Social Modifications of Work Efficiency in Digging by the Ant, *Formica* (*Formica*) *yessensis* Forel[1)]

By

Shinji Imamura

Zoological Institute, Hokkaido University

(*With 6 Text-figures and 1 Table*)

Although digging is one of the commonest behaviors of ants, it has not been intensively studied except for nest structure descriptions (Headley 1949, Ito 1973, Mizutani and Imamura 1980, Talbot 1948, 1964, Talbot and Kennedy 1940, see also in Sudd 1967). The interests for the behavior may be divided into three kinds: How the species-specific nest structures are realized: How ants regulate the amount of digging task: Evolution of the nest structures. Aiming at solving some of these problems serial studies are made, and this first paper deals with the problem of social modifications of ants' efficiency in digging, about which opposing observations have been reported. The question is, "Which phenomenon do ants show, social facilitation or inhibition, during digging ?"

Chen (1937) observed social facilitation in digging by workers of *Componotus japonicus*. He confined two or three workers together for six hours in a half-pint glass bottle which was floored smoothly with moist soil to allow the animals to dig. The excavated soil was collected for later measurement of the dry weight. Then the animals were separately placed in newly prepared containers of the same kind for the same time, in order to compare the total weight they dug with that done under the first condition. He found that the workers dug nearly four times as much soil in groups as in solitude. The difference was statistically significant and must have been caused from grouping. Contrary to this result, Sakagami and Hayashida (1962) faced the directly opposite phenomenon in studying work efficiency by heterospecific ant groups composed of a labor parasite and its host species, *Polyergus samurai*+*Formica fusca*, or *F. sanguinea*+*F. fusca*, and also by homospecific groups of *F. sanguinea* or of *F. fusca* by 24-hour tests using horizontal tubes packed with moist soil in one end. Sudd (1972) reconfirmed the decreased efficiency in groups of *F. lemani* workers in three-hour tests applying a soil-bottomed vertical cell with platforms. The experimental designs adopted by the authors were thus basically similar to each other, comparing the weight of soil excavated under solo with that dug by groups in the same kind of containers

1) Studies on the digging behavior of ants. I.

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during the fixed time in each case. And Chen's result has come to be questioned. Although the present study is preliminary, it gives us some new findings, aiming at explaining the discrepancy shown in those previous reports.

Experiment A. The Various Social Modifications

Material and Method

About three hundreds of *F. yessensis* workers were collected by digging up a nest in Ishikari Shore, Hokkaido, Japan, and fostered with saturated sugar water in a glass basin floored with moist sand brought from the habitat. Restless aggressive (Ra) workers and clustery coward (Cc) ones were adopted for separate experiments. In order to select Ra individuals, a pair of forceps was put forward to workers walking on the laboratory nest surface, and only those that bit at it were chosen as test animals. Fourty individuals were thus selected. These workers were reared in another basin (RB) providing sugar water and moisture but no sand to make handling easy. The experiment was continued for three days. On the first day each individual was placed solitarily in the test cell (Fig. 1) for one hour, and

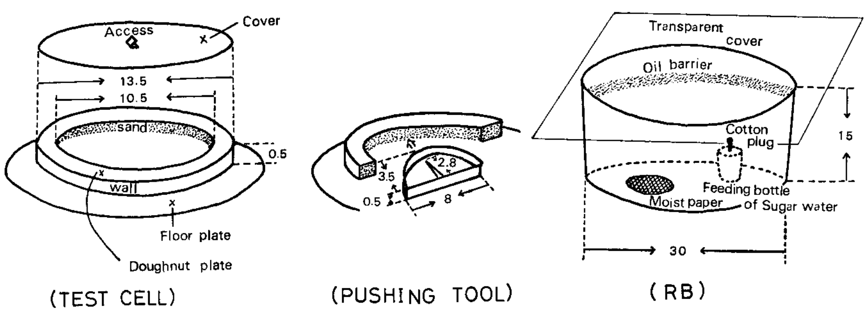

Fig. 1. The test cell is made all of 0.5 mm thick transparent plastic plates. The sand has been passed through a mesh of 0.28 mm and mixed with water in the ratio of volume 4:1. To pack it uniformly under the doughnut plate, a pushing tool was used; each push was stopped when the plastic semi-circle was transformed to touch the needle inside, thus establishing a similar tightness. RB: The resting basin. Scale in cm.

was allowed to dig in the sand under the doughnut plate and put or scatter it in the central space. At the end of the test time, the dug sand placed in the space was collected, and its weight was measured after drying. Twenty cells were prepared at one time, and the 40 individuals could be tested in two runs. On the second day the same workers, excluding three that were found dead, were tested as groups of eight individuals. The groupings were made in a random manner. Four groups could be made for one run of trials and each group was placed in a cell of the same kind as above for one hour. The dug sand was collected for later measurement.

Thus, 32 (4×8) groups were tested, repeating random grouping. On the third day the 37 workers were tested again in solitude as on the first day.

The same series of tests were tried with 40 Cc workers. In order to select such individuals, the artificial nest was broken and all the workers were poured in a large basin. After a while some of them formed clusters here and there, though others kept on walking around freely, and the clustering ones were carefully picked up one by one with a pair of forceps so that the cluster should not be disturbed. Thus, 40 workers were selected, and all of them survived the three-day experiment. Fourty (5×8) groups were tested.

Results

Weight of sand each worker dug in solutide is termed the solo efficiency (henceforth SE), and for comparison with this, weight of sand each group dug was divided by eight to obtain the mean achievement of the members, which is termed the group efficiency (GE). As for the Ra workers, the mean SE with s.d. was 57 ± 95 mg on the first day, and 81 ± 110 mg on the third day. The mean GE was 170 ± 48 mg on the second day (Fig. 2). By a separate experiment a mean SE has been shown to change nearly linearly during three days (Fig. 3), so the mean SE on the second day is estimated as about 69 ($=57\pm81/2$) mg. Thus, the high mean

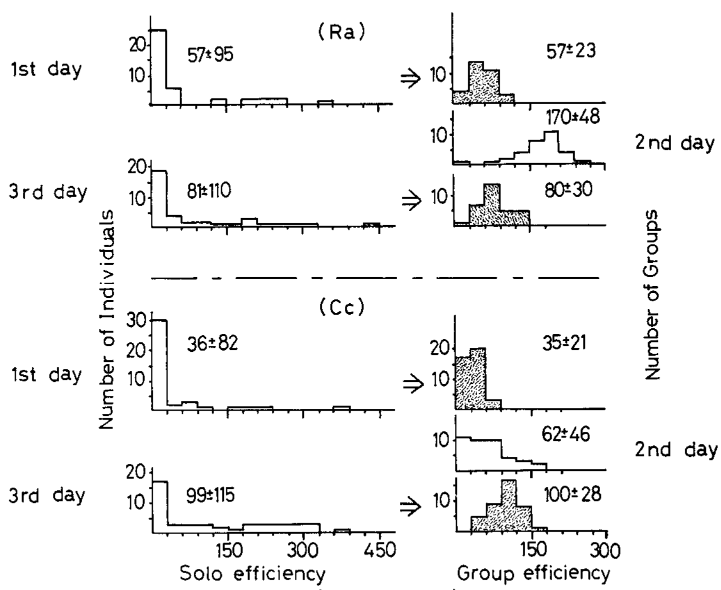

Fig. 2. The dry weight of sand dug in 1 hour in solitude (left) or in groups (right), shown in the open histograms. The shadowed ones give group efficiencies free from any group effects, estimated from the solo performance in each case. Ra and Cc, in text.

GE seems to show the occurrence of social facilitation. However, the standard deviations are not directly comparable between the SE and GE, for each value of GEs is a mean achievement making the s.d. artificially smaller than those of SEs. A special device was therefore needed and the following way was chosen. By means of using a random number table eight SE records were taken out from the 40 SE records on the first day, and from the reamining 32 another eight were selected in the same manner, and by two more repetitions four groups were obtained. And the mean value was calculated in each group. These mean values are assumed as GEs free from any group effects. Further, by repeating such series of random groupings and mean calculations for eight times ($4\times8=$) 32 GE estimations were obtained. This process is comparable to that taken in measuring actual GEs on the second day; the GEs thus estimated are meaningfully compared with those actual GEs. The standard deviations of the estimated GEs were 23 mg based on the first-day SE records and 30 mg on the third day, and they are significantly smaller than that on the second day [$F=2.560$, $P(F>2.386)=0.01$]. Here the following possibilities may be thought of. First, some combinations of workers were to

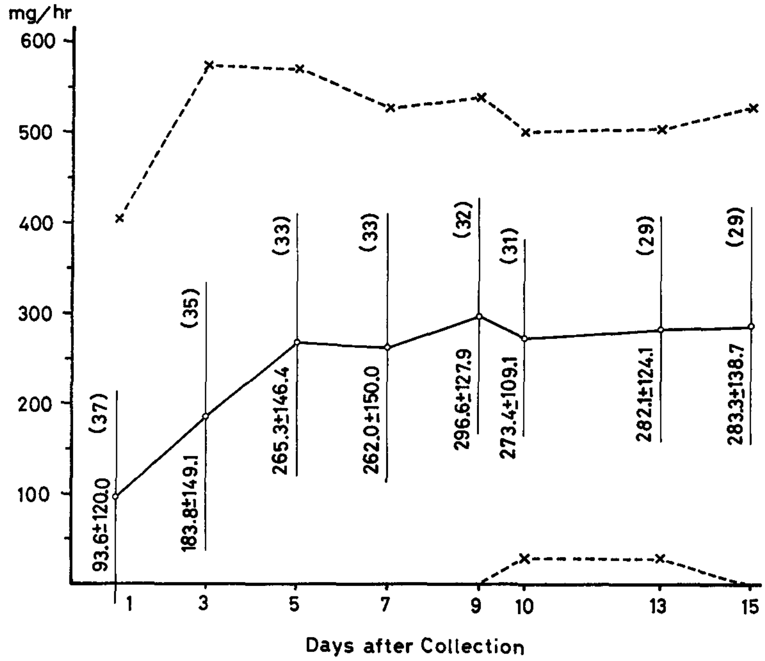

Fig. 3. The daily change of the mean solo efficiency and the s.d. assessed under the same condition as in Figs. 1 and 2. The broken lines show the individual maximum or minimum, and the numerals in parentheses are numbers of workers tested, gradually declining for death. Data on *F. yessensis*.

take more facilitatory effect than others for some fixed properties with them. Second, the facilitatory effect in each group was to fluctuate only accidentally, without any particular fixed causes. As shown below, the group effect in Cc workers was quite different from the above case, suggesting the importance of the first possibility. Even within the selected Ra workers interindividual relation may be various enough to cause the large s.d. observed.

As to the Cc workers, the mean SE with s.d. was 36 ± 82 mg on the first day, and 99 ± 115 mg on the third day. The mean GE with s.d. was 62 ± 46 mg on the second day. As the mean SE on the second day is estimated as 68 $(36+99/2)$ mg, the mean GE didn't show any apparent group effect. However, it was certain that there was some group effect also in the Cc workers, since the s.d. of GE on the second day was significantly larger than those of GE free from the group effect [$F=2.700$, $P(F>2.114)=0.01$]. The fact that the mean GE was similar to the mean SE while showing a larger s.d. may mean that in some groups the effect was inhibitory but in others facilitatory, balancing out each other to give that mean GE similar to SE. The presence of the inhibitory effect is strongly suggested in that there were nine groups showing zero GE. If without such inhibition, this high frequency should not have been reached. The probability that a given group was to show zero GE without the inhibition but by being formed exclusively of SE-zero individuals was estimated as follows. The number of SE-zero individuals was 29 on the first day and 15 on the third day, and that on the second day would have been between the two. Taking 22 $(=29+15/2)$ as the estimated number, the probability for such a group formation to occur was ${}_{22}C_8/{}_{40}C_8=0.004$. The probability that this event should occur nine or more times in the 40 groupings was further lower.

The presence of social inhibition was apparent also in the behavior of aggregation formation. It is safely assumed that before starting excavation the workers had to receive effective stimuli from the moist soil (cf. Sudd 1969). However, those workers that once clustered remained motionless until the end of the test time. If they had not clustered, they or at least some of them could have had some chance of receiving the effective stimuli for starting digging. Thus, clustering seems to have caused the social inhibition. On the other hand, the presence of social facilitation was suggested in the excavation of a common tunnel by several individuals working together. Since the sand surface was uniformly or smoothly prepared, excavation of a common tunnel indicated that either the incipient hole made by the first digger or this individual herself stimulated other workers for the task. This stimulation seems to have led to the social facilitation, assuming that working together do not make the diggers bother each other. In most groups of the Cc workers one cluster and excavation of a common tunnel by the other members took place. This might show that both social facilitation and inhibition occurred in each of these groups, and the GE was decided at the counteraction of the two factors. In some groups the facilitation should overpower the inhibition and in others vice versa. This assumption well suits the data giving the mean GE similar to the estimated mean SE while exhibiting the far larger s.d. than that estimated under the condition free from group effects. Thus, clustering seems to be the cause of the social inhibition as well as the mutual grooming mentioned by Sudd (1972), and the excavation of a common tunnel may mean the presence of the facilitation among the diggers.

Experiment B. A Non-Visual Signal Facilitating Digging

Material and Method

The excavation of one hole by several workers indicated that either the incipient hole or diggers themselves stimulated other workers to dig there. The latter possibility was examined here.

Test individuals were selected carefully. About 500 workers of *F. yessensis* were freed in a basin (ϕ 30 cm) which was floored smoothly with moist sand, and were allowed to dig. After a while excavations started. Most of the workers passing by excavation spots paid little attention to the task. Such workers might not be able to react to the mentioned stimulus. Therefore, only those individuals that were digging together at common holes were selected for the experiment. They would be able either to react to or send out the mentioned stimulus, or possibly in both ways. That most workers are not responsive to such a stimulus is reasonable; if all workers should react, other tasks but digging would be avoided sooner or later in natural nests, and the harmonious colonial life must break down. If the mentioned stimulus is really present, there can be only some workers that are responsive to it. Fourty eight individuals were selected for the present experiment.

The test cells are illustrated in Fig. 4. Two cells were used as a pair. In each of them one worker was placed and allowed to dig out sand from the small box for one hour. The experiment was done under two conditions for every worker. (1) The cells were placed apart from each other. (2) The cells touched with each other at the netted window, and to prevent vision through the window a piece of fine insect net was put between. The weight of sand a worker dug under the first condition is termed the solo efficiency (SE) and that under the second condition the semi-solo (or semi-pair) efficiency (SSE). In this experiment the SE and SSE were compared in each worker. Assuming that diggers send out a non-visual signal facilitating others' digging, the SSE of an individual may be higher than her SE if her partner performs excavation and sends out the signal from the other side of the net. Put the other way, if the SSE appears to be higher, even though statistically, the existence of such a signal can be assumed.

Results

Each worker was tested once under the condition apart and then once under the touched condition after about half an hour. Under the latter condition 28 workers each had an active partner which dug any amount of sand during the time, and the other 20 each got an inactive partner. When both workers dug in the touched condition (eleven pairs), they were taken as active partners to each other, and in case when only one worker dug (six pairs), she was the active partner to the other ant that was the inactive partner to her, and when both did not dig at all (seven pairs), they were inactive partners to one another. Thus, in classifying whether a worker was an active partner or an inactive one only her SSE was considered first, as the purpose was to test if the signal is emitted as a worker digs.

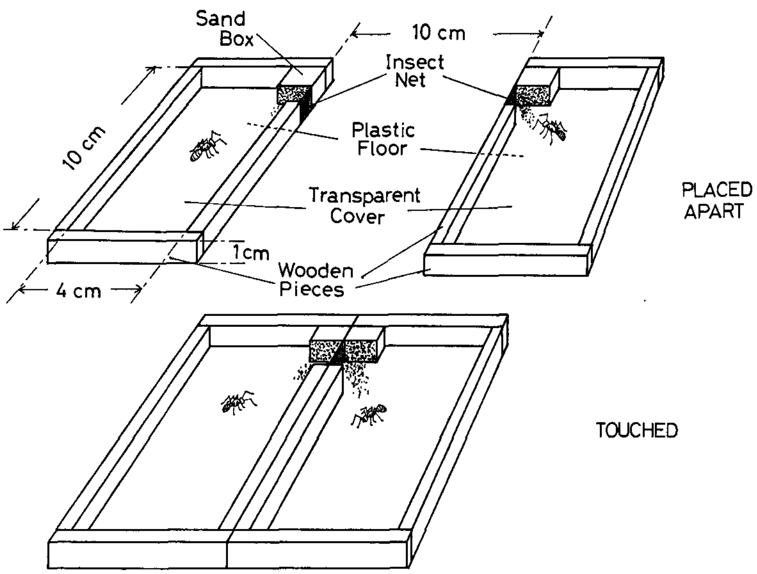

Fig. 4. The pair of cells to test the presence of a nonvisual signal stimulating digging between the workers.

Activity change (SSE–SE) in each worker showed that as to the 28 workers each provided with an active partner, the mean change (M) with s.d. was 58 ± 72 mg, and the possible range of the mean value was $30 < M < 86$ mg at 95% significance degree. As to the other 20 workers with inactive partners, the mean activity change (m) with s.d. was 4 ± 57 mg and $-23 < m < 31$ mg. The M is larger than m at 99% significance degree. Thus, it was apparent that active partners had the facilitating effect, while inactive partners had little such effect (Fig. 5). And the effect was realized through a non-visual signal. As shown in the figure, the two groups seemed to be nearly identical to each other in their efficiencies as solo diggers. Therefore, if the activity changes in the 28 workers had occurred without respect to the partners, a similar activity change should have taken place also in the 20 workers.

Nextly, the effect of partners' SEs was examined. The SEs of ten of the 28 active partners were zero, and workers provided with each of these solitarily inactive ones showed the activity change 76±88 mg, the mean value being significantly larger than zero. The other 18 workers provided with partners active under both conditions gave the activity change 47±63 mg, a significant increase. But the difference between the two mean values was insignificant (Table 1). As to the 20 partners inactive in the semi-pairs, on the other hand, seven of them were active in solitude. Workers provided with these solitarily active ones showed the activity change 34±69 mg, though this was not a significant increase. The other 13 workers whose partners were inactive under both conditions gave the the change -12±45 mg, an insignificant decrease. However, the difference

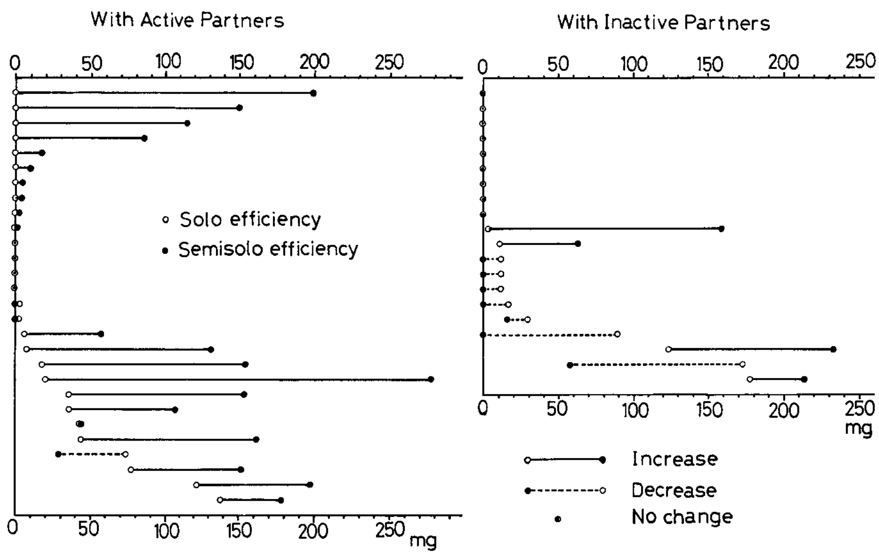

Fig. 5. The activity change in individuals. The workers provided with active partners and those with inactive partners are shown separately.

between the latter two mean values was significant at 90% confidence level. Thus, the seven partners that had dug shortly before may have been somewhat stimulating partners, and the 13 partners that were wholly inactive may have had a weak retarding function. That such effect of partners' SEs was not detected in the 28 workers may have been because it was covered with the later effect from the SSEs. Further, it should also be examined whether the SE values of the workers are related to their own activity changes. As for the 28 workers with partners active in semi-pairs, 14 of them showed the zero SE, and their activity change or increase was 43±67 mg (>0). The other 14 being active in solitude gave the change 73±77 mg (>0). The difference between the mean

Table 1. A statistical analysis of the effects of her partner's SSE and SE, and SE of herself on the activity change in each worker. C: The probability that the ratio of individuals showing activity increases should be equal to or less than the actually observed one given by real numbers in brackets on the right, calculated on the assumption that each worker achieves an increase at the probability of 0.5. When the C is larger than 0.5, a higher probability for the increase should be assumed with each worker. $C=(1/2)^n \sum_{r=0} \binom{n}{r}$. t: The value obtained under the null hypothesis, the mean activity change=0, in each population. F: A comparison data for the s.d. difference between the two populations. T: A comparison data for the difference between the mean values. Gothics, significant activity increases at 95% or more confidence levels, and italics, at 90% level. (+) Active. (0) Inactive.

Partner's SSE (+) and			
partner's SE		SE of herself	
(+) or	(0)	(+) or	(0)
t=3.165	**t=2.731**	**t=3.547**	**t=2.401**
P(t>2.982)=0.01	P(t>2.685)=0.025	P(t>3.373)=0.005	P(t>2.160)=0.05
C=0.952(12/18)	**C=0.999(9/10)**	**C=0.993(11/14)**	*C=0.971(10/14)*
F=1.951	P(F>2.494)=0.05	F=1.321	P(F>2.580)=0.05
T=1.007	P(T>1.706)=0.10	T=1.139	P(T>1.706)=0.10
Partner's SSE (0) and			
partner's SE		SE of herself	
(+) or	(0)	(+)	(0)
t=1.304	t=−0.962	t=0.294	t=0
P(t>1.943)=0.10	P(|t|>1.782)=0.10	P(t>1.813)=0.10	P(t>1.72)=0.10
C=0.227(2/7)	C=0.011(2/13)	C=0.274(4/11)	C=0.002(0/9)
F=2.351	P(F>2.996)=0.05	**F: significant, though incalculable**	
T=1.817	*P(T>1.734)=0.10*	T: insignificant, though incalculable	

values was not significant. As to the 20 wokers provided with partners inactive in semi-pairs, nine of them showed zero SE, and their mean activity change was 0±0 mg. The other 11 were solitarily active, and the change 7±79 mg, an insignificant increase. There seems to be little difference between the mean values, but the s.d. of the nine workers was significantly small. This seems to show that turning active requires some special stimulations from outside or inner psychophysiological changes taking place only occasionally. That the s.d. values (67 and 77) in the 28 workers did not show significant difference from each other may have been derived from the strong effect of the partners active in semi-pairs. It is concluded that the presence of the partners active in semi-pairs had the major importance in the activity increase, though partner's SEs may also have had some effect. This indicates that the stimulus is sent out mainly during the behavior of digging. Further, ten in the eleven pairs in which both individuals were active in semi-pairs showed coupled increases of the activity. This may mean that most diggers are able to stimulate others.

Finally, behavioral observations have left one problem; The beginning of digging by one worker did not immediately cause the behavior in the other individual. Therefore, emission of an effective signal may only sometimes take place, or the receptor worker may not always be responsive, owing to some psychological conditions changing in herself, or she needs a summation process of the stimulation before responding. In order to show which explanation is correct, what the signal is should first be clarified.

A Possible Source of the Stimulating Signal

Wilson (1958) and Crew and Fletcher (1974) reported that the mandibular gland substance can release digging in *Pogonomyrmex badius* and *Paltothyleus tarsatus* respectively, though the substance is widely regarded as an alarm pheromone in many ant species (Blum 1974, Blum and Brand 1972, Wilson 1971). In the present study it was confirmed that this substance comes out at the moment when the mandibles are forced to open. This is easily observed by forcing the mandibles of a separated head of *Camponotus japonicus* to be opened with a needle under a binocular microscope of about 20 ~ 50 times magnification. By repeating the opening and closing of the mandibles, the emission is observed at each opening though the amount of the substance coming out decreases gradually. Since the gland is equipped with no muscles, emission of the substance requires extra pressure from the body fluid. It seems that when the mandibles are opened the glands are pulled forward, receiving extra pressure from the body fluid in the head cavity, and by this pressure some of the substance is pushed out and runs along the groove on the mandibular surface (Fig. 6). The other way for the ants to obtain such pressure seems to move the infrabuccal chamber or the pharynx. Further, by moving these organs coordinately with mandibles ants may achieve some delicate control of the pressure. Therefore, diggers may emit the substance in accordance with the quick mandibular movement, and the substance emitted may stimulate other's excavation. In relation to this assumption, it may be expected that the activity change in a worker is correlated with her partner's SSE. But the

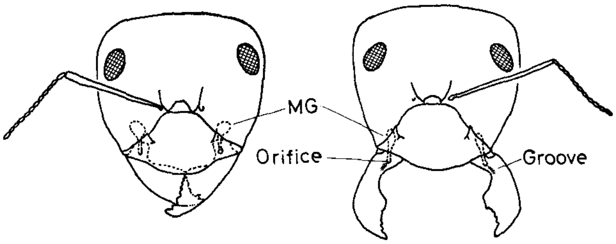

Fig. 6. The forced emission of mandibular gland (MG) substance. By forced opening of a mandible a droplet of the substance comes out and runs along the groove.

correlation was relatively low (r=0.23). This may mean that the SSE is largely affected by her own motivation to dig, or that the amount of the substance emitted per standard digging performance varies individually. The possibility that the mandibular gland substance is widely a chemical releaser of digging in ants is not neglected even though there have been only two studies reporting such an éffect. The glandular substance may be multifunctional, being something of an excitor, and what behavior it elicits may depend on the receptor animal and/or some external stimuli.

Discussion

The previous authors (Chen 1937, Sakagami and Hayashida 1962, Sudd 1972) reported the occurrence either of the social facilitation or of inhibition in each species studied, but the present Experiment A has shown that both phenomena take place in one species with different types of workers exhibiting different group effects. Sudd (op. cit.) showed that in groups animals spend much time for social grooming, a behavior of course impossible for solo ants, and the time loss was correlated with the decreased efficiency in groups compared with that in solo working. Therefore, it seems probable that the social inhibition of digging occurs in every group, as grooming and mutual antennation are the dominant responses when workers meet. But this effect will not persist if the facilitation cuts in with a stronger power. Exp. B indicates that diggers send out a non-visual signal that stimulates nearby workers to join in the task, and the latter ones facilitate back the former. Therefore, when one worker starts digging at her own "will" in spite of the inhibition or objection from the interindividual behaviors, some workers in the mood for digging will be stimulated to dig and there will be the social facilitation among the diggers exclusively. The first worker has to have a particularly strong motivation to dig. After all, the group efficiency will be largely affected by the relative strength of the inhibition from the interindividual behaviors and of the facilitation among diggers. It is now required to assay the two effects separately. How can this be done ? Let's imagine a concrete case. "Two workers are placed together in a cell. Some time later one worker starts digging, breaking the inhibition from the interindividual behaviors. For a while she keeps on digging by herself, sometimes making contacts with the other. The contacts reduce her digging efficiency, while the signal she emits stimulates the other. If her stimulating effect on the other is stronger than the inhibition counter enforced by the latter, the latter is made to dig, and the cooperative digging is realized". Three stages are classified here: Period before digging (BD): Solo digging though with occasional contacts with the other ant (SD): Cooperative digging (CD). The effect of the partner worker would be inhibitory in the first two stages but facilitatory in the last stage. In comparison with the condition of perfect solitude (one worker in one cell), the first stage BD should last longer, and the work efficiency on the second stage lower, but the efficiency on the last stage higher. The work efficiency here is defined as, weight of soil dug/practical time spent for the task. When the effects from the first two stages overpower that of the last stage, the result is the social inhibition, and vice versa. BD and SD can be measured or assayed directly and by repeated tests the mean values can be obtained with each worker. And CD is obtained by subtracting the sum of the first two from the total (by means of incorporating some kinds of estimations).

I assume that the mutual opposition in previous studies was caused by the inadequate experimental method which did not treat the inhibitory factors and the facilitatory one in a discriminative manner, or the results could have been basically similar. The only difference seems to be that in Chen's experiment the facilitatory effect was dominant but in others' the inhibition subduced the facilitation. Which effect overpowers would depend partly on the shape and size of test cells. As the inhibition is caused from those interindividual behaviors, narrow or small cells, such as those adopted by Sakagami and Hayashida (op. cit.) and Sudd (1972), in which the workers frequently meet each other would let the ants perform the inhibition, and spacious ones like those used by Chen (1937) and the present author would allow the ants to realize the facilitation. Further, the quality or type of wokers also affect the group efficiency as shown in Exp. A, the Ra (restless aggressive) workers achieving the facilitation mainly and Cc (clustery coward) workers the inhibition considerably. Although Sudd (op. cit.) used aggressive workers of *F. lemani*, they showed the inhibition. This may be due to the small cell adopted or a case of species difference. Sakagami and Hayashida (op. cit.) did not choose particular types but tested a great number of individuals, showing the inhibition. This may mean that the mean group effect in a whole natural colony falls in the inhibitory range, considering also that narrow tubes were used which were somewhat resembling the narrow spaces in natural nests. That the mean effect is inhibitory may be adaptive for the ants, as nondiggers in the system of labor division, who occupy a large part of the colony population, should not stimulate each other to dig. But there would be the facilitation among diggers exclusively. Although facilitation may be weakened in the narrow nest space and even cancelled out thoroughly, it is still more adaptive for the ants to have it than nothing. Chen (op. cit.) used good diggers selectively, and the facilitation took place. In Exp. A the Ra workers, which showed the facilitation, were presumably hunters. Those individuals were collected in May and tested in early June, when budding is particularly frequent in this species on Ishikari Shore (Ito 1973), and it is hunters that dig or start the bud nests (cf. Imamura 1978). Therefore, the workers tested are assumed as having been good diggers at least in that season. Those workers showing the facilitation in Exp. B were also good diggers selected carefully, though collected and tested in August, when the budding season was over. Contrary to them, the Cc workers, which were clustering ones presumably in natural nests, did not show the facilitation as the dominant phenomenon. Summing up, labor division should be considered in studying the group effects, on the basis that the inhibitory factors and the fcilitatory one are discriminated from each other. The present classification in Exp. A was taken first for the convenience sake; to show the inhibition the Cc workers seemed to be the best subject, and, as the opposite, non-clustery (or restless) ones had to be tested. Among restless workers aggressive ones were chosen as a representative population for their behavioral unity, which was helpful in achieving the random groupings on the second day, which were pre-requisite to the later analysis with GE free from group effects which were estimated by means of using random numbers.

Moreover, to clarify the mechanisms realizing the facilitation is required for detailed analyses of the phenomenon. Although only the mandibular gland substance could be suggested as a possible source of the stimulation, there may be others to be pursued. In order to explicate this problem, the role of the substance should first be tested. For this purpose I tried to seal the glandular orifice with several sticking chemicals or bee wax, but these materials were soon wiped off as the mandibles were rubbed against the clypeus at closing. I tried also to plug the orifice with a tibial hair which fitted it perfectly without bothering mandibular movement, but this treatment seemed harmful to the animals; after a night they moved only slowly and never dug. The operation may have injured them physically, or the stoppage of the substance emission may have discouraged them seriously. The direct microscopic observations on digging intact workers of *Camponotous japonicus* have not been successful to confirm the emission under 20 X magnification. But this may be possible with ants provided with larger mandibular gland, such as *Calomyrmex* whose mandibular gland substance is smeared on the floor of the nest when alarmed (Brough 1978). Thus, the emission of the substance during digging and stimulation of other workers by it remains as a hypothesis.

Finally, it may be questioned why the mutually opposite traits exist in one species. During the evolutionary course of the species one of the traits could be selected for it was adaptive, then the direct opposite trait should be mal-adaptive. The presence of such two traits in one species is thus puzzling and no complete answer is given, but I will just place an idea that the fact is not necessarily against the theory of natural selection. When solitary ancestor individuals came to form a community, they reduced digging since much intranest space could be shared. Here the social inhibition was required to be selected for. However, the nests inhabited by many individuals inevitably grew larger than in the solitary days, and another problem arose; the complexity of nest structure had to be kept minimum, or the individuals being fit to using simple structures could not make good use of the big nest. Therefore, several workers had to cooperate to make one large chamber instead of separately excavating many small chambers. Here the stimulating signal was necessary to attract workers that were in the mood for digging, so that the cooperative excavation could be realized. The stimulation ability may have been selected also to concentrate the work at certain moments in the life history as the quick establihsment of chambers enables their longer use. The stimulation was selected not to increase the amount of digging task each indidivudal was to do in her whole life, but to concentrate work. Thus, the acquisition of the mutually opposing traits seems not impossible.

Summary

Social modifications of digging activity were studied with *Formica yessensis* Forel with the following results:

1) The mean weight of soil dug by eight restless aggressive workers in a group in 1 hr gave the distributions (mean with s.d.) 57 ± 23, 170 ± 48, 80 ± 30 mg during three successive days respectively. Thirty two groups were tested. The first and the third ones are those estimated under the condition in which there was no group effect at all, based upon the data of their solo performances, but the second one was actually observed. The comparison shows that the social facilitation took place, raising the mean value conspicuously to 170 mg, and further the effect of grouping was various among different combinations of the workers, as shown by the significantly larger s.d. 48 mg.

2) The groups of eight clustery coward workers showed 35 ± 21, 62 ± 46, 100 ± 28 mg, the first value and the third one estimated as above. The s.d. on the second day was significantly larger than the others, suggesting the occurrence of some group effects, though the mean value 62 mg did not show any group effect. That there were nine groups exhibiting no digging on the second day was little probable ($P < 0.001$) if it were not for some social inhibition. Perhaps, clustering caused the inhibition.

3) In either type of the workers, excavation of a common tunnel was observed, suggesting the possibility that the diggers sent out a signal stimulating other workers to join in the task. In groups of clustery coward workers, social facilitation may also have taken place, balancing out the inhibition and consequently giving the intermediate mean value.

4) By comparing the weight of sand a worker dug in solitude with that she did in the presence of a partner in the next cell sectioned from hers by three pieces of fine insect net, it became evident that workers dig more efficiently when provided with active partner diggers, and the stimulating signal is a nonvisual one, propagated through such nets or substratal vibration.

5) Anatomy of the head of *Camponotus japonicus* suggests that the mandibular gland substance may mechanically be emitted in accordance with the mandibular movement during digging. The substance may be the stimulating signal, as it has been shown to elicit digging in *Pogonomyrmex badius* and *Paltothyleus tarsatus* though it is widely known as an alarm pheromone.

6) Assuming social grooming and clustering reduce ants' efficiency in digging, the social inhibition seems everywhere workers meet. But diggers are assumed as facilitating each other. By the relative strength of the opposing factors the group activity would be largely affected. The discrepancy in previous studies may be understood as being caused by the difference in the relative strength which was probably due to the choice of worker types and the shape and size of the test cells.

7) The presence of the mutually opposing traits in one species is puzzling from the evolutionary view point, requiring further investigations.

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