of holding back the sticks with pincers, I inserted them upright into the hill, which produced quite an unexpected effect. Such sticks were stubbornly and persistently jerked at by the ants of both groups even in the cases in which they were driven deep and offered strong resistance. The ants of the first group, which promptly abandoned the *lying* stick, persisted in jerking at the vertical one even for 30 min. When it lasted for a long time, many workers flocked together around the stick and tugged at it in a common effort until the stick was pulled out of the ground and laid down in a position horizontal (in relation to the surface of the mound).

A similar experiment, but with the use of matches, was conducted by Chauvin (1958) who, however, believed that the ants tried to remove strange objects from their nest. It turns out that even the sticks taken from the dome untouched by man's hand are pulled out with an equal obstinacy as those touched by man. The only difference is the fact that those touched by man, after being pulling out of the ground, are in almost all cases carried down and removed from the surface of the nest, while the remaining ones are thrown down on the spot or used for construction.

On the other hand, no response was observed to the sticks placed horizontally in the wall of an ant-hill.

Experiment 5

I planted a stick in a vertical position into the opening of a nest which was just being stopped by the builders. In doing so, I seemingly helped them in their work, but their response was similar to the previous one: all workers which happened to be nearby started to drag the vertically placed stick outwards. If it was long and heavy, such work might even last for some scores of minutes. I never observed ants which would leave the stick in its vertical position.

The general tendency exists, therefore, to remove the sticks which are placed vertically on the surface of the mound.

Observation

Experiments 4 and 5 brought back to my mind a phenomenon previously observed in the nests of *F. sanguinea*. This species does not as a rule build mounds and only sometimes accumulates some conifer needles or sticks on top of the nest. I observed more than once that these flat nests were on the whole devoid of vegetation even in the case when the nest was situated among tufts of grass or heather. I never gave a good deal of thought to this fact, assuming simply that the plants undoubtedly perished because their roots were undercut below the soil. Now, after the experiments described above, my interest has been aroused — after all, such a twig of heather, growing on the nest, is a sort of a stick vertically "stuck" in it.

I observed a few nests of *F. sanguinea* situated among the tufts of heather. It turned out that almost all shoots projecting from the soil were peeled of bark close to the ground surface. Most of them, already quite dry, fell away, while some others, just withering, were still present. Fresh twigs were systematically barked by the ants. After marking these ants, it turned out that they were the same workers who were engaged in construction.

Thus, barking twigs which grow out of the nest and, consequently, causing their wasting away are among the building functions.

On the one hand, on the basis of the experiments reffered to above we may draw conclusions as to certain constructional mechanisms, but, on the other, the two groups of workers described might be extreme examples of an extensive individual variability in the ants' behavior (which, it must be noted, was generally recorded). In this case, the individual variability would be manifested by a different degree of the skill of applying hereditary building reactions.

However, in the cases in which these experiments were continued for a certain time in one and the same nest, the results described above became less and less clear. Within one or two days, the workers assigned to the second, inefficient group, began to change their behavior, less frequently trod on the stick being just dragged by them, jerked at it for a shorter time when it offered resistance and, finally, more and more rapidly abandoned it to look for another stick. Thus, the differences between both groups of workers, so striking previously, became obliterated with time. Different manners of behavior, which seemed to reflect individual differences, did not prove to be permanent.

For this reason, I was obliged to conduct further observations distributed over longer periods. For this purpose, I had to identify the workers who were beginners in thier building activities (*see Methods*).

II. Studies on the variability of behavior in the course of time

Below, I give some of the typical examples of changes in the behavior of workers during the performance of their building operations, selected from hundreds of observations.

The note "...(first, second, etc.) day of construction" stands for the fact that I can take full responsibility for the determination of a moment at which a given ant began its building manipulations and for the sequence of days on which such operations were performed. For the cases in which I cannot take such a responsibility, the note runs "...(first, second, etc.) day of observation".

If a previously building individual subsequently eluded my observation for a certain time and it was unknown what it was doing in the meantime, it was recorded as "after ... days".

Roman numerals, put on the margins, denote stages of learning (*see Results*).

F. rufa B-26

1st day of construction:

hours:

I
12:00 The ant violently jerks at a stick, at the same time standing on it;
12:10 Gets off the stick and starts jerking at another place;
12:11 The stick begins to move and gets promptly stuck in obstacles; the ant once more steps on it and starts to jerk.

Nothing important was observed.

II
18:05–18:25 Jerks at the sticks; sometimes treads on them, but in a while gets off theem; some of the sticks are moved by the ant but soon are stuck; the ant chaotically tries to change its position and find another place to grasp; at the same time, climbs the stick and at once gets off;
18:25 Cleans itself;

18:28 Enters the nest;
18:55 Gets out of the nest, walks over the top of the mound;
19:35 Enters the nest, does not reappear any more.

After five days:

10:10 Carries the sticks fairly efficiently, but throws them disorderly; the movement of the stick clearly depends on the character of obstacles encountered on the way; being unable to move the stick, the ant abandons it and seizes another one;
15:05 Enters the nest;
15:35 Gets out of the nest but eludes observation.

After 20 days:

V
- 10:20 Builds a dome, carrying sticks and depositing them in a depression on its top; puts them down in one place; if an adjoining stick is pushed during this operation, the ant adjusts its position;
- 12:15 Carries a pine needle split at the end; when one of its ends gets stuck in the ground, jerks a few times and then abandons the needle (*see F. exsecta* B-7);
- 12:16 Ascends the mound carrying a stick, puts it in a depression on the top;
- 13:20 Carries a stick holding it by the end and keeping it in a horizontal position in front of itself; when the front end gets stuck in an obstacle, retreats, raises the stick vertically and thus negotiates the obstacle.

F. rufa Z-3

I
1st day of construction:

- 10:07 Unsuccessfully jerks at the end of a large stick;
- 10:12 Climbs the stick, jerks, standing on it;
- 10:22 Abandons the stick;
- 10:23 Seizes another stick and jerks at it, also in vain;
- 10:35 After chaotic tugging, abandons the new stick;
- 12:20 After jerking at a stick, on which it stands, gets off it and moves it;
- 12:21 A few centimeters further, the stick gets entangled once more; after a few minutes of tugging at it, gives it up;
- 12:30 Climbs another stick and jerks at it;

despite its several successes on this day in moving the stick, each time after getting off the stick, the ant has repeated its error of standing on the sticks and simultaneously jerking at it; a considerable degree of activity.

2nd day of construction:

- 9:25 Working; very active;
- 12:20 Less frequently steps on a stick jerked at;
- 13:10 Jerks at a large stick but rarely climbs it and when it does, rapidly gets off it (of ten jerks, three are performed when standing on the stick);
- 14:02 More and more rapidly abandons a stick when unable to move it;

II
- 15:00 Absent from the nest dome;
- 16:50 Jerking at sticks; changes them quickly until finds one which may be moved; drags them in various directions;
- 18:10 Enters the nest.

3rd day:

Walks over the nest and its vicinity, sometimes enters the nest.

4th day:

The same.

5th day:

Walks about the area but does not build.

6th day (3rd day of construction):

9:55 Building; gives up the sticks which cannot be moved;
10:20 Seizes a stick, drags it; when caught by a knot, the ant tugs at it for a while and then grips in another place thus releasing it from an obstacle; continues dragging it, but in a somewhat different direction;
10:35 Carries a stick; when stuck in the dome, the ant pushes it for a while, then gives it up and takes another one;
III
12:30 On this day, the ant has not even once stepped on the stick it dragged; sticks are moved but rather inconsistently, when stuck, the insect leaves them where they are; according to the observer's estimation, even light sticks, carried high up and which do not get stuck in obstacles, are thrown about disorderly;
16:07 Enters the nest.

F. rufa Y-47

1st day of observation:

16:30 Carries a pine needle; when it has got stuck in the ground, the ant continues pushing and thus driving it yet deeper;
16:43 Runs about the mound; seizes sticks, carries them for some distance and drops them in various places;
I
16:50 Standing on a stick, the ant seizes it and tries to move; every now and then lets it go and seizes in another place a millimeter or so further; finally, gets off it and tries various grips, but the heavy stick continues to resist;
16:57 Gives up the stick.
The ant is very active, rapidly moving.

2nd day of observation:

Does not build; now and again, leaves the nest, walks about for a few minutes and hides.

3rd day of observation:

Similar behavior.

4th day of observation:

10:15 Carries sticks; encountering a difficult obstacle, jerks at a stick for a long time, but never steps on it;
II
11:05 For a longer time, jerks at a stick which turns out to be too heavy; gives it up;
14:30 Carries a large stick uphill; when it has gotten stuck, promptly abandons it;
III
14:55 Carries a small stick onto the top of the mound and drops it there;
15:15 Carries sticks, but drops them in places where they have got stuck.

After 13 days:

16:15 Very active, builds efficiently;
V
16:26 Carries a pine needle, holding it vertically like a banner and thus avoiding obstacles;

V
16:35 Adjusts a stick loosened by its weight;
17:15 Stops up the opening; putting a new stick, each time adjusts the position of former ones if they move under its legs.

F. rufa B-55

1st day of observation:

I
13:55 Tries to move large sticks; very active;
14:00–16:00 All the time, struggles with various sticks, mostly standing on them and devoting a few or more minutes to each of them;
16:17 Seizes a pine needle and drags it behind itself; depending on the terrain configuration changes direction of its movement as if "rebounding" from the obstacles;
16:22 Gets entangled in an obstacle and drops the needle; seizes sticks and promptly lets go of those which have been mounted in the ground by other ants; very rarely steps on a stick, when does promptly gets off;
16:40 Toils, dragging a stick four times as thick as its abdomen and several times longer than its entire body.

2nd day of observation:

II
12:30 Until this hour has not manifested any activity, although by then it has left the nest several times;
17:40 Tries to drag a stick when standing on it, but rapidly gets off it; when it resists even then, gives it up; jerks at another large stick which does not give way; several times tries to seize other large sticks and abandons them after a struggle;
18:05 Holding a small stick by the end, carries it in front of itself; when it meets an obstacle, continues pushing and does not retreat; finally, gives it up; walks back and forth for 3 min; five times seizes heavy sticks and not being able to move them gives up;
18:20 Enters the nest;
On this day, the ant frequently cleaned itself, while on the previous day it worked without intervals.

3rd day of observation:

Walks over the nest but does not build.

After 12 days:

V
11:10 The ant is busy building;
12:00 Efficiently grates the nest opening;
12:10 Carries a stick; when it has got stuck, releases it by a single, strong, backward jerk; walks more than 20 cm from the nest opening, moving along an almost straight line and negotiating obstacles;
13:15 Drags a long stick, holding it some distance from the end; when it has got stuck with its front end, the animal promptly drops the stick, goes to the other end, seizes it and releases the stick from the obstacle by a backward jerk; afterwards, once more takes hold of the front end and continues dragging it behind itself; also drags another stick.

F. exsecta Y-1

1st day of construction:

I
16:10 Standing on a stick, jerks at it for a longer time; after being marked with a dye, scurried away; up to 16:25 is visible in the nest opening.

2nd day of construction:

11:05 Leaves the nest opening and promptly hides in it once again;
11:20 Gets out of the opening, walks about on the dome for 2 min and disappears once again; after a while reappears;
11:55 Seizes a dead fly and drags it over the surface of the dome for a few minutes; afterwards, attempts to pull the fly into the nest opening but does it clumsily, loses it outside the nest and enters the opening;

II
12:25 Seizes a stick, carries it for a few centimeters and drops it;
14:35 Climbs the top of the dome, takes a stick and rams it in the nest nearby; repeats this operation a few times, each time in a new place; when it happens to tread on the stick, promptly gets off it.

3rd day of observation:

10:00–12:15 Walks over the dome, now and then entering the nest, reappearing resumes walking;
15:10 Crouches in the opening of the nest.

4th day of observation:

9:30 Tugs at a stick mounted in the ground; sometimes climbs it but immediately gets off;
10:05 Drags a stick; when it sticks, drops it;
10:30 Efficiently carries a small, one centimeter long stick, drops it near the top of the mound;
10:50 Struggles for a long time with a long stick without treading on it.

F. exsecta B-14

1st day of observation:

14:45 Walks over the nest.

2nd day of observation:

II
12:30 Drags a stick, holding it by its middle; encountering resistance continues dragging without changing position; carries a pine needle, when it has got stuck in the substratum and taken a vertical position, the ant stays for a moment suspended at the upper end of the needle and tries to find a support for its limbs; after a moment, gets off the needle;

III
15:45 Jerks at various sticks, moving some of them; when they resist — drops them;
15:55 Seizes a long pine needle in the middle; when it sticks, drops it;
16:03 Lays down a stick at a distance of 2 cm from the nest opening being just repaired; drags a long, thin blade of grass; after a long struggle, tears away a piece of the blade, carries it and lays it down outside the nest opening;

16:15 Lays down a stick on the opening;
16:53 Brings sticks and deposits them on the opening;
16:58 Carries sticks to the very top of the dome; some of them are very large;
17:21 Sometimes carries building materials into the nest opening and sometimes onto the top of the nest. IV

3rd day of observation:

11:05 Building; carries building materials and deposits them on the opening;
11:25 Approaches a dead fly but does not touch it;
11:55 Building;
13:27 Together with B-13, the ant fikhts *Myrmica laevinodis* which has climbed the nest;
13:30 Three non-marked workers and eleven builders, including B-14, are running over an artificially made hole;
13:38 The ant efficiently stops the hole referred to above;
14:15 Grates the opening;
14:30 Y-1 throws down a stick carelessly, B-14 promptly picks it up and accurately places on the opening. V
An unusually rapid rate of acquiring efficiency!

F. exsecta Z-2

1st day of observation:

15:40 Pulls out a stick, mounted in the dome, carries for a certain distance and drops it; tugs at another one;
16:42 Cleans itself; enters the nest;
16:55 Jerks for a long time at each stick it seizes; likewise, it tugs at a stick held back with pincers;
17:01 Crosses the opening which is being covered and throws a stick behind it; II
18:20 Only five out of 30 sticks carried by the ant are laid down on the opening which is being covered; the ant behaves chaotically and keeps pulling out the sticks which are already mounted in the dome;
18:25 Enters the nest.

After five days:

16:10 Building (a considerable activity on the nest);
17:15 Meanwhile, the ant has carried 20 sticks and deposited all of them on the opening (artificial); promptly drops all resisting sticks; a faultless activity;
17:30 Sometimes takes large and sometimes small sticks; small ones are thrown into the gaps visible in the opening, long ones are laid down outside in the form of a grill; collecting sticks may be considered as accidental, but laying them down — certainly may not; it should be emphasized that small sticks *do not fall* into the opening accidentally but *are thrown purposefully* by the ant with a single, sure movement; V
17:55 A stick, seized by the ant and held back by the observer with pincers, is immediately dropped by the animal.

F. exsecta B-20

1st day of observation:

V
- 13:30 The ant immediately begins to cover an artificially made hole;
- 13:49 Efficiently grates the opening;
- 14:35 The most intensive building activity;
- 14:55 The ant builds virtually all by itself; it has already grated the entire opening; when it was absent, the observer two times loosened cross-bars placed by the ant; each time, returning to the nest, the ant noticed the change and promptly adjusted a wobbly stick to its previous, firm position.

F. exsecta B-13 (marked previously when its building function was studied; it is not unlikely that this took place 18 days earlier, but it has not so far been observed).

1st day of observation:

14:45 Walks over the nest.

2nd day of observation:

IV
- 15:55 Seizes sticks by the end and drags behind or carries them in front of itself depending on their weight;
- 16:25 Likewise;

V
- 16:30–16:46 Crouches in the nest opening;
- 16:55 Now, the ant is working on the side of dome opposite to the previous one;
- 16:58 Crouches in the nest opening and after a while covers it with building materials; brings loose, small sticks and places them with a single movement into the opening; afterwards, each time adjusts adjoining sticks loosened in the course of this operation (previously, it did not do that);
- 17:18 Taken in hand for a while, becomes alarmed for a very short time and afterwards returns to its work at the same opening;
- 17:21 Enters the nest, dragging behind a stick, mounts it inside as an inner layer of the grill which covers the opening;
- 17:30 Builds in another place but equally efficiently;
- 17:35 Walks for a minute over the nest, feeling some of the sticks; walks further and brings a stick found outside the nest (previously, it did not descend the dome);

VI
- 17:45 Crouches in the opening;
- 17:50 Covers this opening; after having brought a double pine needle, the ant placed it so that the joint was situated above the opening; afterwards it entered the opening, stuck out its head and, gripping the joint of the needle, moved it parallel to the surface until the end of the joint was suspended directly above the middle of the opening; then, it withdrew inside the nest and, with a single, faultless movement, pulled the double needle into the nest;
- 18:05 A stick, carried by the ant with its end foremost, has got stuck under another, fairly long stick protruding from the ground at an acute angle; then, not changing the position of its body and legs, the

ant made a single, semicircular motion with its head, swung the stick around and above the obstacle and carried it further on; it VI brought the stick to the opening and, with a single pushing motion, placed it perpendicularly under other sticks already covering the opening so that together they formed a grill.

3rd day of observation:

11:05 Walks over the nest, after a while starts building;
11:20 Approaches a dead fly but does not touch it;
13:00–13:20 Builds efficiently;
13:27 Together with B-14, fights *Myrmica laevinodis* which climbed the nest;
13:30 Together with three unmarked workers and eleven builders, runs around an artificially made opening;
13:34 Covers *another* opening;
13:38 Enters the artificial opening (*see* above) for a while, but returns to the former opening and continues covering it; throws small pieces of litter into the opening, adjusts sticks covering the opening and which have been loosened during this operation; takes out of the opening the sticks which wobble under its legs and deposits them near the opening; another worker, which is inside the opening, takes out VI a small piece from the jaws of the former and deposits it on the bottom of the opening;
13:49 Places a stick near the opening and enters it; seizes this stick from inside and shifts it, by a movement of its head, over the opening to its other edge, thus forming a cross-bar under previously mounted sticks; a similar operation is repeated several times;
14:22 Carries successively two small pieces and two sticks, mounting them each in a *different* opening;
14:27 Carrying a stick, walks over the very edge of an opening into which it has previously deposited building materials; carries this stick to another opening which is just being covered;
14:35 Likewise;
frightened away, after 25 min returns to its building activity.

5th day of observation:

Absent.

6th day of observation:

Absent.

7th day of observation:

15:30 Efficient constructing activity;
16:45 Walks over the nest;
16:48 Crouches in the opening, after a minute gets out; walks;
17:00 Crouches in the opening;
VI 17:20–17:43 Likewise;
17:43 Constructing activity;
17:45 Crouches in the opening; very small activity on the nest; after a night's downpour, there is a great heat; no constructing ants are visible.

F. exsecta B-3

1st day of observation:

15:30 Constructing activity;

15:40 An artificial opening is made in the cupola of the nest; driven by panic, the ant promptly dives into this opening;

15:45 Together with four other ants, the animal under study is active at construction, but its activity is the most intensive and efficient of all of them; throws small pieces into the opening and grates it by means of sticks;

16:10 Walks away;

16:40 Building nest; puts a thin, 3 cm long stick precisely next to the opening and goes to bring another one; in its absence, the stick has been loosened and slightly shifted by the observer; returning with another stick, the ant adjusts the loosened one and puts it in previous position; when the experiment was repeated, the returning animal seized the shifted stick in its jaw, held it motionlessly for a minute, then dropped it and entered the opening where it spent three minutes in a motionless position;

V

16:55 Builds once again; according to the investigator's observation, the stick put down a moment ago, is quite firmly mounted, but when trodden upon by B-3, carrying a new building material, gives way under its legs; the ant drops the material, carried to the nest and adjusts the stick more firmly.

2nd day of observation:

16:24 Enters the opening and crouches in it;

16:27 Goes inside the nest.

F. exsecta B-7

1st day of observation:

14:45 Carries a double pine needle, holding it by one of the ends (not by the joint); when the other end gets stuck in the ground, the ant — not changing the position of its body — tears away, by a swinging movement of its head, one part of the double needle from the other and walks away carrying this part;

15:30 The same happens with another needle!

15:40 When the stick it carries gets stuck with its front end, releases it by a backward movement (not by turning it); when another stick gets caught very strongly, gives it up;

15:55 Moving backwards, carries a stick holding it halfway up its length; encountering the upright obstacle, the ant rears and thus carries its stick over the obstacle;

VI

16:00 Another worker holds a live, struggling fly; the ant under study approaches them cautiously and promptly goes away;

16:10 Walking forward over the wall of the dome, drags so long and thin a stick that it sags under its own weight and catches on obstacles with its other end; the ant inclines its head so as to raise the distal end of the stick and thus negotiates the obstacle; it does not try to turn the stick although it is thin like a needle;

17:15 Building nest.

F. rufa B-3

1st day of observation:

VI
10:00 Active; building operations in the opening;
10:25 Carries a large stick, holding it in front of its body; when the stick gets stuck with its front end under another one, for a few seconds tries to release it and afterwards drops it, seizes the obstacle and removes it from the way; returns to the stick, seizes and carries it, holding it in previous position; after bringing it to its proper place, works it into the grill of the opening;
13:15 The stick it carries gets stuck with its front end under a cone lying on the ground; releases it by a single, circular (side- and upwards) movement and continues walking;
17:00 Except for short intervals, all the time builds efficiently;
17:05 Enters the nest;
18:10 Emerges from the nest and adjusts sticks in the opening;
18:27 Carries in front of itself or drags a heavy stick; when it gets stuck under another heavy and hooked stick lying on the way, the ant jerks at it for a dozen or so seconds, then lets it go, removes the obstacle, returns to its burden, seizes it and continues carrying it in previous direction;
19:15 Until this moment, the ant has actively built its nest.

DISCUSSION

As mentioned before, the first superficial observations of the variable behavior of ants building nests, seemed to provide new facts testifying to a great individual variability of these animals. It has, however, resulted from further studies that the behavior of each individual under study differed not only from that of other specimens observed, but also — in the course of time — from its own previous behavior.

Thus, not all of the differences, observed in the behavior of the workers, are caused by individual variability. Below, I shall discuss precisely those facts I collected which cannot be attributed to the individual variability and I shall try to explain their nature.

It has been revealed by the analysis of the behavior of particular workers in the course of time that the changes observed in the behavior of each of them, as they performed their building operations, are unidirectional. They take place with the time within which a given building function is performed, and they are so regular that six fundamental successive stages of activity could be distinguished, characteristic of each beginner worker. Of course, these changes take place gradually and it would be even possible to make a further division of particular stages into yet shorter periods. In my opinion, this would, however, decrease the clearness of the presentation of my conclusions and, therefore, I contended myself with the most basic division.

In the second stage of my experiments, Roman numerals denote precisely the stages to which individual workers' activities should be assigned. Particular stages are discussed below [1].

Stage I: Acquiring the skill of moving a stick

A worker, which for the first time seizes a stick, grips it with its jaws at any place and mostly steps on it with all its limbs, which by no means is purely accidental. It is caused by the structure of the ant's jaws which compels the insect to place the axis of its body parallel to the stick it is seizing, and stepping on it [2] is the simplest form of such a parallel position. Consequently, in the case of a beginner worker, on the whole the stick does not move at all even with the ant's greatest efforts. Somewhat different is the case of a pine needle which is too narrow to stand along comfortably or to step on and, therefore, it usually gets between the ant's legs and is moved without any great effort.

Thus, an ant is not anatomically adapted to its most fundamental operation, that is, carrying building materials. My observations have shown in turn that ants are also devoid of a *hereditary skill* of overcoming difficulties resulting from this fact. This is in opposition to an undoubtedly *hereditary tendency* to seize and carry sticks. This is the reason why in the first stage of its building activity, a worker tugs for a long time at a stick it has seized, not letting go of it and not changing its behavior, although it mostly fails in all its efforts. In the course of such a struggle, the ant sometimes happens to change accidentally its position in relation to the stick. If the resistance offered by the stick is caused only by an improper attitude of the ant towards the stick, that is, by standing on it, successive changes in the ant's position may ultimately lead to the conditions under which the stick may be moved.

[1] To simplify the definitions, I continue to apply the name of "a stick" to each elongated building material (which may be, e.g., a pine needle); precisely such an elongated material will be here discussed mostly, since (1) it is most typical of the construction of anthills in the species under study and (2) the transportation of such a material and the subsequent use for the construction of nests requires the highest skill of the ants. If necessary, in contradistinction to "stick", I use a word "piece" meaning various small building material indefinite in shape.

[2] The anatomy of the jaws of a mammal or a bird compels them to take a *perpendicular* position of their body in relation to any longitudinal object they are going to grip with their jaws or beak. This is the anatomical reason why they never step on the object they carry and why they move it in their first trial without effort. In this case, this is by no means evidence for the superiority of their nervous system over that of ants.

After a few such cases, the periods of futile jerking without changing position become shorter and shorter. After a few tugs, the ant drops the resisting stick, seeking to grip it at another place, and repeats this operation until it seizes it accidentally in such a manner that the stick becomes dislodged (that is, until it gets off the stick).

This gradual shortening of the time of each inappropriate grip, the same as in fact all processes here described, takes place at a different rate in particular individuals.

The ant still continues stepping on the stick. Speeding up the changes in its position and changes in the place at which it grips, speeds up in turn reaching an effective position which, however, is still attained accidentally after many ineffective trials. Gradually, the ant gets off the stick after fewer and fewer changes in its position. Finally, the moment comes when it completely stops stepping on the stick, and even if it happens in the course of tugging at the stick, the ant promptly corrects this error.

Thus, moving the stick, if it is not immobilized by environmental factors, ceases to be a problem for a worker in most cases as early as on the first day of its building activity and in some cases even after a few hours (*F. rufa* B-26, Z-3, Y-47, B-55, *F. exsecta* Z-1).

Stage II: Acquiring the skill in eliminating sticks unsuitable for carrying

A stick may resist the efforts of a worker for the reasons which do not depend on the latter. It may be deeply driven in the ground or its weight may be too great for the strength of a worker. In such cases, no change in position can produce desirable effect and a worker may even for a very long time tug at it, repeatedly changing its attitude, until it gets discouraged and gives it up. Sometimes, the ant jerks so stubbornly that it pulls out a stick mounted in the dome of a mound and damages its structure.

At the beginning, such a futile struggle may last a long time (to 5 min). However, a worker which has already reached stage I of learning, that is, which has mastered the skill of moving the sticks from their places, more and more rapidly, even after a few ineffective pulls, abandons the immovable object and looks for another. This also takes place after a smaller and smaller number of trials.

A worker which has already passed the first two stages may be easily distinguished at first glance. After two or three tugs, such an ant gives up a resisting stick and sets out in search of another one (*F. rufa* B-26, Z-3, Y-47, B-55, *F. exsecta* Z-1, B-14, Z-2).

Stage III: Acquiring the skill of moving building materials

From the moment when a stick has first been moved, a worker ant begins to face a new, great difficulty, that is, the necessity to avoid obstacles when carrying in its jaws a long object.

In this stage, it is a matter of pure accident whether the stick is carried or dragged behind. It depends on the position taken by the worker at a moment of moving the stick from its place in relation to the direction in which it intends to carry it, although, in the case of light and short sticks, it mostly carries its burden in front of itself since in such a position it may more easily turn and change the orientation of its body. If, therefore, the position in relation to the stick compels the ant to carry it in front of itself, then sooner or later the stick will get stuck in the construction of the nest and once again begins to offer resistance. This causes — according to the principle of a normal behavior of a worker — a new chaotic struggle which frequently results in the stick being finally pulled out from the ground. If the position of the ant has not in the meantime been changed it continues to carry the stick in front of itself and after some time all this happens once again. After a few or some dozen or so times, the ant more and more often and, finally, even at once moves back, releasing the stick from an obstacle. The ant still does not know how to avoid obstacles and the stick continuously gets stuck with the same frequency, but the general speed of movement has increased as a result of increasingly more efficient releasing of the stick from the obstacles. Due to the fact that each release is effected by pulling, the operations of carrying the stick in front of the ant's body and dragging it behind begin to alternate. Gradually, these two manners of moving the stick become adequate to a definite situation, and not accidental. This leads to more and more efficient avoiding of the obstacles.

In this incessant struggle against obstacles, the ant cannot maintain the direction it gives to the object carried. It is rather the ant itself that is directed by the position of the stick and the way along which it may be pushed through obstacles. Consequently, the direction in which the stick is carried is rather indefinite and the sticks are thrown at random each time in a different place (*F. rufa* B-26, Z-3, Y-47, *F. exsecta* B-14).

Stage IV: Acquiring the skill of directing the building material carried

As a worker more and more rapidly and efficiently releases the stick it carries from various obstacles, it acquires the skill of resuming the previous direction of its movement. More and more distinct becomes

also a certain general rule, that is, if there is no definite damage in the mound, the direction taken by the building workers leads on the whole towards the top of the mound (*see* Chauvin 1959).

The increasing efficiency is expressed in the fact that a worker in this stage more and more frequently returns with building materials to the place in which it has previously deposited some sticks or small pieces. Thus, we have to do not only with the skill of avoiding obstacles, but also with that of overcoming them and steering clear of them (*F. exsecta* B-14, B-13).

Stage V: Acquiring the skill of the free manipulation of building material and assembling structures

In this stage, the ant each time returns to the place in which it has previously deposited building materials, and its carrying sticks, blades, etc. ceases to be an operation in itself. Now, the worker repairs its mound, adjusts irregularly scattered sticks if they give way under its weight, levels any depressions that might be previously formed and grates nest openings (*see* Chauvin's description, 1968).

Each item of building materials is now specifically used and the adequacy of this activity may on the whole be estimated by the observer. If it would be possible to eliminate all workers which are in earlier stages, no one would be entitled to claim that the ants' work is chaotic and that its results depend on purely accidental factors (*F. rufa* B-26, Y-47, B-55, *F. exsecta* B-14, Z-2, B-20, B-13, B-3).

Stage VI: Individual self-improvement

In stage VI, a worker has already learned all fundamental knowledge necessary for performing building operations. Now, the phases of improvement and an increase in the rate of work take place. Unfortunately, I could not manage to subject them to any objective division. This was caused by the fact that, on the one hand, advances of ants were not as marked and rapid as in earlier stages and, on the other, they were more individualized and were displayed in different and accidentally observed operations.

Here, I must simply refer the reader to the descyriptions of excellent solutions of the problems found by the workers of *F. exsecta* (B-13 and B-7) and *F. rufa* (B-3). It is worth while to read them once more.

The facts presented above do not leave any doubts that:

1. the behavior of a worker changes as it performs its building function;

2. these changes are unidirectional, that is, they reveal the tendency to an ever increasing degree of improvement of a worker in the performance of such a function.

This phenomenon may be the result of either a physiological maturing of the workers, which takes place precisely in the course of the performance of this function, or a process of learning how to perform it.

In view of the fact that mostly young workers were the object of my studies, there was a possibility that for a completely efficient performance of their functions they still needed to pass through a period of general physiological maturation. After a detailed analysis of the results, this hypothesis has, however, been rejected, since individuals which for a certain period stopped their building activities, subsequently returned to the same stage of improvement at which they interrupted their work. This hypothesis was yet more strongly denied by experimental forcing (by strong damage to the dome of a nest) of old individuals to undertake the building function. If the hypothesis in question were true, all such individuals should build effectively, which, however, was not the case.

There was also another possibility, related to physiological maturation, that is, maturation for the performance of a *given function,* as is the case of honey-bees. The honey-bee worker, forced by an experimenter, may adapt itself to performing certain functions outside the innate order, but this requires some time to adapt the insect to such functions.

If, in our experiments, we had to do with a similar phenomenon, then, in the workers which stop for a certain time performing their building operations, this hypothetical process of physiological adaptation would have to regress and an ant, after resuming its work, would start once more from stage I, which is, however, contradicted by the facts (B-26, Z-3, Y-1, Y-47).

Thus, neither the maturation to a given function, nor a general maturation are phenomena by which we might explain the self-improvement of the ants I studied.

Rejecting the hypotheses discussed above it remains only to accept the alternative that the improvement of an individual's skill during the performance of building operations is a result of the process of *learning.*

According to Sudd (1967, p. 167): "In other cases however it has very clearly been shown that ants can learn, but how they use this power in their natural lives is not so clear".

In view of the fact that the entire literature devoted to ants' learning deals only with locomotor learning and the subject of my studies was manipulatory learning, I do not think it necessary to discuss this litera-

ture, the more so as it may be found in Sudd's recent monograph cited above.

To analyze the process of learning building functions by ants, we have to separate primarily all hereditary reactions from these animals' building behavior. A need to release these reactions, and overcoming difficulties in releasing them have to constitute the motivation for acquiring new reactions by way of learning.

I succeeded in distinguishing the following hereditary building reactions:

1. Seizing building materials

Unfortunately, little can be said about the mechanisms which evoke this reaction. It is beyond any doubt that to undertake a building function, an ant has to be strongly stimulated to do so (Dobrzańska 1959), but I did not succeed in finding stimuli which make an ant undertake precisely this function and to seize this and not that building material.

2. Moving the material seized

The tendency to move a building material, already held in the jaws, from its place, is undoubtedly a hereditary reaction of a worker. Perhaps this drive resolves itself into a primitive need for movement in a stimulated animal. It is beyond any doubt that a beginner worker does not discern whether or not the stick seized by it is suitable for carrying, and at the same time, the strong stimulation mentioned above compels it to seek ways of moving it from its place, regardless of the resistance it offers. Frequently, it jerks, therefore, at too heavy a stick or even pulls out a stick already mounted in the nest, thus loosening the entire structure around this stick.

Setting a building material in motion is for an excited worker a satisfaction of a motive and, therefore, a positive stimulus. If, on the other hand, the building material, dragged by the animal, offers resistance, it becomes for the ant a source of negative stimulation. Identical effects are produced by the immobilization of each animal which is in a state of excitation. Under such conditions, ants frequently drop the resisting sticks and start to clean themselves, which is a typical displacement activity (B-55, Z-2, B-26).

Thus the reaction under study of setting in motion the building material seized is a motive for learning in stages I and II, that is, during the period when the animal acquires the skill of setting the stick in motion and eliminating the sticks which are unsuitable for carrying.

3. The tendency of taking the building material onto the top of the mound

A term "tendency" is justified, because a statistical principle is here involved.

This phenomenon has been noticed by Chauvin (1959), who mentioned that nearly half the number of all carrying workers took the building materials onto the top or near the top, while the other half, for no observable reasons, scattered them on the way, which he considered as the tendency to carry upwards. It is clear from my observations that dropping the material halfway to the top is in the domain of unskilled workers which are unable to cope with the many difficulties they encounter on the way.

It should be borne in mind that prior to reaching stage IV, it is not the ant itself but the shape of stick and configuration of the path, on which it is carried, that are decisive concerning the choice of the route. The percentage of cases in which the top is reached would be vastly increased if only the postsage IV ants would be taken into account. Of course, there is always some number of damaged and uneven places on the surface of the mound in which building materials are deposited even by skilled workers. It seems, however, that even this phenomenon may resolve itself into the tendency to go uphill, because each depression in the wall of the cone causes the formation of a bend of a straight line, that is, the uphill way and represents a pseudo-summit. This satisfies the ant's motivation and becomes a stimulus to deposit material in such a place.

It can be stated, therefore, that the hereditary tendency to take building materials onto the top of the mound is a motivation for learning in stages III and IV when the ant acquires the skill of moving and directing the building material.

The final shape of the mound is determined by the resultant efforts of *all* workers carrying building materials, regardless of the stage of learning reached by them. A certain self-regulation of the shape seems here to take place: if for some external or internal reasons (for instance, as a result of frequent rains or a shortage of workers caused by some cataclysm), the mound takes an excessively flattend shape, this allows even less skilled workers to climb the summit and deposit building materials, which in turn causes an upward extension of the mound cone and consequently an increase in the steepness of its slopes. On the contrary, the increase in the steepness of the slope, makes its approach difficult for any larger number of insufficiently skilled workers, which in turn causes the flattening of the mound.

4. Putting sticks in a position parallel to the surface of the mound

From experiments 4 and 5 (1st experimental part), it follows that both the skilled and beginning workers always tend to *lay down* the sticks on the surface of the mound and not to set them up in a vertical position. It may well be that this is precisely the reason a worker in stage V never drops the material brought to the nest, but mounts it in a definite position. I checked this experimentally by loosening such mounted sticks which were subsequently mounted once again by the workers. This principle is confirmed by the fact that small building materials (pieces) are as a rule dropped into openings which, in this way, are filled up; tiny pieces are in practice shapeless and there is no fear of their taking an upright position.

I tested the biological sense of this principle literally with my own hands, with which I shaped old, flattened mounds abandoned by their inhabitants. In doing so, I took care to observe the principle of the horizontal arrangement of the sticks. It turned out that even a violent downpour could not drench such a mound. On the other hand, vertically driven sticks became "gutters" through which water penetrated inside the mounds.

Barking the twigs of heather which grows on the nests of *F. sanguinea,* described with the observations of experimental part I, is a contribution to the building reaction under study. I have failed to determine whether the ants peel only the bark because the wood of heather is too tough for their jaws, or because the twigs are already wasted away before being bitten through. There is also the possibility that this became a hereditary activity, that is, only the bark is bitten off the twigs since it is quite enough to reach a desired effect by a relatively small effort. In any case, the ants remove from their nests all vertically projecting twigs, over which water would otherwise flow down to the nest.

The principle of putting the sticks horizontally is at least one of the motivations for learning in stage V, that is, when the ants acquire the skill of a free manipulation of building materials and assembling structures. A stick, thrown carelessly, frequently falls down the opening taking a vertical position. In order that it might maintain a horizontal position, initially given to it by an ant, it should be strengthened in this position by a worker and mounted in the entire structure, which requires a considerable skill of manipulating it. Skilled workers are, therefore, often observed as they adjust and strengthen the position of building materials which give way under the ants' legs. Such materials have either been given up by the beginners, or secondarily loosened by the workers of stage II which frequently pull out already mounted sticks.

Thus, we have formulated at least some of the elements of motivation for learning building functions. This motivation consists on the whole in satisfying the drive to carry the seized building materials onto the summit of the mound and mounting them in this place in a horizontal position.

The fact of self-improvement of the workers in performing building operations, described above, may be classified as instrumental CRs manipulatory in character and whose essence consists in the influence exerted by an animal on objects which surround it (Konorski 1967, chapter 8). As an effect of the building drive and maybe also of the need for movement itself, the animal seizes the stick, repeatedly changing the place of grip, with simultaneous movements of its head and entire body. When some of these movements cause a more efficient shifting of the stick or releasing it from an obstacle, such movement becomes fixed. It should be remembered that each stoppage of the animal's movement by the stick which has got stuck is a negative stimulus, and vice versa, each possibility of moving with the stick once again is a positive stimulus. The elimination of inadequate movements is the more difficult as there are sticks which cannot be set in motion at all, since the resistance of the obstacles exceed the strengths of an ant. This is a source of negative stimuli, the avoidance of which — by giving up such sticks after a few trials — is the most difficult element of learning in initial stages.

Thus, instrumental reactions are formed, according to the principle of trial and error, as an effect of the drive for moving building materials which, in my opinion, is hereditary. It is revealed of course only when an ant starts its building activity. A positive or negative stimulus only satisfies the animal drive or, after a temporary satisfaction, leaves it under a continuing influence of such drive (Konorski 1967).

It may well be that in an ant insufficiently accustomed to its environment and consequently being in the first stage of learning, halts release a drive of fear, as the ant is incapable of discriminating between the halts of movement related to the stick being jammed in an obstacle and the halts of movement resulting from the ant itself being caught by its enemy, by some predatory animal, etc. This is probably caused by the fact that an ant, being in a state of building drive, instinctively clenches its jaws on the building material seized and it is only after a long training that it learns to unclench them when it is impossible to move the stick. Thus a beginning worker gets in a way trapped by its own reflex when the stick gets stuck and violently stops the movement of the animal spasmodically clinging to it. I think that, from the biological viewpoint, each stoppage of its movements, not yet investigated by the ani-

mal, is associated with fear, evoking a reflex of struggle even before the orientation reaction takes place and elucidates the causes of the halt. Otherwise, it would be too late for struggle, defense or flight. At any rate, the stoppage of movement of a excited animal is always a strong negative stimulus, while the release is a strong positive stimulus. The two stimuli, acting alternately, cause the rapid acquisition of instrumental reflexes which resolve themselves into the worker's skill of avoiding obstacles in movement.

The determination of how the building drive is released and which stimuli influence it seems to me be a difficult problem. We already know for certain that it is not automatically formed during a definite life period of a worker, that it does not depend on its age. We also know that this drive is revealed violently, as shown by a great activity of the workers which for the first time start this operation. Considerable individual differences are also displayed: while some of the workers build for weeks (I do not know whether there are workers which do it without intervals), some others give up this activity after a few hours and pass on to other operations. At any rate, the drive is either extinguished for reasons unknown as yet, or is revealed with considerable force manifested in the activity of building workers.

It is manifest that the thesis on learning natural functions by ants is proven in this paper on the basis of a description of changes in the functions and motor models of the ants examined. The reader may be struck by the lack of certain data such as a time within which particular stages of learning were mastered, a decrease in the number of errors, shortening the periods necessary to solve particular problems, etc.

A great difficulty of studying ants under natural conditions consisted primarily in the fact that the individuals under study could be observed over two, three and, less frequently, four (and, in addition, mostly not successive) stages of learning. The only exception was *F. exsecta* B-14 which, due to its very rapid (nontypical) learning, could be observed over four successive stages.

Difficulties of drawing learning curves did not resolve themselves in the circumstances mentioned above. There was also a great variability of the natural environment in which the ants' activity was observed, that in fact made comparing numerical data impossible. Each time, each worker was carrying building material which differed in shape and weight, a difficulty that to a certain extent could be removed (*see* Experiments 2 and 3). However, it is utterly impossible to compel workers (and even one and the same worker) to follow each time the same route and consequently to encounter the same obstacles. This precludes any comparisons of the time within which they cover such a route.

To undertake a building function, an ant has to be strongly excited and, therefore, it behaves "nervously", its movements are quick and its position is frequently changed. This "nervousness" decreases as the ant learns and improves its efficiency, as is the case of workers in stages V and VI which build with composure (their motivation is satisfied to a greater extent). However, we are interested, in initial stages, in the rate at which the changes in an individual's behavior take place and in their mutual comparability. And this is precisely so difficult to perceive that I had to give up even such a seemingly simple operation as measuring, by means of a stop-watch, the time of maintaining particular positions by a worker tugging at a stick. My trials in this respect turned out to be so problematic and inaccurate that I preferred not to make use of the unreliable data thus obtained.

Thus, a discontinuity of observation, variability of conditions which could not be systematized, and a considerable mobility of the animals under study precluded my collecting more or less reliable numerical data as a result of field studies. I think that collecting this would have been possible by the application of the method of filming under laboratory conditions, which is, however, technically difficult.

Consequently, my conclusions were drawn on the basis of *summing up* dozens of individual observations, of which a few exemplary ones are described above in the detailed part of the present paper. Assembling all data indicates an absolutely unequivocal and unidirectional character of the changes that occur in the behavior of *all* (of many hundreds) workers observed.

What is more important, I succeeded in determining criteria, on the basis of which it is possible to discriminate accurately between an advanced worker and a beginner and, in my opinion, this is evidence for a definitive change in behavior as an effect of practice, that is, learning.

Since changes in behavior in stage VI become less comparable and more and more individualized, a skilled worker is, in my opinion, an ant which reached stage V. At first glance and on the basis of a brief observation of a given ant, it is impossible to decide whether it is in stage V or VI. For this purpose, such a worker should be observed for a longer time. In addition, it is not certain whether during such a period, this ant will have an opportunity to display a high degree of its skill. This is the reason why there are probably more workers in stage VI than it is possible to observe. The discussion of the behavior of these individuals is among the problems of the individual variability in the behavior of ants. In the light of the present paper, this variability has to be examined anew.

If, on the other hand, we are concerned with workers which have reached stage V of learning, such ants may be faultlessly distinguished

from less skilled ones on the basis of their behavior in one only building cycle (that is, from the moment at which they seize the building material to the moment at which they put it in its place of destination). Below are accurate criteria of the building behavior, allowing one to distinguish a skilled worker:

1. It never steps on the building material seized by it;
2. It drops a resisting stick after a few (at most three) tugs (except for upright sticks);
3. When carrying a building material, it keeps moving in a chosen direction, not changing it under the influence of the obstacles encountered;
4. It deposits this material in the place of building in a definite manner; this may be checked experimentally by interfering with the system worked out by the ant, which always evokes its reaction.

The last item of this list, together with the fact that a skilled worker does not attempt to seize each stick found on the way (as the beginners do), but walks for a long time before choosing one of them, make one ask the question: does there exists so high a degree of training of an individual that there may be a definite *picture* of a stick suitable for a given structure and a *plan* of mounting it in this structure. I was not able to check and answer this question even approximately. I did not succeed in finding any objective criteria of value or of the suitability of building material for a given place in the nest. Undoubtedly, there are many features, imperceptible for an observer, which may be of a certain value for an ant. However, does such a differentiation of building material by ants actually take place? Selecting building materials by advanced individuals need not necessarily be a symptom of the selection for the purposes of a definite structure. It may well be a selection of sticks most suitable for transportation, which as a matter of fact also requires skill.

The behavior of the worker of *F. exsecta* B-13, which was plugging a few openings at a time, carrying each stick to a different place, might testify to a planned selection. This may be understood in the following way: instead of looking for a stick suitable for a given opening, the worker took any stick at random but afterwards fitted it in such places in which it could be mounted. On the other hand, we may also reason that this worker operated without any plan and that after all each stick may be suitable for any structure with the ant's acquired skill of mounting the material into the nest.

Thus, this problem, remaining so far in the realm of pure speculation, is insoluble and requires concrete proof for one or the other standpoint.

SUMMARY

The building behavior of ants consists of hereditary and acquired elements. Hereditary reactions are: seizing building materials, transporting them on the summit of the mound and putting them down parallel to the surface. Acquired reactions are: the skill of selecting building materials suitable for transportation, carrying it (despite ants' anatomical conditions), overcoming obstacles and mounting the material into the structure of the mound. The presence of manipulatory learning in ants alters the views on their individual differences and on the plasticity of their nervous system.

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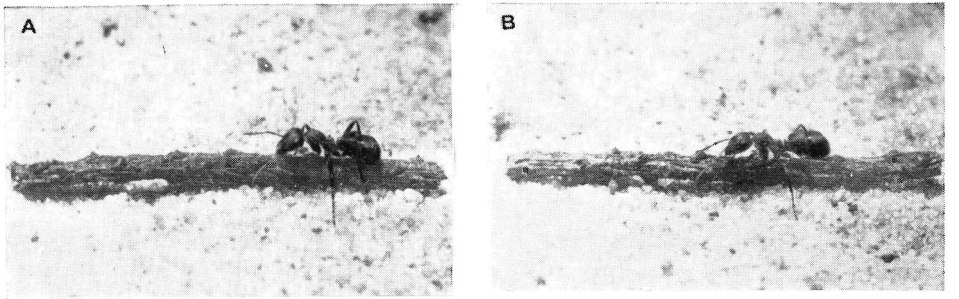

Fig. 1. The ant climbs the stick (*A*) and jerks at the same time standing on it (*B*).

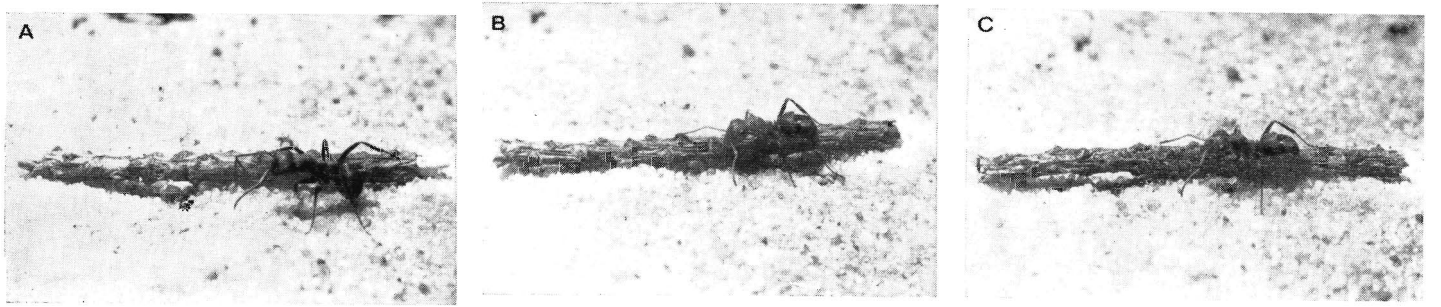

Fig. 2. The ant gets off the stick for a longer time (*A*), climbs it in another place (*B*) and jerks again standing on it (*C*).

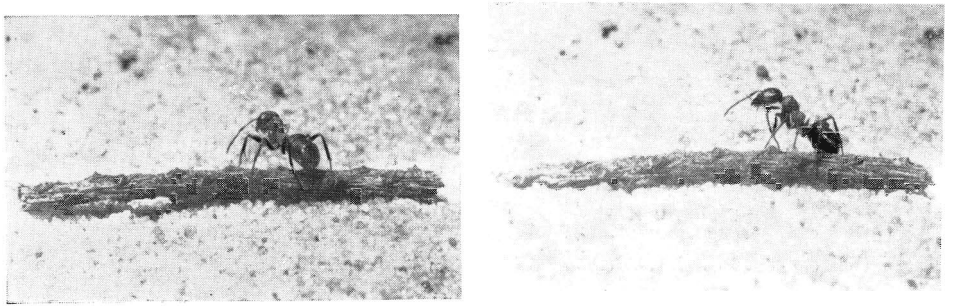

Fig. 3. The ant frequently drops the resisting stick and starts to clean itself, which is a typical displacement activity.