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ACTIONS OF HALLUCINOGENS ON ANTS (*FORMICA PRATENSIS*)—II. EFFECTS OF AMPHETAMINE, LSD AND DELTA-9-TETRAHYDROCANNABINOL

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Abstract—1. D,L-Amphetamine sulfate, D-lysergic acid diethylamide tartrate (LSD) and delta-9-tetrahydrocannabinol (THC) were administered to ants in several doses either orally in food, or by injection into the abdominal cavity.

2. Amphetamine, injected in doses of 1 or 10 μg/ant caused an increase in intraspecific aggression. Sugar-water containing 1 or more mg/ml amphetamine was generally refused.

3. Application of 20 ng LSD or more by either route typically impaired locomotion. Dependent on the dose administered, these symptoms vanished, or led to death.

4. To dissolve THC, we mixed 10 vol% of Tween-80 with physiological NaCl-solution, or with sugar-water. Drug doses of 2 μg injected, or 3–4 μg orally did not cause conspicuous changes in behavior.

INTRODUCTION

The increasing abuse of psychogenic drugs in human society is an important problem to solve. To this purpose, we are engaged in exploring the mechanisms of drug action and behavioral alterations caused by these substances (Waser, 1971; Waser *et al.*, 1976). Many hallucinogenic drugs are structurally related to norepinephrine, dopamine or 5-hydroxytryptamine. The almost universal occurrence of these neutrotransmitters in animal kingdom (Fischer, 1971), and the importance of social components involved in the cause of drug dependence stimulated our aim to test psychogenic substances in social insects.

We selected ants for these investigations because their reduced flying capacity allows experiments under controlled laboratory conditions. The biology and behavior of ants is well known and was summarized by Sudd (1967) and Wilson (1971). However, pharmacological experiments on ants are scarce. Steiner & Pieri (1969) administered substances with presumed neurotransmitter function iontophoretically through a multibarrelled microelectrode to the ants' brain and recorded the activity of these neurones at the same time. Kostowski and his group investigated in a series of experiments (1965–1975) the effect of many substances on the aggressive behavior of ants and on the bioelectrical activity of their optic lobes.

In this paper, we examined the behavioral and toxic effects of amphetamine, LSD and delta-9-THC in individual ants. In a previous report (Frischknecht & Waser, 1978) we summarized our investigations on the uptake of orally administered LSD and THC into the ants' brain. Another publication concerning the effects of these substances on social behavior of ants is in preparation.

MATERIALS AND METHODS

Animals

We always used worker ants of the species *Formica pratensis* Retz, taken out of a colony on the "Pfannenstiel" (13 km south-east of Zurich). We kept them in our laboratory in a formicar (60 × 60 cm) with their genuine nesting material and we made sugar-water (250 mg/ml sucrose) available to them.

Drugs

The following drugs were used: D,L-amphetamine sulfate (Cantonal Pharmacy, Zurich); D,L-methamphetamine-HCl (Cantonal Pharmacy, Zurich); D-lysergic acid diethylamide tartrate (Sandoz, Basle); (−)-trans-delta-9-tetrahydrocannabinol, purity 97% (DHEW Public Health Service NIHM).

Procedure

The drugs were either injected into the ants hindquarter, or administered orally in the food.

For drug injections, amphetamine (0.05, 0.5, 5 or 50 mg/ml) as a sulfate and LSD-tartrate (1, 10 or 100 μg/ml) were dissolved in 0.8% NaCl-solution. With THC (1 mg/ml), 10 vol% of Tween-80 were mixed with the solvent. The ants were narcoticized with ether until they lay down and their coordinated leg movements disappeared. Glass capillaries, calibrated to 2 μl, were used as microinjection needles. The needle was inserted from caudal direction through the unchitinized membrane between the first and second gastric tergites into the ants abdominal cavity. In all cases we noted the time interval from injection to awakening from narcosis, beginning of crawling, running and showing aggressive behavior. The first two activities occurred spontaneously, aggressive behavior was provoked by the approach (threat posture) and touching with a probe (seizing). Moreover the occurrence of peculiar activities was recorded and the general condition of the insects was estimated according to their locomotion ability 2 hr after injection.

With large groups of ants, or in experiments where more frequent doses were used, only oral drug application is feasible. Amphetamine (0.1–50 mg/ml as sulfate) was dissolved in sugar-water containing 250 mg/ml sucrose. LSD-tartrate was mixed with the food in concentrations of 1 μg/ml–1 mg/ml. THC (1 mg/ml) was suspended in an emulsion of sugar-water containing 10 vol% of Tween-80. In all experiments the food was offered to starved ants. The uptake was observed and the subsequent occurrence of behavioral effects and deaths were noted.

With regard to subsequent analyses of drug effects on social behavior of ants, two questions have to be asked:

(1) Does a preference exist between drug- and control-food?

(2) Does the drug uptake alter usual grouping of ants?

Food preference was tested between sugar-water (250 mg/ml sucrose) and food containing 100 μg/ml LSD, or between control-food containing 10 vol% Tween-80 and solutions with 1 mg/ml THC added. In all experiments, 50 worker ants were fed after 3 days of starvation with either control-food or drugged food. After another 3 days of fasting, they received control- and drugged food simultaneously. During the first 10 min we recorded food preference by taking a photograph every 2 sec with a super-8-camera (Vivitar 98 PM, single picture shooting). We counted the number of ants visiting control- and drugged food, determined the percentage of visitors ingesting food for longer than 4 sec (3 pictures) and computed the mean duration of a single food uptake.

To investigate the distribution and group formation of ants, bipartite formicars (32 × 25 cm) were used, holding 50 ants in either half. After 2 or 3 days of starvation, the ants in one compartment had free access to control-food (250 mg/ml sucrose, or sugar-water containing 10 vol% Tween-80) for 1 hr, whereas those in the other half were fed with drugged food (100 μg/ml LSD, respectively 1 mg/ml THC). 2, 9, 24 and 48 hr after food uptake, two photographs at an interval of 1 min were taken of the formicar with a miniature camera (Minolta SRT 101). To evaluate the pictures, either compartment was subdivided into 16 squares and the number of ants determined in each of them. In cases of doubt the ants were localized according to their head. Corresponding to the type of food and the time after feeding, the percentages of ants in the four corner-squares were compared to those in the four central-squares. To evaluate the group formation tendencies, the mean number of neighbours in the same square were computed.

RESULTS

Drug administration by injection

The results of these experiments are summarized in Table 1. Control injections of 2 μl 0.8% NaCl-solution did not cause any detrimental effect in addition to those observed after anesthesia alone. The ants recovered from ether narcosis and began to crawl on average after 5 min, began to walk after 14½ min and showed the typical defense reactions (seizing and threat posture) after 30 min. The behavior of these ants was not impaired 2 hr after injection of NaCl-solution. Nevertheless, after 24 hr, several deaths were recorded. Dissections suggested intestinal injury and infection as the most probable causes of death.

Injections of 0.1 μg amphetamine showed the same results.

Six in ten injected with 1 μg amphetamine writhed very much when anesthesia faded. They couldn't walk within the first half hour on average. Especially worth noting was that 30–90 min after drug administration 5 in 10 ants began spontaneously to fight one another. After 2 hr 1 in 10 had been killed and the other nine walked about continuously in an excited fashion.

Writhing again set in after injections of 10 μg amphetamine in 6 out of 10 ants within a few minutes. Only one ant was able to walk 2 hr after drug administration (5 others within 4–18 hr). On the other hand several ants still suffered from writhing and convulsions. They reared and fell down. One ant seized its own antenna. After 20 hr two ants were vigorously fighting. Another one circled continuously on the spot with only short interruptions.

Injections of 100 μg amphetamine caused serious toxic effects. Only 3 in 10 ants were able to crawl between 3 and 15 min after drug administration. Afterwards all ants lay on their side or back and moved their legs and antennae infirmly. None of them recovered from the effects of this high drug dose.

After injections of 2 ng LSD, about twice as much time elapsed as in the controls with NaCl alone, before the ants began to crawl, to walk and aggressive behavior could be provoked. Nevertheless behavior was not altered and 2 hr after drug administration all ants moved completely normally again.

Likewise after injections of 20 ng LSD, the ants began to walk belatedly and seizing and threat-posture were retarded. The locomotion was rather unsteady and hesitant often for hours. Afterwards 6 ants regained normal movement while the other 4 continued to display fumbling motions with their forelegs in the air at each step.

Injections of 200 ng LSD significantly retarded the occurrence of all observed criteria. The mean latencies were: 20 min to crawl, 40 min to walk and 60 min to show defensive postures. After 2 hr, four ants

Table 1. Drug administration by injection into the abdominal cavity of ether narcotized ants (10 ants/dose)

Drug	Dose	Solvent (2μl)	Latency to Crawl	Walk	Seize	Threat	State 2 hr after injection
—	—	0.8% NaCl	5 min.	14½ min	24 min	30½ min	O.K.
Amphetamine	0.1 μg	0.8% NaCl	ns	ns	ns	ns	O.K.
Amphetamine	1 μg	0.8% NaCl	ns	***	*	ns	partly aggressive
Amphetamine	10 μg	0.8% NaCl	*	***	***	***	partly convulsions
Amphetamine	100 μg	0.8% NaCl	***	***	***	***	severe poisoning
LSD	2 ng	0.8% NaCl	**	***	ns	*	O.K.
LSD	20 ng	0.8% NaCl	ns	*	**	**	impaired walking
LSD	200 ng	0.8% NaCl	**	**	***	***	do. + uncoordinated
—	—	do + 10% Tween	5½ min	17 min	28 min	32½ min	O.K.
THC	2 μg	do + 10% Tween	ns	ns	ns	ns	O.K.

Significantly retarded occurrence of criteria compared with controls:
* $P \leq 0{\cdot}1$.
** $P \leq 0.05$.
*** $P \leq 0.01$, (n.s.: not significant). Wilcoxons ranked-order test.

Table 2. Effect of orally administered drugs in ants (10 or 20 ants/experiment)

Drug	Concentration	Number of experiments	Food uptake	Occurrence of drug effects*	Mortality 5 days	Mortality 10 days
Amphetamine	0.1–0.5 mg/ml	5	very good	no	—	—
Amphetamine	1–50 mg/ml	17	poor	—	—	—
Amphetamine	1–5 mg/ml	3	good	uncertain	0–5%	—
LSD	1–10 μg/ml	9	very good	sporadic in full-fed ants	0–5%	0–15%
LSD	30–50 μg/ml	11	very good	sporadic in full-fed ants	0–10%	0–20%
LSD	100 μg/ml	9	good (delayed)	frequent in full-fed ants	10%	25%
LSD	300–500 μg/ml	8	good (delayed)	always in full-fed ants	15%	45%
LSD	1 mg/ml	4	moderate	in all ants	40%	100%
THC	1 mg/ml	2	very good	no	0–5%	

* For specification see text.

moved uncoordinatedly and two typically fumbled with their forelegs at each step. Nevertheless, mortality was not increased.

Injections of 2 μl 0.8% NaCl-solution containing 10 vol% of Tween-80 used as solvent for THC, did not exhibit any differences to NaCl-controls.

After injections of 2 μg delta-9-THC, the same effects as with the control were observed and no behavioral changes were noticed.

Oral drug administration

In all experiments the ants were fed on sugar-water containing 250 mg/ml sucrose. First we determined food uptake quantitatively. After three days of starvation, mean body weight of 24 individual worker ants was estimated to be 11.2 mg (minimum 6.0 mg, maximum 17.7 mg). The hindquarters of these ants were extended and body weight was increased to 15.2 mg 1 hr after feeding with sugar-water (extremes 10.5 and 21.4 mg). Taking the specific weight of the sugar-water into consideration, the food uptake amounted to 3.6 $\pm$ 0.2 μl.

The findings of all experiments with oral drug administration are summarized in Table 2. In each series 10 or 20 ants/test were used.

Amphetamine was dissolved in concentrations from 0.1–50 mg/ml in sugar-water. Starved ants ate much food containing 0.1–0.5 mg/ml amphetamine but later on no behavioral effects were conspicuous. From 20 series with drug concentrations of 1, 2.5, 5, 10, or 50 mg/ml amphetamine, food uptake was very poor in almost every case. The ants simply tasted the solution and then retreated from it. They often rubbed their mandibles on the ground, or vigorously attacked the food reservoir. In only 3 of the 20 experiments, which included the smaller concentrations i.e. 1, 2.5 and 5 mg/ml of amphetamine was food taken up well. But later on, no behavioral defects could be detected. In two series however, ants carried nestmates several times into a corner of the formicar. Individual workers transported up to 4 ants per min in a stereotyped manner, and within 15 min over 150 such activities were noted. This carrying did not occur in control experiments and was rarely seen otherwise in our laboratory. Mortality was not increased by feeding ants with sugar-water containing up to 5 mg/ml amphetamine.

The mostly poor uptake of food with 1 or more mg/ml amphetamine might be due to the slightly bitter taste of the drug. Sugar-solutions containing the bitter substance, quinine (0.5 mg/ml), were always refused by ants. Likewise food containing methamphetamine was either tasted only (1 mg/ml) or rejected (5 mg/ml) completely.

From a series of 41 experiments with sugar-water containing LSD in concentrations of 1 μg/ml to 1 mg/ml, a good picture of the drug effects on behavior was established. Locomotion was slowed down and the ants moved with little steps. These ants often fumbled with their forelegs in the air at each step. The head was kept elevated and the antennae were stretched out and agitated. These ants often avoided the approach or touch with a probe instead of showing threat posture and seizing.

The uptake of sugar-water containing 1–50 μg/ml LSD was always very good. But only occasionally, ants with extremely extended hindquarters showed the above-mentioned drug effects. The uptake of food holding 100 μg/ml LSD was sometimes delayed. Nevertheless, the next day numerous ants had extremely filled gasters, indicating a good food uptake. A good many of them showed the typical LSD-effects described above. But these effects disappeared in almost all cases, thus increasing the mortality rate only slightly. With sugar-water containing 300 or 500 μg/ml LSD, ants initially hesitated to eat but later on food uptake was good. All ants with extremely extended hindquarters showed intense drug effects. In part, a second phase of LSD-intoxication was reached. The locomotion of these ants became uncoordinated. They lost the ability to balance and fell over. These ants had increasing difficulties to stand up again, showed a general impaired condition and often died within a few days. Thus mortality after 10 days was significantly increased. Uptake of sugar-water containing 1 mg/ml LSD was only moderate. Nevertheless all ants showed drug effects within a few hours and always reached the second phase of intoxication. All of them died within a period of 10 days.

The studies using Tetrahydrocannabinol had the

Table 3. Preference tests between control-food (C) and food containing drugs (D)

Series	Last feeding three days ago (C or D)	Test-feeding C and D		Number of ants visiting C	D	% Visitors feeding ≤ 4 sec C	D	Mean duration of food uptake at C	D
1 a	SW	SW	LSD	42	35	56	46	29 sec***	14 sec***
1 b	LSD	SW	LSD	38	33	63**	48**	31 sec	26 sec***
2 a	Tween	Tween	THC	35	37	58	54	25 sec	22 sec
2 b	THC	Tween	THC	38	41	65	64	23 sec	25 sec
				Wilcoxon test for matched pairs				Wilcoxon ranked-order test	

SW: Sugar-water (250 mg/ml sucrose)
LSD: SW containing 100 μg/ml LSD-tartrate
Tween: SW holding 10 vol. % Tween-80
THC: Tween containing 1 mg/ml delta-9-THC
Levels of significance:
* $P \leqslant 0.1$.
** $P \leqslant 0.05$.
*** $P \leqslant 0.01$. (others not significant).

difficulty in oral drug application of its low water solubility. 1,2-propylenglycol as well as olive oil were not eaten, but after it became smeared over antennae and eyes of careless ants, it caused excitations and bursts of intraspecific aggression. Finally we suspended the THC in sugar-water containing 10 vol % of Tween-80 as an emulsifier. The uptake of such a solution with 1 mg/ml THC was very good. But subsequently no distinct behavioral changes could be observed, not even after repeated drug administration.

In the succeeding experiments, the following four food qualities were used:
SW: Sugar-water (250 mg/ml sucrose)
LSD: SW containing 100 μg/ml LSD-tartrate
Tween: SW holding 10 vol% Tween-80 as an emulsifier
THC: Tween containing 1 mg/ml delta-9-THC.

Food preference tests

The results of 10 food preference tests between SW and LSD, with 50 ants each, are summarized in Table 3 (series 1).

The frequencies of visits were slightly (but not significantly) increased for SW compared with LSD, independent of whether the ants were control- or drug-fed 3 days previously (series 1a, respectively 1b). The number of visitors feeding longer than 4 sec was greater at SW than at LSD (1a ns., 1b $P \leqslant 0.05$). Furthermore, the mean duration of a single food uptake was significantly shortened at LSD in ants having first contact with the drug (1a $P \leqslant 0.01$). These findings suggest a preference for SW compared with LSD during the first 10 min following food presentation.

In an analoguous series of 10 experiments (Table 3, 2a and 2b) food preference between Tween and THC was investigated. No difference whatever in number of visitors, percent which eat and duration of uptake could be detected, independently of whether the ants were new (2a), or had drug experience once (2b).

Group formation tests

The results of five experiments with SW- and LSD-fed ants, analogous to the series with Tween and THC are summarized in Table 4.

The distribution of the 50 ants among the 16 squares of either half of the formicars in SW/LSD- and Tween/THC-experiments displayed striking resemblance. With all four food qualities the ants preferred the corners-squares compared with the centre-squares. This preference was most pronounced 9 hr after food uptake (greatest gathering in the corners and lowest accumulation in the centre), whereas 48 hr after feeding this latency was weakest. Differences between control- and drug compartments were rare: 2 hr after THC-uptake the gathering of ants in the four corner-squares was increased compared with Tween, and 9 hr after LSD-feeding the accumulation of ants in the four centre-squares was lower than with SW. The mean number of neighbours in the same square decreased from nine to 24 hr following oral

Table 4. Distribution and group formation of ants in bipartite arenae, subdivided in 16 squares

	Food	Time after food uptake 2 hr	9 hr	24 hr	48 hr
Percentage of ants in the 4 corner squares	SW	32.3	37.8	36.0	29.7
	LSD	33.6	43.2	36.5	33.2
	Tween	35.8**	38.8	33.4	32.8
	THC	42.8	42.5	36.3	31.1
Percentage of ants in the 4 centre-squares	SW	13.7	13.5**	18.5	18.5
	LSD	16.0*	10.5***	19.8	19.2
	Tween	11.7	11.2	16.2	20.4
	THC	12.6	11.5	15.3	18.4
Mean number of neighbours in the same square	SW	6.7	7.1	6.5	6.6***
	LSD	6.1	6.4**	5.1	5.4
	Tween	7.1	6.9	9.4	8.0
	THC	7.2	7.1	8.5	6.8

Statistics: Comparisons between times with Wilcoxon ranked-order test. Comparisons between control- and drugged food with Wilcoxons test for matched pairs. Levels of significance:
* $P \leqslant 0.1$.
** $P \leqslant 0.05$.
*** $P \leqslant 0.01$. Others not significant.

administration of LSD and 48 hr after LSD-uptake it was significantly reduced compared with SW-controls. Altogether, LSD slightly reduced the tendency of group formation 1 and 2 days following drug uptake in comparison to the controls, whereas THC had no influence on the distribution of ants in a formicar.

DISCUSSION

Sugar-water with amphetamine concentrations of 1 mg/ml or more was generally refused in our experiments with worker ants of the species *Formica pratensis*. Other species seemed to be not so selective. In preliminary investigations with *Formica cinerea*, uptake of food containing 5 mg/ml amphetamine was very good. Kostowski (1966) administered amphetamine orally to *Formica rufa* in a dose of 1 mg/g of ant, for which drug concentrations of 3–5 mg/ml in the food might have been necessary. Kostowski likewise did not find any conspicuous drug effects: aggressive behavior towards Geotrupes beetles was not changed and spontaneous bioelectrical activity of the head ganglia was not impaired (Kostowski *et al.*, 1965). This contrasts with results of Floru *et al.* (1969) in hornets. They found, even after small oral doses of 0.3–1.3 μg/g, unrest, hyperwakefulness and aggression towards members of their own colony. Amphetamine in oral doses of 12–35 μg/g inhibited all social activities, caused convulsions and some hornets even died. In our experiments, amphetamine was injected for the first time into the abdominal cavity of ants. After administration of 1 or 10 μg/ant (about 75 respectively 750 μg/g) we could also observe unrest, increased intraspecific aggression and convulsions. Altogether, these results suggest, that the effectiveness of amphetamine is very much higher in hornets than in ants.

LSD caused typical and conspicuous changes in locomotion of ants. We found these impairments after injection of 20 or 200 ng of LSD-tartrate (about 1.5 respectively 15 μg/g), as well as after oral drug application. Sugar-water with 100 μg/ml LSD (resulting in doses of about 25 μg/g) caused these effects in a good many of the full-fed ants. At drug concentrations of 300 or 500 μg/ml (about 75–125 μg/g), some ants showed toxic effects in addition, and the uptake of food with 1 mg/ml LSD always caused the death of the ants within 10 days. Likewise Kostowski *et al.* (1972) established the sporadic occurrence of ataxia and unusual movements in ants after injection of 30 μg/g LSD. Unfortunately these behavioral impairments were not described in detail. In addition these authors reported a decrease in interspecific aggression 1–3 hr after drug application and changes in EEG pattern. In an earlier paper, Kostowski (1966) found one to three hours after oral administration of 25–100 μg/g LSD a decrease, and 18–24 hr after drug application an increase, in ants' aggression against Geotrupes beetles. Again, Floru *et al.* (1969) ascertained drug effects at very low LSD-doses in hornets. Taken orally 0.6–1.2 μg/g LSD caused hypersensitivity, increased aggression, slowed locomotion, spastic movements and tonic convulsions. Our results do not indicate an increased aggressiveness in LSD-treated ants. On the contrary, they often avoided contact when touched, instead of showing defensive reactions. Perhaps this might be connected with a tactile hypersensitivity or altered sensory perceptions. The reduced tendency for grouping one and two days after feeding with LSD could be explained by the same mechanisms. The significant decrease in group formation occurred between 9 and 24 hr after LSD administration, thus coinciding with the period of maximal drug concentration in the brain of these ants (Frischknecht & Waser, 1978).

THC, the active principle of hashish was administered in our experiments for the first time in insects. But neither injection (about 150 μg/g), nor oral application (250 μg/g) caused any conspicuous changes in behavior.

For continued investigations of drug effects on social behavior of ants, the following findings of this paper are important:

(1) In tests with large groups of ants, or for repeated drug application, the substances have to be given in food.

(2) Amphetamine seems to be unsuitable for this purpose, since mixed in sugar-water it caused the food to be refused or only poorly consumed.

(3) Uptake of sugar-water containing LSD-tartrate was good (delayed at higher doses) and led to dose dependent drug effects. For further investigations, a drug concentration of 100 μg/ml seems to be reasonable. At this dose behavioral changes occurred, but there was only little evidence of toxic effects.

(4) THC was consumed in sugar-water holding 10 vol% of Tween-80. Food containing 1 mg/ml THC caused no conspicuous behavioral changes or toxic effects. Because of increasing difficulties to dissolve the drug in higher concentrations, we used this concentration of 1 mg/ml THC for further experiments.

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