

Short-Term Activity Cycles in Ants: A Phase-Response Curve and Phase Resetting in Worker Activity

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Single, isolated worker ants are known to become spontaneously active and to respond to interactions with other, active ants. Here I explore the consequences of an interaction between two worker ants on the timing of activity. Isolated worker ants become active after an interval that is characteristic for each individual. The effect of an interaction between two worker ants is strongly dependent on when the interaction takes place. The effect of an interaction is always to decrease the expected interval until the onset of activity. By studying the effect of an interaction on subsequent intervals of activity, it is possible to reject the hypothesis that the change in timing of activity is due to a change in the characteristic period of activity. Rather, the data are consistent with the hypothesis that an interaction causes a phase shift in the normal activity oscillation. The phase-response curve is derived from the observational data. A knowledge of the dynamics of the interactions of individual ants is necessary in order to begin to reconstruct the patterns of colony behavioral activity.

KEY WORDS: activity; ants; rhythms; ultradian rhythms; phase-response curve.

INTRODUCTION

The temporal pattern of behavior is one of the fundamental characteristics of any behavioral trait. In order to understand the mechanisms or the adaptive significance of an action, it is essential to understand not only the action itself, but its context. The context includes other individuals to whom the action is

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directed as well as its temporal pattern. Characterizing the temporal pattern of behavior can give insights into its mechanism by revealing cues for behavior and natural time scales on which mechanisms operate.

We can exploit some of the characteristics of social insects to study the temporal pattern of behavior. Social insects introduce a level of complexity intermediate between that of individuals and that of populations. The actions of one individual may influence the actions of other members of a colony without necessarily affecting other colonies in a population. Social insects therefore provide a convenient level of complexity to study the dynamics of interactions among individuals. There is the additional advantage to the study of social insects in that temporal patterns of behavior at the colony level need not be the same as the temporal patterns of individuals (Cole, 1991). Between-group selection (Wade, 1985) (i.e., kin selection) can operate on the colony temporal phenotype by changing either the temporal patterns of individuals or the way in which individuals couple their actions to one another.

The purpose of this paper is to examine the mechanisms by which ants couple their patterns of activity to one another. There are two points of rationale for this study. The first is to begin to explore the behavioral mechanism by which an individual effects a change in other members of its social group. The second is to understand the dynamics of an interaction between two individuals so that a model of the behavior of a colony can be derived from the actions of its component workers. I demonstrate that when pairs of ants interact with one another, the effect is to phase shift the normal, underlying propensity of a single ant to oscillate between periods of activity and inactivity.

Colonies of the myrmicine ant *Leptothorax allardycei* (Mann) exhibit oscillations in the level of activity with a period of about 0.5 h (Cole, 1991). While the activity of single ants does not show clear evidence of periodicity, periodic peaks emerge when larger numbers of workers are allowed to interact. I examine the consequences of an interaction. In particular: Does an interaction result in a predictable, repeatable alteration of the activity of a nestmate?

MATERIALS AND METHODS

The behavior of isolated, individual worker ants of *L. allardycei* was videotaped in order to obtain information on periodicity of single workers. The workers were confined within an arena 15 × 15 mm between two glass microscope slides that were held apart by a 2-mm balsa wood partition. I recorded behavior with a Dage-MTI Model 65 high-resolution video camera on a Panasonic NV-8950 VHS recorder. The field of view of the video camera coincided with the size of the arena. Single workers were placed within the arena, allowed to acclimate for 30 min, and videotaped for 6 h. Videotapes were reviewed to determine the interval between bouts of activity.

The behavior of pairs of worker ants was assayed similarly. Two worker ants from the same colony were confined together and videotaped for 6 h. The videotapes were analyzed to determine when interactions took place and the intervals between bouts of activity and between interactions and activity. An interaction is defined as occurring when one ant makes physical contact with another. Physical contact is required for activity to spread among individuals (Cole, in preparation). Observations of activity on two sides of a screen partition that allowed air, but not ants, to pass showed that the activity of the two halves of the colony was independent. There is no evidence that a diffusible substance conveys information to other ants about their state of activity. Interactions that occurred during periods when both ants were active or when there was more than a single interaction during one period of inactivity were not scored for this experiment.

For each worker ant the average interval between bouts of activity when there was no interaction between the ants was standardized to a value of 1 to remove possible individual variation. The interval between the onset of inactivity and the interaction as well as the interval between the interaction and the onset of the next bout of activity is given as a fraction of this unit interval.

RESULTS

The results are given in three parts. In the first I discuss the predictability of the length of the inactive phase of the activity cycle of single workers. In the second, I present the results of interactions between pairs of worker ants. In the third section I test whether the interaction between two ants results in a phase shift of the oscillation of single-ant activity or whether the effect of an interaction is to change the period of the oscillation.

The Predictability of Single-Ant Activity

A frequency histogram of 27 periods of inactivity is presented in Fig. 1. For each individual the mean interval between activity bouts is standardized to 1. If activity occurs completely at random and is described by a Poisson process, then the frequency distribution of the interval between bouts of activity should be negative exponential. (The distribution of waiting times in a Poisson process is negative exponential.) Rather than a negative exponential, the distribution has a nonzero, central, mode. The data fit a normal distribution (χ^2 -square, $P > 0.5$) but do not fit a negative exponential distribution ($P \ll 0.001$). The variance in the time between bouts of activity is fairly large ($SD = 0.28$), but clearly activity is much more likely to occur after some interval. Therefore, while there is variation in the length of a period of inactivity, it is not correct to say that the activity of single ants is entirely unpredictable. Vir-

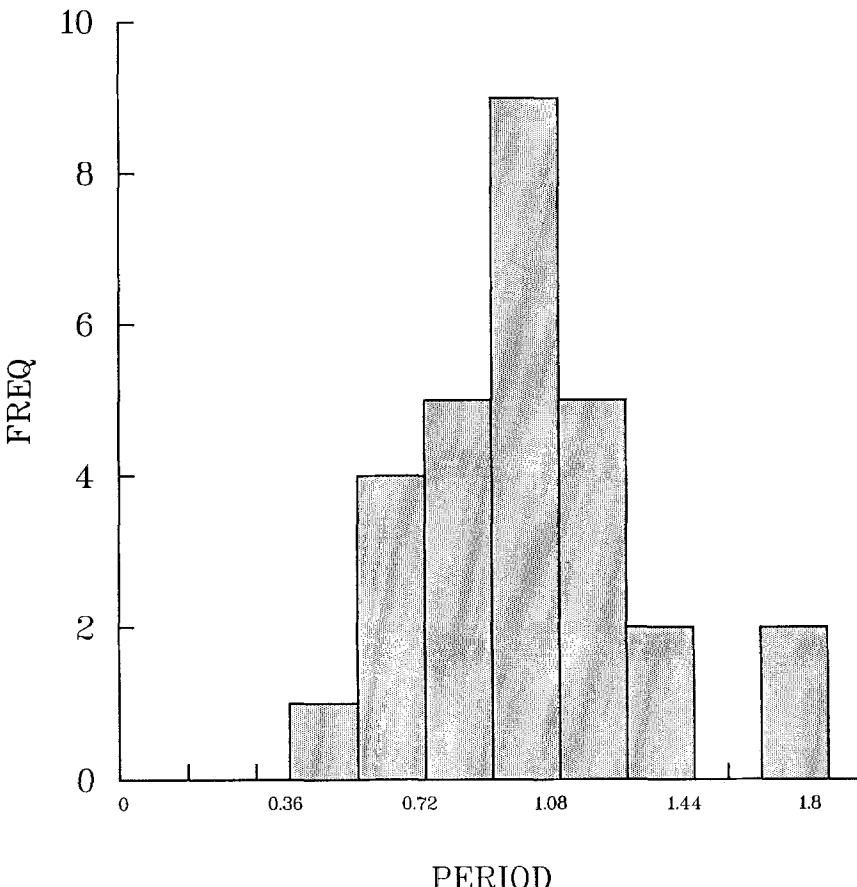
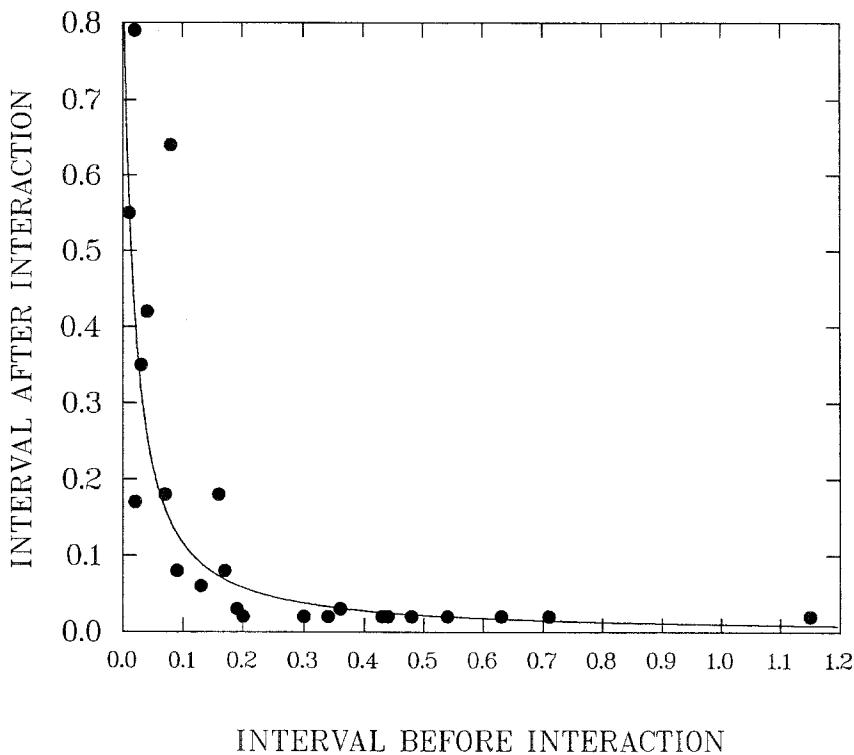


Fig. 1. Frequency distribution of 27 activity periods for isolated worker ants.

tually all of the bouts of activity occur between .5 and 1.5 times the duration of the unit interval.

Interactions Between Ants

For each interaction scored in this data set, there were two intervals: the interval from the beginning of inactivity to the interaction (before the interaction; *B*) and the interval from the interaction to the onset of activity (after the interaction; *A*). The relation between these two intervals is shown in Fig. 2 for 23 interactions. The null hypothesis is that one ant has no effect on the actions of the other. If one ant has no effect on the activity of the other, then the interaction should simply divide the unit interval into two parts that sum to one.



INTERVAL BEFORE INTERACTION

Fig. 2. The relationship between the interval before an interaction and the interval after an interaction between an active and an inactive ant. The units are standardized to the mean length of the inactive period of the stimulated ant. The curve is the best-fit power function.

That is, the data should occur on a line with a slope of -1 that has a y intercept of 1.0 . Clearly the data in Fig. 2 do not fit this description (the data are significantly different from a slope of -1 , t test, $P < 0.001$). A very good fit is obtained using a multiplicative model: $A = aB^b$ (a constant 0.02 is added to each interval to remove zero values; $a = 0.01$, $b = -1.16$, $r^2 = 0.80$, $df = 21$, t test, $P \ll 0.001$).

The difference between the null expectation ($A' = 1 - B$) and the observed value ($A = 0.01B^{-1.16}$) is the magnitude of the effect of an interaction between two ants. This value peaks with a value of $A = 0.76$ at $B = 0.13$ and declines nearly linearly to near-zero when $B = 1$.

Phase Shifts Versus Period Changes

The result presented in Fig. 2 could be due to several effects. Three possibilities are distinguished in the following experiment. The first is that there is a transient stimulation of activity which does not affect the underlying oscilla-

tion of activity in the stimulated ant. The second is that there is a change in the period of oscillation of the activity cycle of the stimulated ant. The third possibility is that stimulating an ant changes the phase of the oscillation of the stimulated ant. These three possibilities are tested by measuring the period of three consecutive activity cycles from videotapes, as described above. During the first and third of the cycles there is no interaction between the two ants. During the second period of inactivity there is an interaction with the active ant. The lengths of the three successive inactive periods are designated I_1 , I_2 , and I_3 as shown in Fig. 3. If the interaction, denoted by an arrow, induces a transient period of activity, then the underlying oscillation is not perturbed and the final episode of activity should begin when expected. The length of the third period of inactivity should be longer than the first period of inactivity. If an interaction induces a change of period, then the length of the third period of inactivity, I_3 , should be shorter than I_1 . If there is a phase shift, then the period should not be altered, and I_1 should equal I_3 . The final prediction is borne out by the data ($I_1 = 1.1$, $I_3 = 0.9$, $t = 1.48$, $df = 35$, $P > 0.2$).

DISCUSSION

I have demonstrated that an interaction between two ants produces a phase shift in the short-term activity cycle of the inactive ant. The form of the phase-response curve has important implications for the ability of a colony of ants to synchronize their behavior to one another and for the stability of this synchronization. Some of these implications are discussed here.

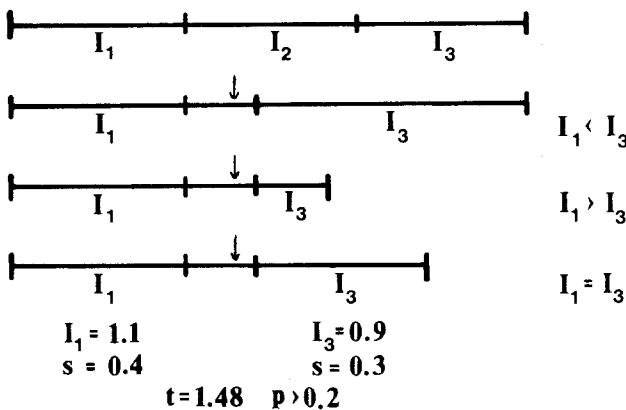


Fig. 3. A diagrammatic summary of the possible outcomes of an interaction: (1) transient stimulation of activity that does not disturb the underlying oscillation; (2) shortening of the period of an oscillation; (3) phase shift of the underlying oscillation. The data best fit alternative 3.

The phase-response curve obtained from the data in this paper is shown in Fig. 4. Since both the Phase at which the interaction occurs and the Phase Response are angular variables, the natural coordinate system for this sort of plot is on the surface of a torus. The major axis of the torus is a single period of inactivity. The minor axis of the torus is the angular phase shift, with one complete revolution being one inactive period. The inactive phase begins at the point labeled A and proceeds counterclockwise. The maximal phase shift occurs at the point labeled B.

An important point about the phase-response curve in this system is that an interaction always produces phase advances, never phase delays. The phase resetting curve, or the plot of the new phase following the interaction versus the old phase, over one cycle, is

$$\phi' = 1 - 0.01 \phi^{-1.12}$$

The slope of this curve is positive for all ϕ . This sort of resetting curve is consistent with changing the period of a clock of a result of a stimulus (Winfree, 1980). The importance of experiment three, which shows that period changes are not occurring, is that it rules out period changes as the cause of a changing phase relationship.

The phase resetting curve for this interaction, if graphed on a toroidal surface, passes once through the hole in the torus. Such a curve is said to have a winding number of one, or to have Type 1 resetting. This is in contrast to a resetting curve which does not wind through the hole in the torus and is called

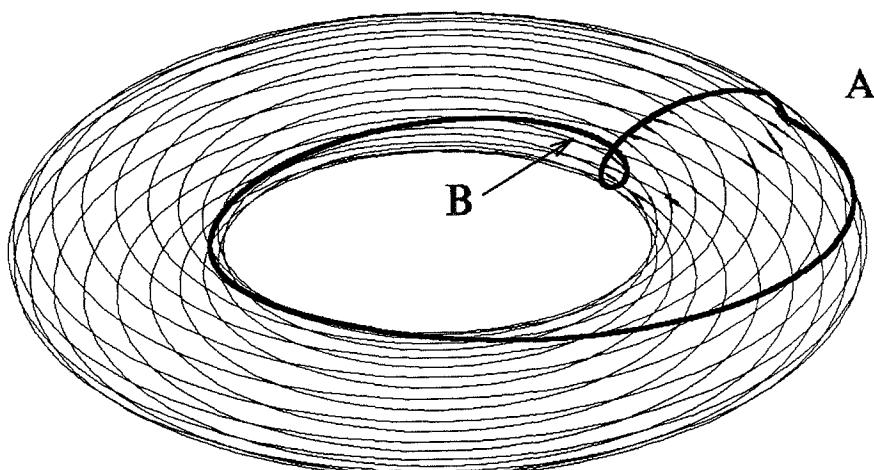


Fig. 4. The phase-response curve for ant interactions. The two axes of the torus are the period of the activity cycle (major axis) and the phase shift (minor axis). The labels correspond to (A) the onset of inactivity and (B) the maximal phase shift.

Type 0 resetting. The effect of an interaction can be quite large ($\Delta\phi_{\max} = 0.76$ at $\phi = 0.13$). Often Type 1 resetting is called “weak” resetting (as opposed to Type 0 resetting, which is called “strong” resetting) because it pertains in the case of the weakest interactions. However, the large magnitude of a phase shift which can be produced argues against the use of this terminology and in favor of the more accurate topological distinction. The simplest sort of Type 0 resetting would occur if one ant became active immediately upon interaction with another ant. In such a case, the inactive ant becomes active, regardless of the length of time since last activity. The phase resetting curve for such an interaction does not wind through the hole of the torus. An example of this sort of response is that given to the release of alarm pheromone. Regardless of the length of time since last activity, stimulation with alarm pheromone produces immediate activity. If colony activity cycles were driven by workers that had Type 0 resetting curves for interactions, then the period of colony activity cycles would be driven by the worker with the shortest activity cycle. Since workers are not, themselves, truly periodic, it would seem difficult to generate a social rhythm with Type 0 resetting.

It seems much easier to construct colony rhythmicity from nonperiodic workers if they have Type 1 resetting curves. If activity cycles are capable of stable Type 1 phase resetting, then the colony activity pattern is buffered from variation. The variation may occur due to differences among workers in the characteristic period of inactivity or to chance variation in interactions between particular workers. The period of colony rhythmicity will be a function not only of the length of the period of the most frequently active worker ant, but also of the shape of the phase-response curve.

According to the phase resetting curve given above, the activity cycles of two ants do not appear to be able to couple synchronously and stably. Perkel *et al.* (1964) and Winfree (1980) show that stable coupling of two oscillators requires that $|d\phi'/d\phi| < 1$ near $\phi = 0$. If the slope of the phase resetting curve is greater than one near $\phi = 0$, then small deviations from synchrony will be magnified, and if the slope is less than one, small, initial deviations from synchrony will decline. In the present case, $(d\phi'/d\phi) < 1$ only when $\phi > 0.13$, and not in the vicinity of $\phi = 0$.

Nevertheless, one apparently observes synchrony of activity among entire colonies (Cole, 1990). There are at least three alternatives. The first is that the synchrony of whole colonies is only apparent. Colonies could contain temporary groups of individuals that oscillate in phase with one another but out of phase with other such groups. The aggregate of colony activity contains temporary assemblages of workers ephemerally phase-locked with one another. This possibility seems at odds with the evidence for sustained oscillations of activity, in which all workers appear synchronized within whole colonies.

The second possibility is that the phase resetting curve of a single ant

interacting with a colony of synchronous ants is different from the phase resetting curve of a single ant interacting with another single ant. A single worker may be responding not to the stimulus of a single individual, but to some summed stimulus of the entire colony. Here the phase resetting curve may have a slope of less than one near $\phi = 0$.

The third, and the most likely, possibility is that the intensity of the phase response near $\phi = 0$ is not as great as estimated. The amount of the phase shift near $\phi = 0$ is estimated from the function fitted to the data in Fig. 2. This function was chosen as the simplest which provided a good fit, however, there is no compelling reason to suppose that it is the true theoretical model. If interactions near $\phi = 0$ have a smaller effect on the timing of subsequent activity than predicted here, then stable, synchronous coupling may be possible. The second and third possibilities cannot be distinguished with the evidence available. Information on the effect of interactions occurring just after the onset of inactivity could differentiate the hypotheses.

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