

## THE BALANCE BETWEEN ANTAGONISTIC INDUCTION AND DEPRESSION OF FLIGHT ACTIVITY IN *APHIS FABAE* SCOPOLI

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### INTRODUCTION

When flight in alienicolous *Aphis fabae* Scopoli is temporarily inhibited by eliciting an antagonistic activity, settling, the flight activity exhibits certain after-effects. The flier's rate of climb may be augmented after the intervening bout of settling (rebound, or antagonistic induction) and it may also be diminished (antagonistic depression). Both these excitatory and inhibitory after-effects can usually be detected within seconds of take-off but they occur in widely varying proportions. The net result is to strengthen or weaken flight in relation to settling (Kennedy, 1965). Temporary inhibition of settling by flight has similar opposite after-effects upon settling activity (Kennedy & Booth, 1963*b*, 1964) (papers in this series will be referred to hereinafter by date only). The balance between the after-excitation and the after-inhibition of each activity when the antagonist interrupts it is thus the key variable that governs the overall course of behaviour. The important question then becomes what in turn governs that balance.

Experiments already reported (1965) and not originally designed to answer this question suggested that the balance of after-effect of settling on flight depends, first, on the excitatory states of the two antagonists at the moment when flight is inhibited by stimulating settling and, secondly, on the strength or duration of that inhibition. However, this conclusion was based partly on indirect comparisons, and the method used for varying settling in order to measure its after-effects on flight was simply to change the type of surface presented for settling, which introduced unknown qualitative differences between the settling stimuli provided in addition to the quantitative variation desired. It also left a large amount of uncontrolled variation in the strength of the settling responses on any one surface. This paper describes further experiments in which settling was subject to controlled, quantitative variation on one unvarying surface. Similarly regulated settling was used to obtain further evidence on the nature of the co-ordinating link between the two successive, antagonistic activities.

### MATERIALS AND METHODS

The aphid and plant material, the recording flight chamber and the methods used in this work have been detailed in previous papers (1963*a, b*, 1964) and the terms used in presenting the results were re-defined by Kennedy (1965). The flying aphid's rate of climb was recorded continuously and the after-effect on its flight of inter-

polating a landing was gauged by comparing the rate of climb during the last 60 sec. before presentation of the surface for landing, with that during the first 60 sec. of resumed flight after take-off. The rate of climb often fluctuated rapidly, especially at the start of a flight, and three measures of it were therefore read off the records as described and illustrated in the previous paper (1965, fig 2): the maximum and minimum rates attained during each 60 sec. and the average rate over the whole 60 sec.

The results given in this paper came from three experiments in which the aphid's settling responses to leaves after landing, and hence the duration of their stays on them between bouts of flying, were curtailed by the operator in order to standardize them. This was done by jolting each aphid off the leaf, and thus stimulating it to immediate flight, by tapping the tube holding the leaf lightly but sharply while the aphid was walking. Further details are given under the individual experiments.

## RESULTS

### *Effect of jolting off a leaf into premature flight*

Several groups of aphids were allowed twenty successive 1 min. flights in Expt. III as already described (1964, table 2). Groups D and E made their interpolated landings on a young host leaf, *Vicia faba*; groups B and C on a mature non-host leaf, *Fuchsia*. Groups D and B were left undisturbed after each landing and thus took off after varying lengths of stay; groups E and C were jolted off the leaf, into flight, as soon as they began walking after completing their first probe on the leaf. At a minority of landings the aphids took off again without probing at all, especially from the non-host leaf. Accelerated walking across the leaf toward the lights preceded take-off and as soon as such walking was observed in groups C and E the aphid was jolted off at once thus anticipating its spontaneous take-off. The results are reproduced in Fig. 1. To facilitate comparisons, the positions of the entire curves D, E, B and C have been adjusted slightly up or down (by at most 2.9 cm./sec.) as required to bring the mean starting rate of climb of all groups, in the first minute, to the same level as that of the control group A.

The undisturbed landings of groups D and B boosted the maximum and average rates of climb and concurrently depressed the minimum rate, by comparison with the records from the control group of uninterrupted fliers (group A). As the series of flights and landings on the host leaf continued (D in Fig. 1) the depressing effect diminished, and in some individuals it disappeared altogether. The behaviour of the group landing on the non-host leaf was similar (B) except that the depressing effect was smaller and disappeared after a few flights so that even the minimum rate of climb soon came to exceed that of the uninterrupted fliers. Those curves may now be compared with the curves from aphids that were jolted into flight off the same leaves. Group E, jolted off the host leaf, shows less boosting of the maximum rate and less depression of the minimum rate of climb than group D, undisturbed on the host leaf, the net result being similar 60 sec. average rates of climb. The effect of jolting the aphids off the non-host (group C, Fig. 1) was again to reduce both the initial depressing and the later boosting effects of the landings. By the twentieth flight there was no significant difference between the rates of climb of the two jolted-off groups,

or between them and another group (F) making brief undisturbed landings on a card (1964, 1965).

Thus repeatedly curtailing settling by jolting the aphids off the leaf into the air did not have the boosting effect on subsequent flight which might have been expected. The effect was much the same as curtailing settling naturally by using a landing surface that provided weaker stimulation of settling and allowing undisturbed take-off.

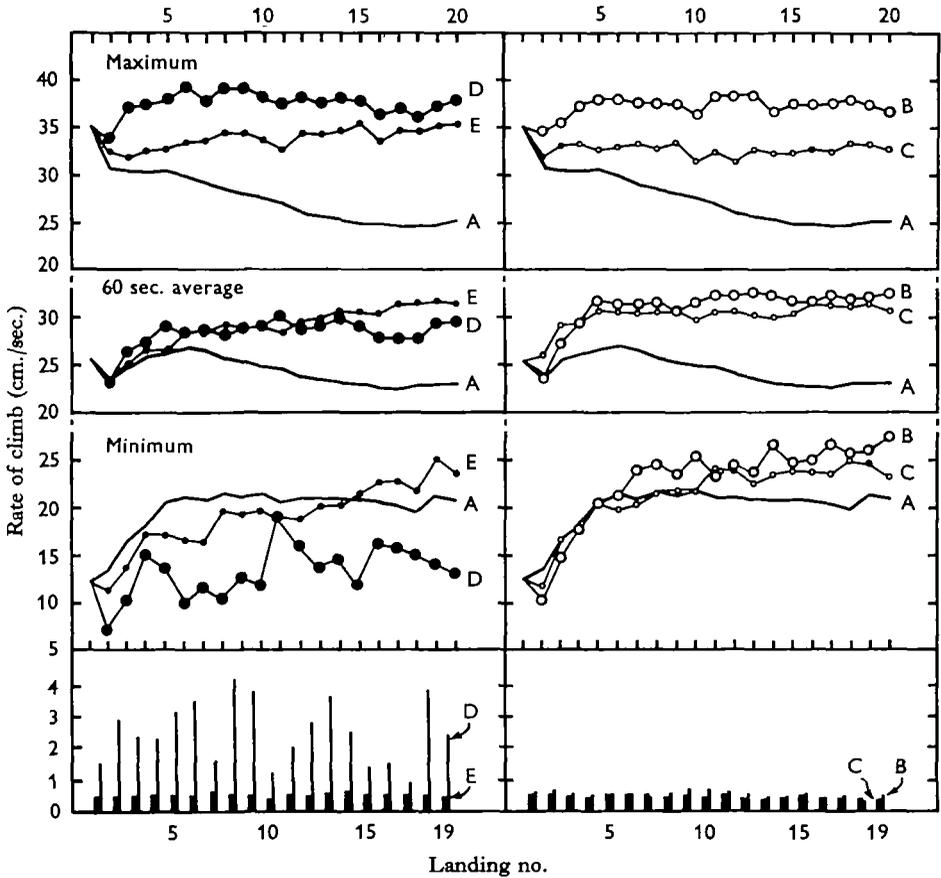


Fig. 1. Minute-by-minute rates of climb during 20 min. of uninterrupted flying by a control group A (means from 30 aphids), and during twenty successive 1 min. flights between landings on a host leaf (groups D and E) or on a non-host leaf (groups B and C) (Expt. III). Groups D (9 aphids) and B (30) left undisturbed at each landing; groups E (20) and C (20) regularly jolted off the leaf after one probe. Maximum, 60 sec. average and minimum rates of climb plotted separately for the same aphids in the same minutes. Below: mean duration of stay on the leaf at each landing, min.: groups D and B as thin columns, E and C as thick ones.

Jolting off had the advantage of permitting controlled variation of settling without changing the landing surface, with some diminution of both the after-effects on flight activity normally obtained with any given landing surface but apparently no other distortion of these effects.

*After-effects of controlled settling on flight*

Expt. IV was designed to compare the after-effects on flight of weak and strong settling, and also of weak and strong flight activity just before settling, using a young host leaf (*Vicia faba*) as the landing surface throughout. A first flight of 10 min. was allowed to each aphid in order to bring it well into the steady 'cruising' phase of flight (1963*a*) before the first landing. Five minutes flight was allowed before each subsequent landing. These two procedures eliminated the initial phase of cumulative increase in the rate of climb which was obtained when the first and subsequent flights were limited to one minute each (Fig. 1).

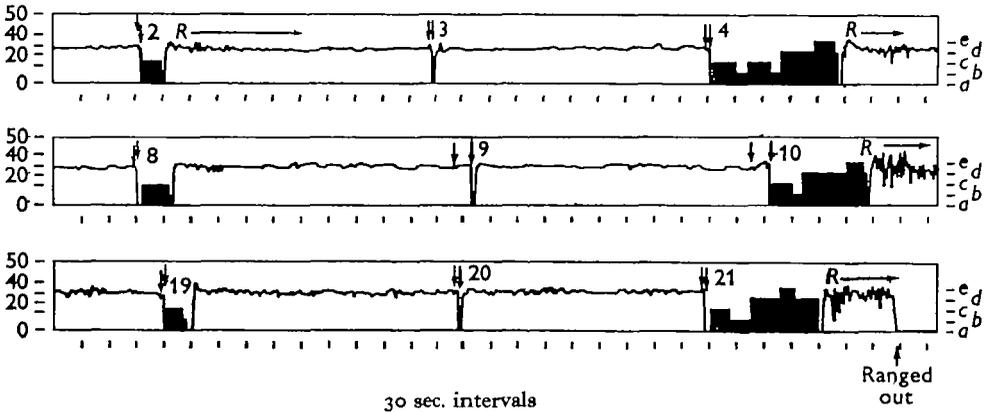


Fig. 2. Three separate excerpts from an original flight chamber record of the rate of climb (irregular line, and scale at left, cm./sec.) and settling responses of an aphid landing repeatedly on and jolted off again from a host leaf between 5 min. flights (Expt. IV). First arrow marks when the leaf was presented to the flier, second arrow the moment of landing on it; adjacent figure is the serial number of that landing. Periods spent on the leaf before jolting off shown as black blocks of varying height indicating the aphid's behaviour according to scale at right. On upper surface: *a*, stationary not probing; *b*, walking; *c*, probing. On lower surface: *d*, walking; *e*, probing. *R* indicates ranging, for the duration of the arrow.

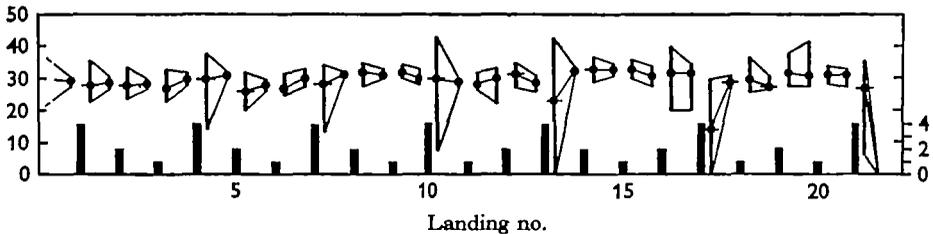


Fig. 3. Entire flight and settling record, condensed, from the same individual as in Fig. 2. Thick vertical strokes joined by thinner lines show rates of climb (left-hand scale, cm./sec.) during the first and last minute of each 5 min. bout of flying between landings. Length of each stroke shows the range of rates within that minute; solid circle on stroke marks the average rate over the full 60 sec. A small cross-bar indicates some ranging. Columns on base-line indicate strength of settling responses at each landing (right-hand scale, see text, pp. 218, 219).

The settling responses made at one landing can be graded on an arbitrary numerical scale according to how far they progress through the sequence which, under favourable conditions, culminates in larviposition (1964*b*): 1, no probe on the exposed upper

surface of the leaf; 2, one probe there; 3, more than one probe there; 4, walking over on to the shaded lower surface and probing there; 5, larviposition. In Expt. IV one of three grades of settling response was permitted at each landing, by jolting the aphid into flight (1) as soon as it began walking after landing, before it had probed at all (total stay 2–5 sec.); or (2) as soon as it began walking again after making its first probe (total stay 20–40 sec.); or (4) after it had made one or more probes on the upper surface and had then walked round on to the shaded underside of the leaf and made one more probe there (total stay 100–150 sec.). These three grades of permitted settling response are shown in Figs. 2 and 3, but for the purposes of summarizing the results in Fig. 4 and of testing the significance of differences, grades (1) and (2) have been combined as 'weak settling', leaving grade (4) as 'strong settling'.

It can be seen from Figs. 2 and 3 that the rate of climb had usually recovered from the after-effects of the previous landing before the 5 min. flight bout was over, for by then the rate had steadied again at about the same level as it was just before the previous landing. The landings were having a persistent effect, nevertheless, for the steadied rate of climb at the end of each 5 min. did not undergo the progressive decline seen in uninterrupted fliers (1963*a*), but tended rather to stay up around the same level until the series of flights was terminated by the aphid ranging out into the darkness and landing on the flight chamber wall. It was thus possible to use the same individual for a number of successive comparisons of the after-effects of weak and strong settling on flight activity of approximately the same strength as illustrated in Fig. 3.

The behaviour of five individuals (including that of Figs. 2 and 3) which it was possible to keep flying for more than twenty 5 min. flights and landings with controlled settling, is summarized in Fig. 4A. During the first 60 sec. from take-off after both strong and weak settling, the rate of climb of these aphids rose to a significantly higher maximum value than it had reached during the last 60 sec. before landing, and also dropped briefly to a significantly lower minimum value. But the gain in rate of climb was significantly greater after strong settling than after weak settling, and so also was the depression (Mann-Whitney tests:  $P < 0.001$  in both cases).

In most respects the after-effects of landings by these long-flying aphids showed no clear secular changes, but in one respect there was a change. The records from the sample individual in Figs. 2 and 3 show that depression of the rate of climb after strong settling became more pronounced as the series of flights and landings continued, while the after-effects of weak settling remained relatively small throughout. Analysis of the combined results from the five individuals represented in Fig. 4A confirmed the reality of this trend. There was a sharp drop in the rate of climb to less than 5 cm./sec. after strong settling in 22% of cases falling among the first five landings of each aphid (10th–35th minutes of flight), in 53% of cases among the 6th to 15th landings (40th–90th minutes of flight) and in 69% of all subsequent cases; whereas the equivalent percentages after weak settling were 0, 6 and 7%. Thus there was a shift in the relative effects of strong and weak settling as flights proceeded, strong settling tending to depress flight more and more while weak settling continued to sustain it. Ranging usually accompanied pronounced depression of the rate of climb and ranging out eventually terminated the series of flights.

Ten other aphids were treated in the same way as the five long fliers of Fig. 4A

but ranged out considerably sooner, after 2-10 landings only. On this criterion they were distinguished as 'weak' fliers; and their mean rate of climb as a group was then found to be slightly but significantly lower than that of the long strong fliers. Fig. 4 B summarizes the combined results obtained from the weak fliers for comparison with the strong fliers above. Strong settling failed to boost the maximum rate of climb of these weak fliers and significantly depressed their 60 sec. average as well as their minimum rate. Weak settling, on the other hand, failed to depress the minimum rate of climb of the weak fliers and significantly boosted their 60 sec. average as well as

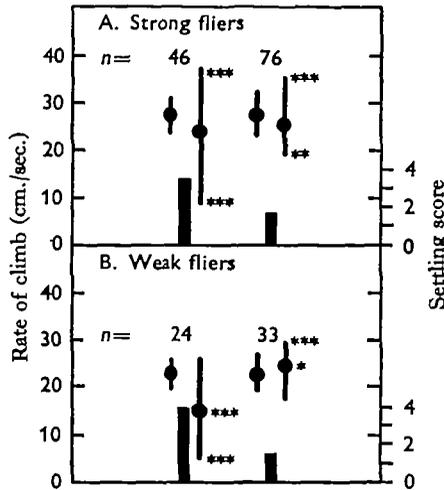


Fig. 4. Summarized effects of strong and weak settling responses on the subsequent flight activity of strong and weak fliers (Expt. IV). Thick vertical strokes show rates of climb as in Fig. 3. Left stroke of each pair shows mean rates during the last minute before landing; right stroke shows mean rates during the first minute after take-off. Black column between strokes shows mean settling score as in Fig. 3 ( $n$  = no. of landings on which each mean is based). Asterisks indicate the level of significance pertaining to the difference between the adjacent 'after' value and the comparable 'before' value on the preceding stroke (Wilcoxon tests; no asterisk,  $P > 0.05$ ; 1 asterisk,  $P < 0.05$ ; 2,  $P < 0.01$ ; 3,  $P < 0.001$ ).

their maximum rate. Thus the weak fliers behaved, from the beginning, like the strong fliers after they had been flying for some time (when their flight would have weakened considerably if they had made no landings: 1963*a*, 1965). To sum up, strong settling boosted flight more than weak settling did in strong fliers, but depressed flight more than weak settling did in weak fliers.

#### *After-effects on flight of unequal stimulation of settling but equal settling performance*

Expt. IV above showed that the after-effect of landings on flight varied according to the strength of the settling response even when the landing surface was the same. It was not necessary to use different surfaces, such as host and non-host leaves, to obtain the different after-effects on flight associated with the different strengths of settling response to the surfaces. This seemed consistent with the previous findings in Expt. III that the aphids' eventual rate of climb after twenty 1 min. flights (above,

p. 216), and likewise their subsequent settling responses on a standard test leaf (1964), differed little, whether the previous landings between flights had been made on a host or on a non-host, provided the strength of the settling responses at those previous landings had been kept artificially at about the same level, by jolting off. However, Expt. III involved comparison of separate groups of aphids each landing only on the host or only on the non-host, and there were progressive changes in the rate of climb before landing (Fig. 1). Expt. V was therefore designed as a more rigorous test of the hypothesis that the nature of the landing surface makes no difference to the after-effect on flight provided the strength of the settling responses actually performed is the same.

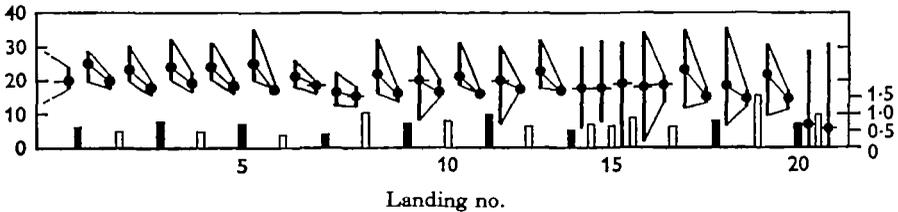


Fig. 5. Entire flight and settling record, condensed as in Fig. 3, from one aphid landing alternately on a host leaf (solid columns) and a non-host leaf (open columns) with jolting off both leaves after one probe. Five min. flight bouts between landings, except where single vertical strokes indicate flights of 1-2 min. only (after landings 13-15, 20, 21) (Expt. V). Columns on base-line show duration of stay at each landing according to scale at right (min.).

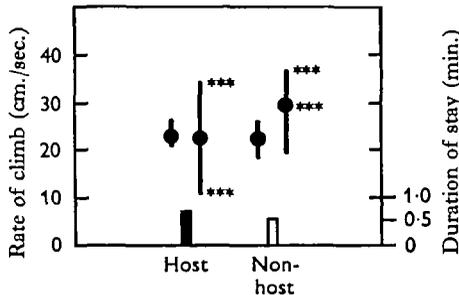


Fig. 6. Summarized effects on flight activity of alternate landings on a host leaf and a non-host leaf with jolting off both leaves after one probe and 5 min. flight bouts between landings (Expt. V). Presented as Fig. 4. Means from 37 landings on host, 31 on non-host.

The same individual was used for a number of comparisons of the after-effects of alternate landings on a mature host leaf (*Vicia faba*) and on a mature non-host leaf (*Fuchsia*) with jolting off both after one probe, while the level of flight activity before each landing remained approximately the same. A first flight of 10 min. was allowed, followed by 5 min. flight bouts between landings and as in Expt. IV this was usually enough for the rate of climb to recover from the after-effects of the previous landing before presentation of the next leaf. After a variable number of such flights and landings the flight became so depressed and wide-ranging on take-off from the host leaf that, from previous experience, the aphid could be expected to range out and so terminate the series of flights. The non-host leaf was then presented before 5 min. had passed, one or more times, with the result that flight activity was sometimes fully

restored and further 5 min. flights and landings on both leaves became possible. This is illustrated in Fig. 5 which represents the complete series of flights and landings of one individual until it ranged out. Fig. 5 also shows that the approximate equalization of settling by jolting off did not eliminate the difference between the two leaves in their after-effects upon flight.

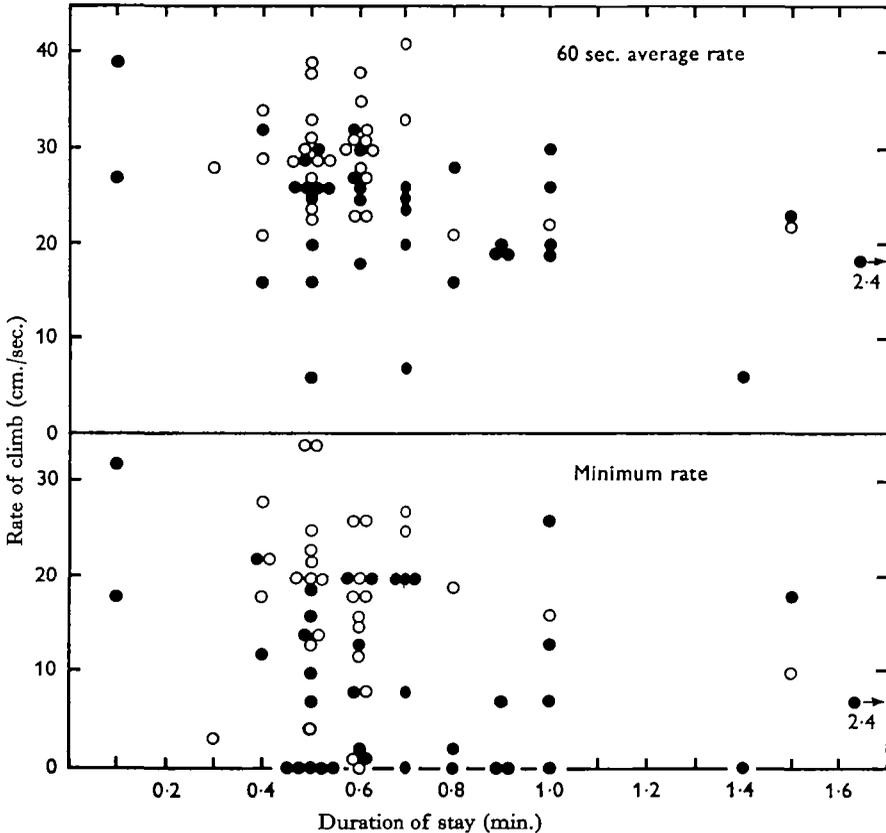


Fig. 7. Relation between duration of stay on a host leaf (solid circles) and a non-host leaf (open circles) and the rate of climb on take-off (Expt. V).

Figure 6 gives the pooled results from five individuals treated like the one in Fig. 5 and includes only the effects of landings following a full 5 min. flight. The rate of climb during the fifth minute, just *before* each landing, did not differ significantly; but the 60 sec. average and minimum rates of climb after landings on the host and non-host leaves differed highly significantly (Mann-Whitney 'two-tailed' tests: 60 sec. average rates,  $P = 0.0001$ ; minimum rates,  $P = 0.0014$ ). As usual, landings on the host depressed the minimum rate of climb significantly whereas landings on the non-host did not. Both leaves boosted the maximum rate, but the non-host did so more and as a result boosted the 60 sec. average rate as the host did not.

The jolting off of the aphids did not entirely equalize their settling and Fig. 7 shows that longer stays (due to longer probes) were more common on the host than on the non-host. But this does not account for the different after-effects shown in Fig. 6.

Within this much narrowed range of stay durations there was no apparent correlation between stay duration and subsequent rate of climb, and the effects of the two leaves differed in the same way as in Fig. 6 even when stays of the same duration are considered, notably 0.5–0.6 min. (Fig. 7).

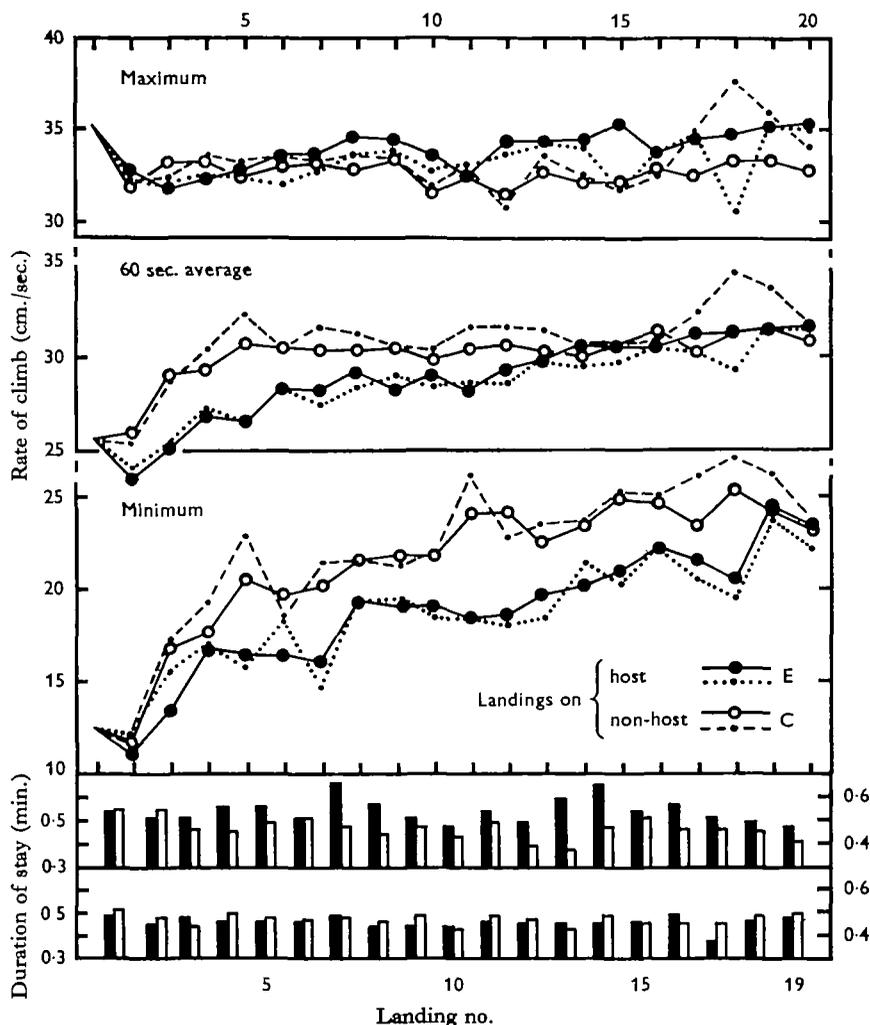


Fig. 8. Minute-by-minute mean rates of climb during twenty successive 1 min. flights between landings on a host leaf (group E) or a non-host leaf (group C) with jolting off both after one probe, presented as Fig. 1 (Expt. III). Dashed and dotted lines—the same for flights following landings of 0.3–0.6 only. Mean duration of each stay at each landing on host shown below as solid columns, on non-host as open columns; upper row, at all landings; lower row, at landings of 0.3–0.6 min. only.

The unambiguous results of Expt. V prompted re-examination of the results of treatments E and C in Expt. III. It was mentioned on p. 221 that the eventual rate of climb of aphids by the time they had made twenty successive 1 min. flights differed little whether they had made their repeated landings on a host leaf (E) or a non-host leaf (C) provided they were jolted off both after one probe. However, when the entire

E and C curves of minute-by-minute rate of climb are compared directly, as in Fig. 8, there does appear a consistent difference between the E and C minimum and 60 sec. average rates. Their eventual coincidence appears to have been due to convergence; if continued the curves would have crossed over (1965). Their earlier divergence in Fig. 8 was smaller than, but in the same sense as, the difference between the D and B curves from aphids which were left undisturbed on the same two leaves and therefore responded much more strongly to the host leaf than to the non-host (Fig. 1).

Again the question arises as to whether this difference in Fig. 8 was due to the small residual difference between the settling responses made on the two leaves before jolting off. Fig. 9 shows that in this experiment the main difference in settling activity

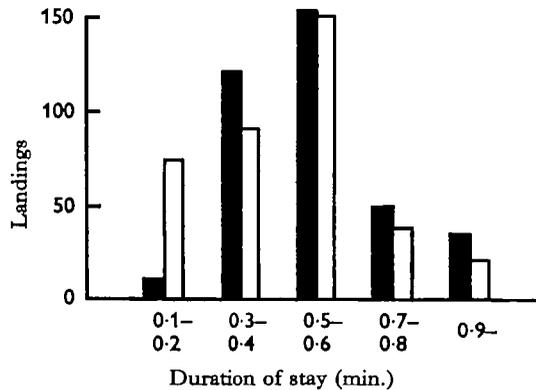


Fig. 9. Frequency distribution of durations of all stays on a host leaf (solid columns) or a non-host leaf (open columns) between the twenty successive 1 min. flights shown in Fig. 8.

was in the number of very brief stays. Stays of 0.1-0.2 min. were those during which the aphid did not probe at all (p. 216) and were rare on the host leaf. Scatter diagrams revealed no correlation between stay duration and subsequent rate of climb, as in Expt. V (Fig. 7), but this test is of doubtful validity for Expt. III because of the variable level of flight activity between landings. With successive landings separated by only 1 min. of flying, instead of 5, there was summation of the after-effects to produce a progressive rise in the rate of climb (Figs. 1, 8) which altered the relative after-effects of different stay durations as demonstrated above (Expt. IV, Fig. 4) and previously (1965). This would obscure any correlation between stay duration and the subsequent absolute rate of climb. It is necessary to consider instead the shape of the entire curves for the series of flights. These have therefore been re-calculated after excluding from the mean for each minute of flight all cases where the aphid's stay on the leaf at the immediately preceding landing lasted less than 0.3 or more than 0.6 min. The remaining stays, within the range 0.3-0.6 min., were on the average slightly longer on the non-host than on the host (Figs. 8, 9) thus reversing the normal situation. The dashed and dotted curves in Fig. 8 show the re-calculated mean rates of climb; they are based on smaller samples and hence more irregular than the continuous curves including all flights regardless of stay duration, but the difference between E and C is not apparently less.

When the aphids were allowed to respond fully to the leaves and not jolted-off, those

aphids landing on the host leaf (group D) displayed not only more depression of the rate of climb but also more frequent and persistent ranging than those landing on the non-host (group B) (1965, fig. 8). There was a similar difference in the incidence of ranging between the jolted-off groups E and C. This is shown in Fig. 10, which again excludes all flights following a stay of less than 0.3 or more than 0.6 min. on the leaf. Individuals omitted from Figs. 8 and 9 because they ranged out before they had completed the desired run of twenty flights are of course included in Fig. 10. In terms of both ranging and rate of climb, therefore, the results of Expt. III are consistent with those of Expt. V.

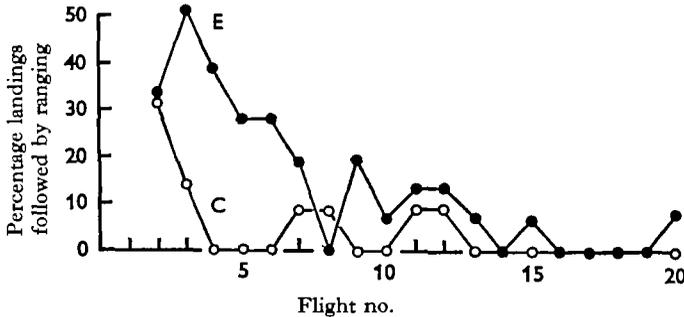


Fig. 10. Incidence of ranging behaviour during twenty successive 1 min. flights between stays of 0.3-0.6 min. on a host leaf (E) and a non-host leaf (C) (Expt. III).

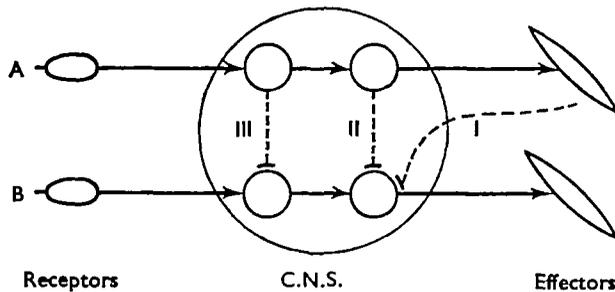


Fig. 11. Schematic representation of three possible links between successive activities, such that stimulation of reflex system A cross-inhibits the antagonistic system B, to produce the observed after-effects on B. I, peripheral link, involving some form of feed-back from the performance of activity A (for present purpose it is immaterial whether the feed-back acts on the motor centre or further 'upstream'). II, central link between motor centres. III, central link further 'upstream', perhaps at the level of sensory analysers. The evidence points to III as the operative link.

DISCUSSION

*Centre and periphery*

Although it is usually assumed that peripheral feed-back provides the co-ordinating link between successive activities such as flight and settling in insects, strong inferential grounds have already been given for concluding that in the aphid the two-way interaction between flight and settling is central, in the first place (1963a, b, 1964, 1965). The results of Expt. V (Figs. 5, 6) supported by those of Expt. III (Figs. 8, 10) appear to settle this point as far as behavioural evidence can do so.

Landings on host and non-host leaves had different after-effects on flight even when apparently equal settling responses were made on the two leaves. The difference of after-effect was then smaller than, but similar to, the difference observed when the unequal settling that is normally elicited by these two leaves was allowed. The stimulation received during contact with the leaves thus appears to produce its after-effect on flight independently of its elicitation of the settling responses; the two actions of the stimulus are parallel, not sequential. When the settling responses are grossly unequal in strength and duration as they normally are on such different leaves, this will of course add to the difference of stimulation received by the aphids before they take off again. Thus the greater difference of after-effect on flight, then observed, does not contradict the idea of independent action for it could be due to the greater difference of stimulation.

If it is the settling stimulus and not the settling activity that affects subsequent flight, then plainly this effect on flight cannot be a result of sensory, hormonal, metabolic or other feed-back from the settling activity (Fig. 11, I). It will be the result of the central inhibition of flight by the settling stimulus as previously inferred (1965). On top of that primary interaction feed-back presumably comes in as an additional effect sooner or later, and it is known eventually to make the transition from flight to settling irreversible (by hormonally controlled flight muscle breakdown) or, alternatively, that from settling to flight (by total exhaustion).

The central link can hardly be at the level of the motor complexes of settling and flight (Fig. 11, II). If it were at that level we should not expect any difference of after-effect on flight when the settling activity is the same. The reciprocally inhibitory cross-connexions between these two reflex systems presumably lie further 'upstream' (Fig. 11, III) than those of lower-order antagonists such as wing or leg raising and lowering. The latter are so coupled at or close to the level of the motoneurons themselves (Hoyle, 1964; Wilson, 1964). On these grounds Wilson (1964) saw no need to postulate a higher control centre for each pattern of motor activity such as flying. He showed, however, that the way motor units are coupled, as antagonists or as synergists, is not fixed. Units which work as antagonists in flying work as synergists in walking, and vice versa. Here surely is a function for higher centres as envisaged in the aphid (Fig. 11): not to co-ordinate the motor units during any one pattern of activity—for Wilson has shown these co-ordinate themselves according to the way they are coupled—but to co-ordinate the insect's different patterns of activity by imposing now one and now another system of couplings.

#### *Induction and depression*

The results of Expt. IV (Fig. 4) provide better evidence for the previous conclusion (1965) that the balance between the excitatory and inhibitory after-effects of temporary inhibition of flight depends (i) on the excitatory states of flight and settling at the moment when flight is inhibited; and (ii) on the strength (including duration) of that inhibition. The stronger flight is just before being inhibited, the less depressed and the more boosted it is afterwards when released from the inhibition. The stronger the settling responses elicited and hence, presumably, the stronger the simultaneous inhibition of flight, the greater is the after-effect on flight one way or the other.

The influence of (ii) the strength of the inhibition of flight was obvious throughout

the experiments but its at first sight confusingly reversible role showed that (i) the excitatory state of the two reflex systems is equally important. Very strong flight activity is strengthened more in every way after strong settling than after weak settling (1965, figs. 9, 11A). Weak flight activity may be strengthened momentarily by strong settling but it is then greatly weakened (Figs. 4B and 5; also 1965, fig. 11B); only frequent weak settling will keep such an insect flying at all. During most of a series of brief flights and landings an aphid's behaviour falls somewhere between these extremes and boosting and depression of flight are both more evident after strong settling than after weak settling. Mutual boosting and depression by settling and flight tip the balance of after-effect on each first one way and then the other, introducing a large element of instability and unpredictability into the course of behaviour when there is rapid alternation of flying and settling (1964, 1965).

The results also confirmed the importance of the excitability of settling, as well as that of flight, in determining the after-effect of settling on flight. The excitability of settling intervenes in two ways. The first way is indirect. When settling is not artificially controlled its excitability determines the strength of the settling responses elicited on a given landing surface. That governs the amount of stimulation received from the surface during the contact ensured by those settling responses, which in turn governs the strength (including duration) of the inhibition temporarily imposed on flight, and hence the after-effect of settling on flight. The second and more interesting influence of the excitability of settling is direct, and can be inferred from the results of Expts. IV and V and, also, less clearly, from many individuals given similarly extended series of flights in Expt. III. The intermittent landings made by these long-flown individuals boosted their rate of climb sufficiently to defer and even prevent the progressive decline of the rate seen in uninterrupted long fliers (1963*a*). In many cases the series of flights was terminated by the aphid ranging out before there had been any overall decline in the rate of climb (Fig. 3). While the excitability of flight was still being maintained in this way, with return to the previous rate of climb on recovery from the immediate after-effects of each landing, these immediate after-effects nevertheless changed as the series of flights lengthened. The immediate depression of the rate of climb on take-off increased, accompanied by ranging. Such an increase in the inhibitory after-effect on flight of the same settling stimulus implies an increase also in its immediate cross-inhibitory effect on flight, and that strongly suggests an increase in the central excitatory state of settling itself. Independent evidence of that last inferred increase already exists. A progressive priming or increase in the excitability of settling has been demonstrated as flying continues, whether or not the flying is interrupted by landings (1963*b*, 1964).

Another stage at which flight is especially liable to depression after a landing occurs within the first few minutes from an aphid's first take-off (Fig. 1; also 1965). It is known that the excitability of settling is very low at this time (1963*b*), hence the ease with which flight is depressed cannot now be attributed to strong cross-inhibitory influence from the 'settling centre' as it can later. It is associated rather with the fact that flight itself is still weak (although more excitable than settling) compared with what it will soon become with or without boosting by landings (Figs. 1, 10; also 1965, figs. 4, 8; 1963*a*).

In conclusion, the balance between antagonistic induction and antagonistic depres-

sion depends on the prevailing balance between the central excitatory states of the two reflex systems (their relative excitability) at the moment when external stimulation excites one of them enough for it to displace the other in overt behaviour; and this balance in turn depends on their previous interaction according to the pattern of stimulation received.

#### SUMMARY

1. A bout of settling activity on a leaf or other surface has both excitatory and inhibitory effects upon subsequent flight activity (antagonistic induction and depression of flight by settling); flight has similar after-effects upon settling; and the changing balance between these reciprocal after-effects determines the general course of behaviour.

2. The strength and duration of settling responses made on landing by free-flying aphids were regulated by jolting them off the surface into flight again prematurely. This treatment diminished but did not otherwise appear to distort the after-effects of a landing on flight and was used to establish the following points.

3. The balance between the excitatory and inhibitory after-effects of any one landing on flight depends (i) on the excitatory states of both flight and settling before the landing occurs, and (ii) on the strength of the settling stimuli received from the surface after landing.

4. The after-effects of settling on flight are predominantly excitatory when flight is already strong relative to settling but predominantly inhibitory when flight is relatively weak; the after-effects of strong settling are consistently greater, both ways, than those of weak settling.

5. Landings on different surfaces known to provide weak and strong settling stimuli still produce their typically different after-effects on flight when the settling responses actually performed on the two surfaces are kept equal.

6. The after-effects of settling on flight evidently do not require any peripheral feed-back (although this can add to the after-effects), and result from central cross-inhibition of flight when settling is centrally excited by external stimuli.

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#### REFERENCES

- HOYLE, G. (1964). Exploration of neuronal mechanisms underlying behaviour in insects. In *Neural Theory and Modeling*, pp. 346-76. Ed. R. F. Reiss. Stanford University Press.
- KENNEDY, J. S. (1965). Co-ordination of successive activities in an aphid. Reciprocal effects of settling on flight. *J. Exp. Biol.* **43**, 489-509.
- KENNEDY, J. S. & BOOTH, C. O. (1963*a*). Free flight of aphids in the laboratory. *J. Exp. Biol.* **40**, 67-85.
- KENNEDY, J. S. & BOOTH, C. O. (1963*b*). Co-ordination of successive activities in an aphid. The effect of flight on the settling responses. *J. Exp. Biol.* **40**, 351-69.
- KENNEDY, J. S. & BOOTH, C. O. (1964). Co-ordination of successive activities in an aphid. Depression of settling after flight. *J. Exp. Biol.* **41**, 805-69.
- WILSON, D. M. (1964). The origin of the flight-motor command in grasshoppers. In *Neural Theory and Modeling*, pp. 331-45. Ed. R. F. Reiss. Stanford University Press.