AN INFORMATIONAL ANALYSIS OF ANTENNAL COMMUNICATION DURING TROPHALLAXIS IN THE ANT *MYRMICA RUBRA* L.

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ABSTRACT

Lenoir, A., 1982. An informational analysis of antennal communication during trophallaxis in the ant *Myrmica rubra* L. *Behav. Processes*, 7: 27—35.

Trophallaxis by ants is accompanied by antennal movements which have an informational value. The succession of contacts permits the transmission of information for triggering, maintaining or stopping the exchange. The use of information theory indicates that antennal contacts during trophallaxis quantitatively transmit much less information than some other systems used by social insects (i.e. the dance of the bees or trails of *Solenopsis*). The information transferred by the signal is never more than 20%; the system is not appropriate to conduct important messages but belongs to a modulatory communication system.

INTRODUCTION

The antennae of social insects are very complex organs containing a large number of varied sensorial apparatuses and whose role is more or less well known (cf. Slifer, 1961 for bees; Kürschner, 1969; Dumpert, 1972; Jaisson, 1969 for ants). Social insects often utilize their antennae for beating in situations as diverse as recognition of congeners, emission of alarm signals, recruitment of nestmates, exploitation of a food source or exchange of food through trophallaxis. Antennal communication is particularly important during recruitment phenomena, with highly stereotyped behavioural sequences, termed "invitation behavior" by Hölldobler (1977). For instance, *Oecophylla longinoda* utilizes no fewer than five recruitment systems to draw nestmates from the leaf nests to the remainder of the nest tree and the foraging areas. In four of these five systems chemical signals are utilized synergistically with antennal tactile signals (Hölldobler and Wilson, 1978).

Antennal communications during trophallaxis are now well known in wasps (Montagner, 1966) and bees (Free, 1956; Montagner and Pain, 1971a, b, 1973). Concerning ants, we may cite the works of Wallis (1961) and Hölldobler (1970, 1973) in *Formica* and that of Torossian (1973) in *Dolichoderus*.

In a prior publication we described the sequences of antennal movements during trophallaxis in *Myrmica* (Lenoir, 1973). It appeared that the reactions of two ant partners are interrelated to a slight extent. It is difficult to predict the behaviour of an ant by observing that of its partner, therefore an attempt was made to analyze more attentively this system by using information theory.

In all types of communication, the simplest system utilizes two signals: the presence of a stimulus or its absence. One of these alternatives thus represents an information unit, i.e. a bit.

A communication system requires the presence of two individuals: one emits the signal, the other receives it. In the present case, the donor ant and the receiver ant are alternatively or simultaneously emitter and receiver. Such a system also requires the presence of an information repertory common to the two individuals. In the case of trophallaxis, this repertory is composed of the different types of antennal movements; the association of the elements (acts) in sequences constitutes the message whose significance is not always clear for the observer who attempts to translate it into his own language. The message is transmitted physically; in the present case mechanically (tactile and proprioceptive).

The message is often disturbed by parasite emissions which are termed noise in terms of the reference channel. Noise in the present case is in two forms. The first is the crowding of the colony: during trophallaxis involving several ants, there is a large quantity of tactile stimulation. There is a second form, which is olfactory perception, which perturbs antennal rituals. When another ant is in the immediate proximity, it can be observed that the antennae of the donor, and occasionally those of the receiver, are momentarily directed toward the third ant.

The remaining characteristic of this communication system is the existence of a learning period. This has been demonstrated in wasps (Montagner, 1966; Montagner and Pain, 1971a, b, 1973). It has been known for a long time that exchanges among young worker ants are imprecise and rare (Heyde, 1924) but the need for a detailed study of antennal sequences in young ants still remains.

All essential conditions are thus present to affirm the existence of an antennal "language" in ants. The information value of this language can be evaluated according to the information theory of Shannon (after Atlan, 1972; Losey, 1978).

MATERIALS AND METHODS

Antennal movements were studied with cinematographic techniques. Colour film was utilized at 80 or 150 frames/s. Only exchanges between two ants were filmed. Several hundred metres of film were studied frame-by-frame, corresponding to seven sequences of trophallactic exchanges (total 90 s, 9700 frames). In two sequences, the exact positions of antennae and contact zones were noted in workers starved for several days.

TABLE I

Frequency distribution of intraindividual two-act sequences of receiver during trophallaxis (Sequence 2)

x_i \ x_j	Funiculus LA	Scape LA	Base LA	Vertex	Interantennal space	Thorax	Base RA	Scape RA	Articulation RA	Funiculus RA	Total	$P(i)$	Eqn. 1 $H(x_i)$	Eqn. 2 $H_M(x_j/i)$
Funiculus LA	2	3	1		1		1	1			9	0.046	0.204	0.112
Scape LA	4	2	10	3	2						21	0.1076	0.3462	0.2165
Base LA	3	8		2	8		1	1	1		24	0.1230	0.3719	0.2933
Vertex		1	1		3	1		7		2	15	0.0769	0.2846	0.1650
Interantennal space		6	6	2			4	5		2	25	0.1282	0.3799	0.3152
Thorax RA				1		3	1		3		8	0.0410	0.1990	0.0742
Base RA			2		3		1	2		2	11	0.0564	0.2339	0.1222
Scape RA		1	1	4	4	1	1	4	8	6	30	0.1538	0.4154	0.4290
Articulation RA			1	2	1	3		8	8	4	27	0.1384	0.3949	0.3363
Funiculus RA		1	1	1	2	1		5	6	8	25	0.1282	0.3799	0.3229
	9	22	23	15	24	9	9	33	26	24	195	1	$H_{(x)max}$ 3.2009	H_M 2.3758

x_i (initial act) and x_j (following act) = contacts of the right antenna of the receiver on the head of the donor; LA = left antenna of the donor; RA = right antenna of the donor; duration = 30 s (80 frames/s); $R = 1 - (2.3758/3.2009) = 0.2577$ (Eqn. 3).

RESULTS

Only the tactile aspect of antennal relationships will be considered here. Each antennal contact on the head of the partner ant represents one informational element. The various zones touched are supposed to be as many different elements. Ten of these zones were distinguished on the head (Table I); we may call them x_i acts. Their succession represents a "message", in which each act appears with a frequency $P(i)$. The diversity of acts supplied by each antennal contact may then be calculated using the formula of Shannon

$$H(x) = -\Sigma P(i) \log_2 P(i) \tag{1}$$

During palpation, the antenna has, in reality, more than one chance of touching two neighbouring regions and the quantity of information per contact thus decreases. Acts are not independent; an act x_j has a conditional probability $P(j/i)$ of appearance after x_i and this phenomenon can be studied with a Markov matrix (first order). The quantity of information H_M is thus defined as

$$H_M = -\Sigma P(i) \, P(j/i) \log_2 P(j/i) \tag{2}$$

which enables us to calculate the redundancy of the message (Table I)

$$R = 1 - \frac{H_M}{H_{max}} \tag{3}$$

Under these conditions, it can be shown that the diversity of acts during antennal movements depends on the type of activity performed by the ants (Table II).

Sequence 1 is the case of a non-recruiting replete ant which regurgitates almost passively, most often maintaining its antennae spread. The diversity is between 1.1 and 1.8 bits, with a redundancy of about 50%. In Sequence 2, however, the ant is a forager which recruits other ants and often attracts them to force them to accept the regurgitation. Its antennal movements contain 2.5—2.9 bits per contact with a lower redundancy of about 26—35%. In all cases, the diversity showed by antennal strokes of the receiver is greater than that of its partner; 2.2 bits with a replete donor and 3.2 bits with a donor which invites. Redundancy is about 20—26%. It thus appears that receiver activity is much more precise than that of the donor.

The transmission of information between two ants was then studied, in order to determine if the behaviour of one ant was influenced by that of the other. Here, we consider the symbol x_i as the emission of a signal by one partner, and y_j the response of the other. Thus, x_i corresponds to antennal contacts and y_j to the antennal response, which may be the spreading of one antenna (Table III). We define $H(y/x)$, a variable quantifying the predictability of the response of one individual to the acts of the other, as

$$H(y/x) = -\Sigma P(i) \, P(i/j) \log_2 P(j/i) \tag{4}$$

TABLE II

Intraindividual values of quantity of information in antennal beatings during trophallaxis in *Myrmica*

	Tactile contacts of the antenna of the receiver on the head of the donor[a]	Tactile contacts of the antenna of the donor on the head of the receiver	
		Left antenna	Right antenna
Sequence 1	Left antenna		
$H(x)$	2.002	1.8163	1.1221
R (%)	20.46	47.26	51.30
nb contacts	60	18	18
Sequence 2	Right antenna		
$H(x)$	3.2009	2.8919	2.5424
R(%)	25.77	26.55	35.36
nb contacts	195	121	65

[a]The solicitor being on side-face, one antenna only was entirely visible and its movements were analyzed.
Sequence 1: donor regurgitating passively (duration = 10 s; 1500 frames).
Sequence 2: forager soliciting a receiver (duration = 30 s; 2400 frames).

TABLE III

Information transmitted by interindividual antennal contacts during trophallaxis

	Acts y_i of the donor following antennal contacts x_i of the receiver	
	Left antenna	Right antenna
Sequence 1		
$H(x)$ (Eqn. 1)	2.1810	2.1945
$H(y)$ (Eqn. 1)	1.6653	1.4429
$H(y/x)$ (Eqn. 4)	1.3268	1.2447
$T(x,y)$ (Eqn. 5)	0.3385	0.1952
x^2 (Eqn. 7)	30.0328[a]	16.7775
df	16	12
Normalized transmission (Eqn. 6)	20%	13.5%
nb acts	64	62
Sequence 2		
$H(x)$ (Eqn. 1)	3.3287	3.3033
$H(y)$ (Eqn. 1)	2.6828	2.7440
$H(y/x)$ (Eqn. 4)	2.4296	2.4463
$T(x,y)$ (Eqn. 5)	0.2532	0.2977
x^2 (Eqn. 7)	106.7074	117.2072
df	132	143
Normalized transmission (Eqn. 6)	9.4%	10.8%
nb acts	304	284

[a]Significant with $P < 0.05$ (x^2 P = 0.05: 12 df = 21.026, 16 df = 26.296, 132 df = 159.53, 143 df = 171.62).

This enables us to calculate the quantity of information transmitted from x to y: $T(x,y)$ which is a measure of the relatedness or shared information.

$$T(x,y) = H(y) - H(y/x) \tag{5}$$

Since the limits of the zones distinguished are arbitrary, $H(x)$ is arbitrary. Thus for example, the ant could have 64 regions of the head that are able to distinguish upon antennal contacts, hence the donor gives up to $\log_2 64 = 16$ bits per stroke. For this reason, we calculated the normalized transmission from the ratio $T(x,y)/H(y)$ expressed as a percentage. It reduces the influence of the number of categories selected arbitrarily by an experimenter for a study (see for example Steinberg and Conant, 1974).

$$t(x,y) = \frac{T(x,y)}{H(y)} \times 100 \tag{6}$$

In this case, the donor reactions to receiver palpations were considered (Table III). The matrix used for Table I was used again but other contacts zones (as mandibles, clypeus, cheeks) and several possibilities to donor reactions (as spreading the antennae, joining them together or maintaining the antennae spread) were added. In all cases, 0.2—0.3 bits per contact were found, which corresponds only to 13—20% of the information in normalized transmission.

The hypothesis of transmission of nul information was tested using Miller's chi-square test (Miller and Madow, 1954, cited by Losey, 1978).

$$\chi^2 \simeq 1.3863 \, N\hat{T} \tag{7}$$

where N = sample size, and $\hat{T}$ = estimate of information shared with $(Nx - 1)(Ny - 1)$ degrees of freedom (Nx and Ny = number of rows and columns in the matrix). Significant values of χ^2 indicate that T is greater than zero.

In Sequence 1, χ^2 is significant only for the left antennal reactions of the donor, which is the most active antenna. It is not significant for Sequence 2. It appears that the quantity of information transmitted between a very active donor and a receiver is very low (Sequence 2). It is surprising to observe a difference between a passive and an active donor; the passive donor transmits information with one antenna (20%) but not the active donor. This result, which needs to be confirmed with other sequences, is probably related to the number of antennal contacts; in Sequence 2 the weak influence of the receiver could be the consequence of the great number of antennal interactions.

DISCUSSION

Application of information analysis is difficult in behavioural analysis. We do not bring here experimental evidence that what we regard as different signals or responses are indeed perceived like this in ants. All these results are

open to criticism because we initially postulated that messages are related to contacts and that the absence of contact has no informational value. We thus recalculated the above findings for Sequence 2 by adding the element of absence of contacts considered as an information. The quantity of information remained practically the same: $H(x)$ for the left antenna was 3.2761 instead of 3.3287, for the right antenna 3.2704 (3.3033); $H(y)$ for the left antenna was 2.6592 (2.6828), and for the right antenna 2.8503 (2.7440).

It may be asked if antennal communication is comparable to observations in other situations. There are relatively few quantitative studies in this field. Wilson (1962) studied the trails of *Solenopsis* and Haldane and Spurway (1954) studied the dance of bees. In both cases, there is an indication of distance and direction, and perhaps of quantity in the case of ants. Furthermore, the *Solenopsis* trail takes a collective message value. The quantity of source information, unknown for bees, is between 7 and 15 bits for *Solenopsis*, which is a very large quantity. The quantity of information transmitted is between 2.4 and 11.2 bits, according to the case, that is about 70% for a source at a distance of 5 cm. Wilson believed that the transmission rate by the dance of bees is of the same order. Thus, both systems are highly effective, much more than trophallaxis. This seems rather logical, since distance and direction require qualitative and quantitative information, whereas the patterns of a trophallaxis may simply require the knowledge of whether a partner accepts the continuation of the exchange or not.

The transmission of "alarm" type information by substrate vibrations in an undisturbed *Camponotus* ant colony is 12% (Fuchs, 1976). The influence of the signal is highly variable, according to the type of activity of the receiver ant; ants engaged in an activity are much more sensitive and so the significance of the signal is influenced by the situation of each individual ant. This is also the case of simple information which raises the level of activity of workers. Stridulations transmitted by the ground seem to have the same type of effect and belong to a modulatory communication system which modifies the activity of the receiving ant (Markl and Hölldobler, 1978). This system is not appropriate to conduct important messages causing drastic reactions. The information transfer during trophallaxis is very reduced and shows a very weak influence of the signal. Therefore, we believe that antennal movements during trophallaxis belong to this category.

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NOTE ADDED IN PROOF

Recent data presented by Bonavita-Cougourdan and Morel during the
annual meeting of the French Section of the Union for Study of Social In-
sects shed new light on the role of antennal contacts during trophallaxis in
another species: *Camponotus vagus*. In this species Bonavita-Cougourdan
demonstrated, with other methods, that there is no accurate communication
between individuals, and Morel observed in young ants that this system pre-
sents a development of behaviour.

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