

CO-ORDINATION OF TWO KINDS OF FLIGHT ACTIVITY IN AN APHID

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SUMMARY

1. The interaction between 'migratory flight', defined as flight oriented vertically and horizontally towards a large overhead light source, and 'targeted flight' oriented towards a yellow leaf-like object seen to one side against a dark background, has been analysed in *Aphis fabae* in a laboratory flight chamber. Landings were prevented by regulating a down-current of air so as to balance the flier's rate of climb and by momentary withdrawal of the target when the flier came close.

2. The longer an aphid had flown before the target appeared the more persistently it homed-in on the target and the more its rate of climb was depressed by the presence of the target.

3. This 'priming' of targeted flight during migratory flight could be counteracted by suitably repeated bouts of presentation of the target. Such a treatment tended rather to prime migratory flight responses to the target stimulus, that is avoidance of the target and increase in the rate of climb.

4. The visual stimulus from the target had both excitatory and inhibitory effects on the rate of climb, mixed in varying proportions. Antecedent events in the behavioural chain governed the magnitude and relative timing of these effects.

5. The excitatory effect usually followed an inhibitory one but it could occur first or even alone, and was thus a separate effect not comparable with post-inhibitory rebound.

INTRODUCTION

In an earlier analysis of the interaction of two activities, flying and settling, in the black bean aphid, *Aphis fabae* Scopoli (Kennedy & Booth, 1964 *et ante*; Kennedy, 1965, 1966), it was found that stimulating one of these two antagonistic reflex systems inhibited the other and this inhibition left an after-effect on the system that had been inhibited. When that after-effect of the temporary inhibition was a net strengthening, the process was called *antagonistic induction*; when it was a net weakening, it was called *antagonistic depression*. These processes appeared to be central, and with repetition of the stimuli they could be cumulative, until one activity came to displace the other one entirely. However, the unequivocally antagonistic relationship between flight and settling in the aphid is not typical of the relationships between many of the behavioural activities of these and other animals. The above after-effects might then

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be peculiar to the interaction of outright antagonists. Thus it seemed very desirable to analyse similarly the interaction of reflex systems which were less antagonistic and more allied than flight and settling.

The two systems chosen for this may be termed *migratory flight* and *targeted flight*. Migratory flight here has the same meaning as 'flight' in the previous experiments, namely, climbing flight directed phototactically toward a large overhead source of light in a laboratory flight chamber. This is the kind of flight which in nature takes the aphid towards the sky and so out of the vegetal cover into the upper air where migratory travelling occurs on the wind (Johnson, 1969; Kennedy & Fosbrooke, 1972). This reflex system has the virtue of being continuously measurable as the rate of climb of the flying aphid towards the overhead light. In the flight-chamber this system also includes positively phototactic responses in the horizontal or yawing plane to the light-window above. Whenever the flier approaches the edges of the window and is therefore heading into the dark it turns back towards the window again. How far out from the centre of the window it strays is a measure of the strength of this horizontal phototaxis. Crossing the light-dark boundary, or 'ranging' (Kennedy & Booth, 1963*a*), marks an identifiable stage in the weakening of the phototaxis.

Targeted flight here refers to the horizontally directed approach-response of the flying aphid to a visually-contrasting object at its own level, in this case a leaf-shaped yellow card seen against the black walls of the flight chamber. Normally this response brings about mechanical contact of the tarsi with the object approached, leading in turn to inhibition of wing-beating and initiation of the settling responses. For present purposes, however, contact with the target was prevented in order to permit measurement of the effects of stimulating the targeted flight response only.

It was known from previous flight-chamber work that this targeted flight response was compound in nature – phototactic, optomotor and akinetic (Kennedy, Booth & Kershaw, 1961). A white pillar against a black background induced many fliers to turn toward and fly straight in to land on it. A black pillar against a white background also attracted fliers but, once arrived within a few centimetres of the pillar, they often paused hovering there and their rate of climb toward the overhead light decreased. These flight-inhibitory elements in the response to the optomotor stimulus from the target provided one reason for classing the targeted flight response as 'allied' to the settling responses made after landing. A second reason was Moericke's (1950, 1955) finding that yellow is the most effective colour both for attracting flying aphids into traps and for arresting walking ones and inducing them to probe the substrate, the first of the settling responses. On the other hand, unlike the settling responses, the targeted flight response is plainly not incompatible with flight or even with climbing flight toward an overhead light, for it occurs by means of flight and even while climbing against a down-current of air toward the overhead light in the flight chamber (Kennedy & Booth, 1963*a* (especially Fig. 7) and 1963*b*).

MATERIAL AND METHODS

Aphid supply

The arrangements for maintaining a continuous supply of fresh, adult winged aphids taking flight for the first time were as previously described (Kennedy & Booth, 1963*a*).

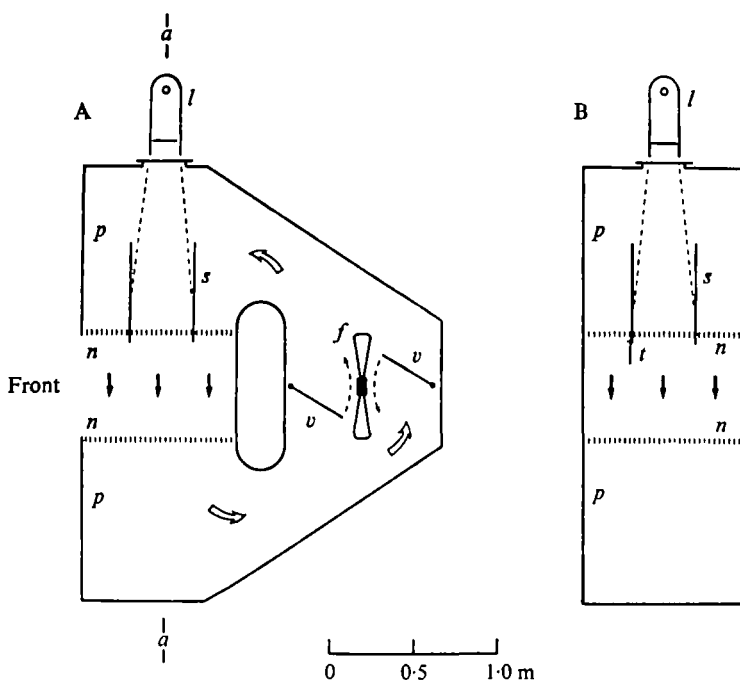


Fig. 1. Sectional diagrams of the aphid flight chamber modified for closed-circuit airflow. A, median section; B, section through *aa*. *f*, fan; *l*, illumination unit comprising lamp, housing, heat filter and glass window; *pp*, upper and lower plenum chambers; *nn*, brushed-nylon screens forming roof and floor of working section; *s*, internally reflecting collar confining light to central area of upper nylon screen; *t*, hinged target 'leaf' in lowered (exposed) position; *v*, flap valves, set for downward flow through the working section (black arrows).

except that the culture was kept at 19 °C (like the non-return take-off box and the flight chamber) and the rearing plants (*Vicia faba* L. cv. Sutton's Green Giant Long-pod), instead of being newly emerged whole seedlings, were seedlings taken at the 2–3-leaf stage and decapitated to leave only a stump supporting the large basal stipule on which the aphids settled to feed (Shaw, 1970*a*). The seedlings were germinated in 'Eff' soil-less (peat) compost and selected ones were decapitated and transplanted into sand, two per 70 × 70 mm square plastic pot, for infestation with forty apterous adult mothers per pot. The mothers were removed 48 h later and after a further seven days when the progeny were in the last larval instar the stipules bearing them were cut off and placed on fresh, leaf-bearing, decapitated bean-plants in the non-return box as previously described (Kennedy & Booth, 1964). The density of the larvae on the stipules was sufficient to produce, according to Shaw (1970*b*), a large proportion of alatae of the migrant type, that is those ready to fly before larvipositing. An aphid to be flown in the flight-chamber was taken immediately after it had been observed to take off and land on a glass sheet in the non-return box. It was induced to walk from the glass on to a detached *Fuchsia* leaf which was promptly transferred to the flight chamber for the aphid's second take-off.

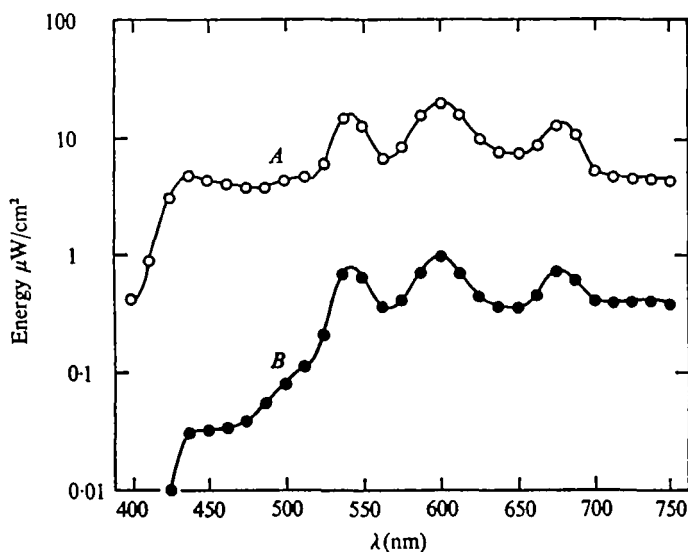


Fig. 2. Spectral energy distribution of light reaching an aphid flying in the flight chamber under the central area of the upper nylon screen, *A*, coming from above; *B*, coming from the yellow target 'leaf' 3 cm away in the lowered position.

Flight chamber

The flight chamber was a vertical wind tunnel cursorily described by Kennedy (1974) and Laughlin (1974). It was similar in principle to that originally described by Kennedy & Booth (1963*a*) but now formed part of a closed-circuit airflow system as shown in Fig. 1. The flow of air through the working section was not confined to the central illuminated area as in the previous model but extended beyond it on all sides. This eliminated the earlier problem of climbing fliers that 'ranged' beyond the margins of the lit area of the roof into the still air surrounding it and so tended to hit the dark peripheral roof. Instead the flier remained in the same downflow at the same height as before, with the bright central patch of roof still in full view. If still photo-tactically positive, it therefore wheeled back into that area again.

The light from the single 400 W quartz Compact Iodide lamp (Mazda 99-0201) above the upper plenum chamber was confined to the white central area of the brushed-nylon roof screen of the working section by a square, white-lined collar which was suspended above and in contact with the roof screen. In addition, a 5-cm-deep 'pelmet' of white card was fixed against the underside of the roof screen along all four sides of the central lit area. The dark peripheral parts of the roof screen were of black brushed nylon, the floor screen of the working section of black brushed nylon and the walls of the working section were lined with black flock-paper. The light coming from the overhead window and that reflected by the target are compared in Fig. 2.

The vertical airflow through the working section was produced by setting up a pressure differential between the upper and lower plenum chambers. This was done by directing unequal proportions of the output from a single axial fan (24-in 'Planette' from Airscrew Fans Ltd, Weybridge, Surrey, who state that it delivers air

Maximum rate of $1.7 \text{ m}^3/\text{s}$ at a pressure of 11 mm of water when driven at 950 rev/min by its 504 W (0.68 hp) motor) to the two chambers, and arranging for correspondingly unequal return flows to the intake side of the fan, by means of the flap valves shown in Fig. 1. These valves provided a very sensitive control of the airflow through the working section and were actuated via a counterbalanced lever system by the operator standing at the open front of the working section. From there he could watch the flying aphid and hold it at 5–15 cm below the roof screen by continually adjusting the rate of downward airflow to balance the aphid's rate of climb toward the light.

One of the flap-valve spindles carried a cam actuating a potentiometer, the voltage across which was fed into a chart recorder to provide a continuous record of the air-speed and therefore of the aphid's rate of climb. The cam had been shaped so that the voltage across the potentiometer varied approximately linearly with the air speed at the flying aphid's level under the centre of the lit area of the roof screen. The air speed in that position had been measured for a range of flap-valve settings (when no aphid was flying) using a modified Head-Surrey self-balancing vane anemometer (Head & Thorp, 1965) which had itself been calibrated in a laminar-flow device permitting the calculation of air speeds from the pressure drop across an orifice plate. The variation of air speed from place to place within the central lit area, for any one setting of the flap valves, was smaller than with the earlier flight chamber (Kennedy & Booth, 1963*a*, fig. 2) and would therefore cause only very small changes of level for an aphid circulating about the lit area at a horizontal air speed of 20 cm/sec.

When a flying aphid began to sink, instead of climbing, the flap valves were used to reverse the direction of airflow from downward to upward, through the working section. A sinking flier could be kept airborne and its sinking speed recorded in this way unless that speed came to exceed about 40 cm/sec, which was the maximum rate of upflow obtainable.

Target presentation

The visual landing target used for all these experiments was a leaf-shaped yellow card, 9 cm high and 4 cm across the centre, which was promptly withdrawn from the flying aphid's visual field whenever the aphid approached within 2–3 cm. Three different modes of presentation were used, and for two of them the target was suspended on a hinged arm from a point just below the roof screen so that the centre point of the target when exposed was about 10 cm from the roof. By energizing a solenoid the target could be swung suddenly edgewise and upwards to lie against the roof screen where it was out of sight behind the pelmet or inside a special white sheath; or it could be allowed to drop back into its vertical, visible position. The solenoid switch simultaneously actuated an event-marker pen to record on the chart when the target was presented or withdrawn.

The principal mode of presentation had the target hanging 2 cm outside the mid point of the pelmet on one side of the central lit area, with the blade parallel with that side and thus facing the centre (Fig. 1*B*). Since the target lay outside the flight path of an aphid circulating within the lit area, this was referred to as the 'off-course' target position. The flying aphid could not approach the target in this position without deviating from the flight path that it followed when no target was present. When the chart showed a withdrawal of the target, therefore, this signified a positive approach-

Table 1. *Experimental treatments*

Mode of target presentation	Treat- ment symbol	Flight dura- tion before first pre- sentation (sec)	Presentation bout (sec)	Presentation interval (sec)	Total aphids started (flying 60 min)	Expt no.
Continuous frontal	F	300	300	600	36 (21)	I
On-course {	D	600	c. 10*	600	27 (16)	
	B	90	180	360	12 (4)	
	B'	90	300	600	6 (4)	
Off-course {	A	90	300	600	6 (6)	II
	H	3,400	200	—	26 (10)	
	J	400	c. 10*	600	16 (10)	
	K	400	c. 10*	60	28 (9)	
	L	400	3,200	—	47 (10)	
	M	400	200	600	36 (10)	

* These brief presentation bouts were terminated at 10 sec, or after the flier had made three approaches, whichever was shorter.

response to the target. The absence of a recorded withdrawal signified that the aphid either turned toward the target but then turned away from it while several centimetres distant; or failed to turn toward it at all. Turns away from the yellow target were never toward the dark and were actually turns toward the white light from the roof window. In this they resembled the repeated turns back toward the window made by an aphid whenever it found itself heading out of the lit area into the dark. For aphids turning away from the target, the horizontal component of the light from the roof window was apparently a stronger phototactic stimulus than the yellow reflected light from the target. No active repulsion from the target is postulated.

A second mode of presentation had the target hanging within the central lit area, 5 cm in from the mid point of the front pelmet and perpendicular to it. It therefore lay directly across the circling path of the flying aphid and was referred to as 'on-course'. With this arrangement the absence of recorded target withdrawals again signified a turn toward the white top light away from the yellow target, when the latter loomed large on close approach. A withdrawal of the target might or might not signify a positive response to the target.

With these targets, on-course or off-course, a *presentation* is defined as a single exposure of the target between lowering it into view and raising it out of sight again. A *presentation bout* is defined as a set period of target exposure, which might cover a single presentation or a number of consecutive presentations, depending on the aphid's responses. If during such a period the aphid made a close approach to the target this was withdrawn to prevent a landing as usual, but it was then promptly lowered again as the aphid wheeled back into the lit area. The flying aphid received visual stimulation from the fixed target in a cyclical manner because of its circling flight path under the roof window. One circuit normally took 3-4 sec, which may be termed a *stimulation cycle*. The shortest presentation bout used in these experiments was about 10 sec, and thus allowed about 3 stimulation cycles.

The third mode of target presentation may be termed 'continuous frontal' presentation. It was effected manually by a second operator wearing a black glove and

Long-sleeved black gown and holding the yellow 'leaf' upright by its stem with its centre kept as nearly as possible in front of the flying aphid and about 5 cm away. This relative position of target and aphid could be maintained despite the movements of the aphid, and without permitting it to land, if the target was constantly oscillated from side to side (edgewise) at 3-4 Hz through about 5 cm. The target was quickly slipped out of the way (again edgewise, to minimize air disturbance) whenever the aphid approached. When on the contrary, the aphid was not homing in on the target and instead constantly 'dodging' it by turning away toward the unobstructed roof light, then the target was moved in front of the aphid again, in constant pursuit.

Treatments

The nine experimental treatments used in the course of two protracted experiments are set out in Table 1. In Expt I the mode as well as the timing of presentations differed between treatments, and three of the four treatments were continued repetitively for as long as each aphid could be kept flying, accidental landings notwithstanding. If the operator failed to withdraw the target in time from the path of an approaching flier and a landing occurred, the treatment was resumed after the aphid had been jolted into flight again. Scrutiny of many records showed that a landing not exceeding 2 sec duration was indistinguishable in after-effect from the usual close approach without landing; such brief landings were therefore ignored. When a landing lasted over 2 sec, that presentation bout was omitted in analysing the results, but subsequent presentations were included. However, the after-effect of such a landing on the rate of climb (usually a boosting of it) could persist for many minutes; hence the effects of presentation bouts proper, without landings, on long-term trends in the rate of climb could not be assessed in this experiment. In Expt II protracted flights were not attempted and more rigorous standardization was possible. The mode of target presentation was 'off-course' for all treatments and any aphid that landed for more than 2 sec was discontinued. Each treatment was repeated (interpolated between others) with fresh aphids until at least ten had continued under it for 67 min. After that time the treatment was usually discontinued.

Analysis of flight records

The flight records permitted measurement of the effects of target presentations on both the vertical and the horizontal components of the aphid's flight activity. The effects on the vertical component or rate of climb of the flier were assessed in two ways. The first was to follow the *extent* of changes in the rate of climb during and just after each presentation bout, and also through a succession of presentation bouts. The latter procedure was not appropriate for Expt I, as already indicated. The rates of climb were measured as averages over 60 sec which could be read to the nearest 0.5 cm/sec from the recorder charts with the aid of a graduated cursor (Kennedy, 1965, fig. 2). An aphid whose rate of climb differed from the controlled wind speed by even this amount would in one minute rise or fall 30 cm, which none did. In Expt II the rates were read at the same successive time intervals after take-off under all the five treatments and these times (see Fig. 5) were chosen to fall immediately before and after the start and the finish of each 200-sec presentation bout in the series composing

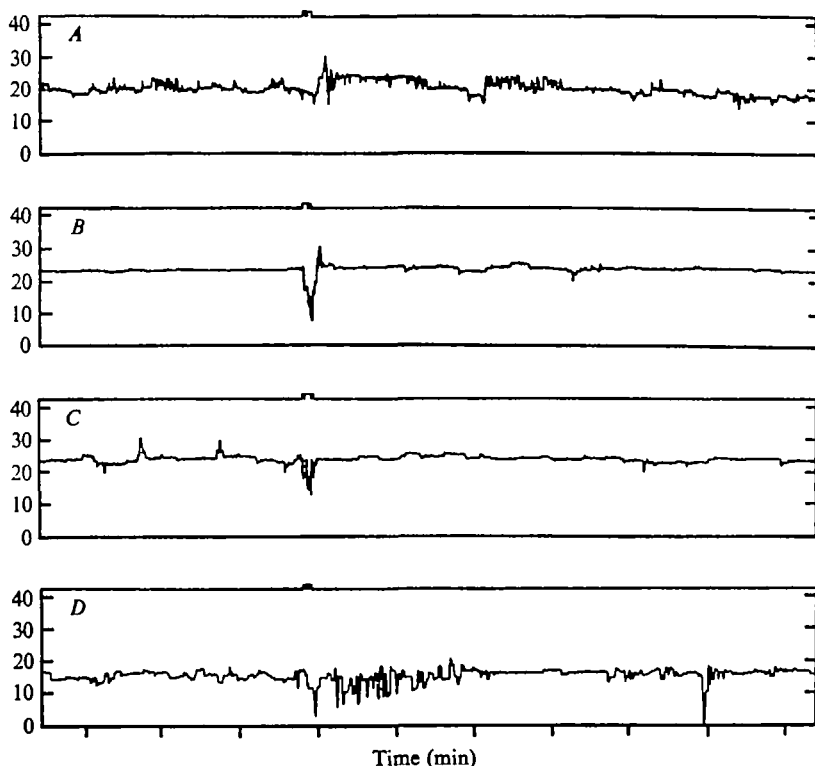


Fig. 3. Graded examples of the effect of presenting the off-course target for 10 sec. Ordinate is rate of climb of flying aphid in cm/sec; abscissa is in 60-sec intervals (lowest trace). Target presented whenever the upper (event marker) line moves to its higher level, and withdrawn whenever it drops to its lower level.

Treatment M. These times also bracketed the start and finish of each presentation bout under Treatments J, L and H, and every tenth one under Treatment K. No attempt was made to quantify rate-of-climb changes during the 10-sec presentation bouts of Treatments J and K, as this could not be done accurately.

The second method used to assess effects on the rate of climb was applicable to Expts I and II alike, including the treatments with 10-sec presentation bouts (D, J and K). This was to summarize the *sequence* of changes in the rate of climb during and for 60 sec after each presentation, simply according to the direction of change relative to the rate during the 60 sec immediately before the presentation began. Thus only three categories of change were recognized, a decrease, an increase and no measurable change. During presentations lasting several minutes (Treatments F, B, A, M and H) a decrease or increase was recognized when the change in average rate of climb over 60 consecutive seconds met the 0.5 cm/sec criterion above, no matter at what stage in the presentation bout this occurred. Thus a decrease and an increase could both be recorded within one presentation period and, if so, their order was noted.

During the shorter (10 sec) presentation bouts a decrease was recognized if the minimum rate of climb recorded during the bout was at least 2 cm/sec less than the minimum during the whole of the previous 60 sec before the presentation began; an increase was recognized if the maximum rate of climb during the bout was at least 2 cm/sec more than the maximum during the whole of the previous 60 sec before the presentation began.

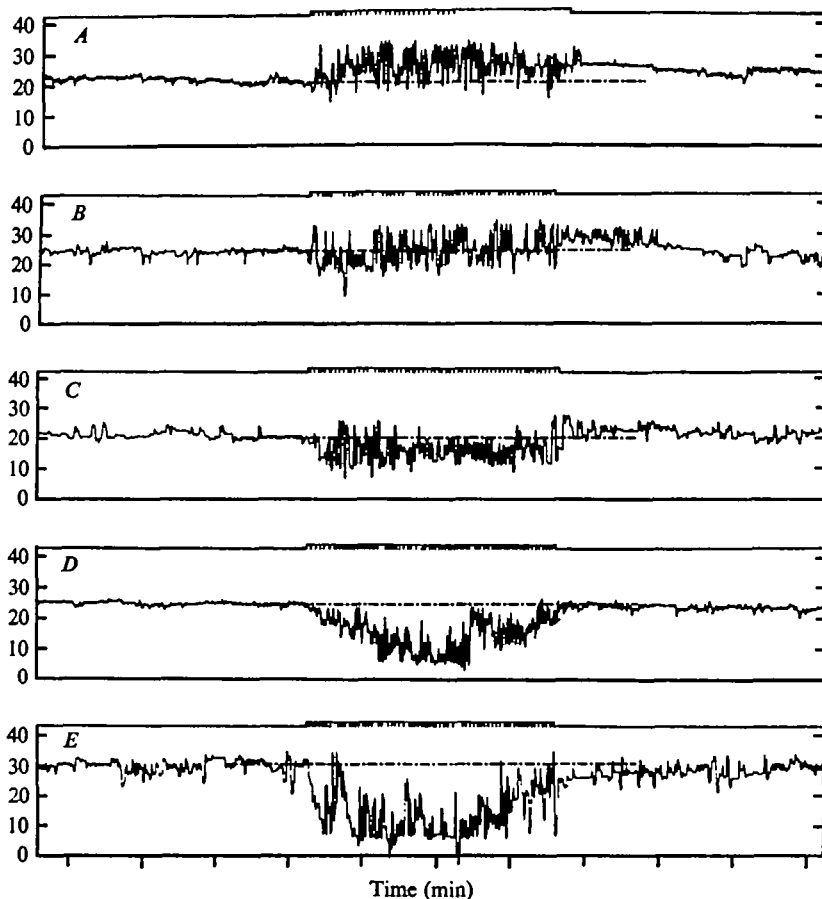


Fig. 4. Graded examples of the effect of presenting the off-course target for *ca.* 200 sec. Particulars as in Fig. 3 with the addition of the heavy broken line to mark the reference level, the average rate of climb during 60 sec immediately before presentation of the target. Note that the aphid in *A* was failing to home in on the target during the latter part of the presentation bout.

2 cm/sec more than the maximum during the 60 sec before the presentation began. Examples of sequences are shown in Figs. 3 and 4. With all presentations classified according to the type of sequence each produced, it was then possible to compare the frequency distributions of the different types, within and between the different treatments (as in Fig. 6).

The effect of a target presentation on the horizontal component of the aphid's flight activity, that is its effect on orientation in the yawing plane, was assessed indirectly, from the recorded frequency of target withdrawals (p. 177). With all treatments except F, the aphid was flying to and fro or round and round below the roof window, and this reiterative flight path brought it near the target once every few seconds. It might then approach the target closely, whereupon the target was withdrawn. It might fail to turn aside toward the off-course target (Treatments A, H, J, K, L and M, Table 1) or it might turn aside toward but then recoil from it; or, when the target was on-course (Treatments D and B), it might turn aside and thus 'dodge' the target. In either of these cases the target was not withdrawn. Thus periods when the record

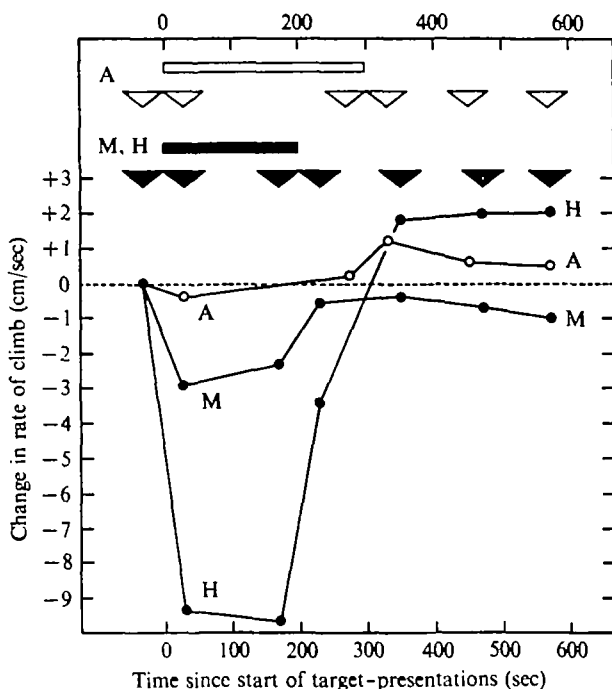


Fig. 5. Mean changes in the rate of climb during and after presentation of the off-course target following an uninterrupted flight of 90 sec under Treatment A, of 400 sec under M and of 3400 sec under H. Each point represents the mean difference between the rate of climb averaged over 60 sec at that time and the 60 sec average rate immediately preceding target presentation (reference level, marked by heavy broken line). Horizontal bars above show the length of the bout of target presentation, and triangles mark periods over which the rate of climb was averaged.

showed that the target was present but had not been withdrawn for 10 sec or more, could be read as periods when the optomotor/phototactic orientation response to the target was not strong enough to overcome the opposing phototactic response to the roof window, which was brighter and larger than the target. When the target was being kept constantly in front of the flying aphid by hand (Treatment F, p. 178) the operator was continuously aware of whether the aphid was orienting toward or away from the target and the periods it spent doing each were recorded whenever they exceeded 5-7 sec.

Probabilities quoted below with the results from statistical tests are all two-tailed.

RESULTS

Effect of the first bout of target presentation after uninterrupted flight

Fig. 5 shows the effect of a first long bout of presentation of the off-course target after three different periods of uninterrupted flight. The mean rate of climb during the first 60 sec of the presentation bout was less than the mean during the 60 sec before the presentation in each case, but the extent of this depression was significantly greater after 400 sec of prior flight (Treatment M) than after only 90 sec (Treatment A) and significantly greater after 3400 sec (57 min, Treatment H) than during either of the earlier presentation bouts (all probabilities less than 0.05).

Table 2. *Percentage of aphids showing a decrease in rate of climb and positive orientation to a target presented after various periods of uninterrupted flight. Total aphids in brackets*

Mode of target presentation	Treatment symbol	Time to first presentation (sec)	During first 10 sec of presentation bout		Over whole presentation bout	
			Rate of climb decrease	Orientation to target	Persistent orientation to target	Ranged out
Off-course	A	90	17 (6)	83 (6)	50 (6)	0 (6)
	J				—	—
	K				—	—
	K	400	69 (127)	86 (127)	—	—
	L				—	—
	M				71 (35)	21 (29)
	H	3400	95 (17)	94 (16)	95 (17)	35 (17)
On-course	B+B'	90	12 (17)	53 (17)	14 (14)	0 (14)
	D	600	48 (27)	93 (27)	—	—
Continuous frontal	F	300	77 (35)	74 (35)	31 (13)	17 (24)
Column	—	—	1	2	3	4

Mann-Whitney U test). The difference in degree of depression was greater than either Fig. 5 or the statistics suggest because the most depressed aphids could not be included. These aphids became negative to the roof light in the presence of the target and 'ranged out' towards the dark walls with zero rate of climb (Kennedy & Booth, 1963*a*), and the proportion doing so rose with the duration of prior flight (Table 2, col. 4) (this trend is not in itself significant). Accompanying this increasingly depressing effect of the off-course target on the rate of climb was an increasing tendency to turn towards it (Table 2, col. 3) ($P < 0.05$, Fisher Exact Probability test with Tochev's modification).

Fig. 6 displays these differences between Treatments M and H in terms of the individual sequences of change in the rate of climb during and just after the first presentation bout (see Methods, p. 180). Out of a total of sixteen long-flown aphids exposed to the first presentation under Treatment H, 87 % showed a depression of the rate of climb both during and after the target presentation (see also Fig. 9B), whereas, although 97 % of the shorter-fliers (M) showed an initial depression, 16 % then recovered during the presentation bout (as in Fig. 4B) and a further 19 % rebounded immediately after the target was withdrawn (as Fig. 4C).

Changes during the first 10 sec of the first presentation bout, long or short, may be compared in all treatments. Column 1 in Table 2 confirms the increasingly depressing effect of the off-course target on rate of climb as prior flight lengthens ($P < 0.05$, χ^2 test), an effect also suggested by the analysis of long presentations above. Again accompanying this effect is an increased tendency to turn towards the target during the first 10 sec of the first presentation bout (Table 2, col. 2) (this trend is not significant).

Similar differences were observed in response to the on-course target although here only the changes during the first 10 sec are comparable (Table 2, cols. 1 and 2). During this period, fewer aphids showed a decrease in their rate of climb ($P < 0.02$,

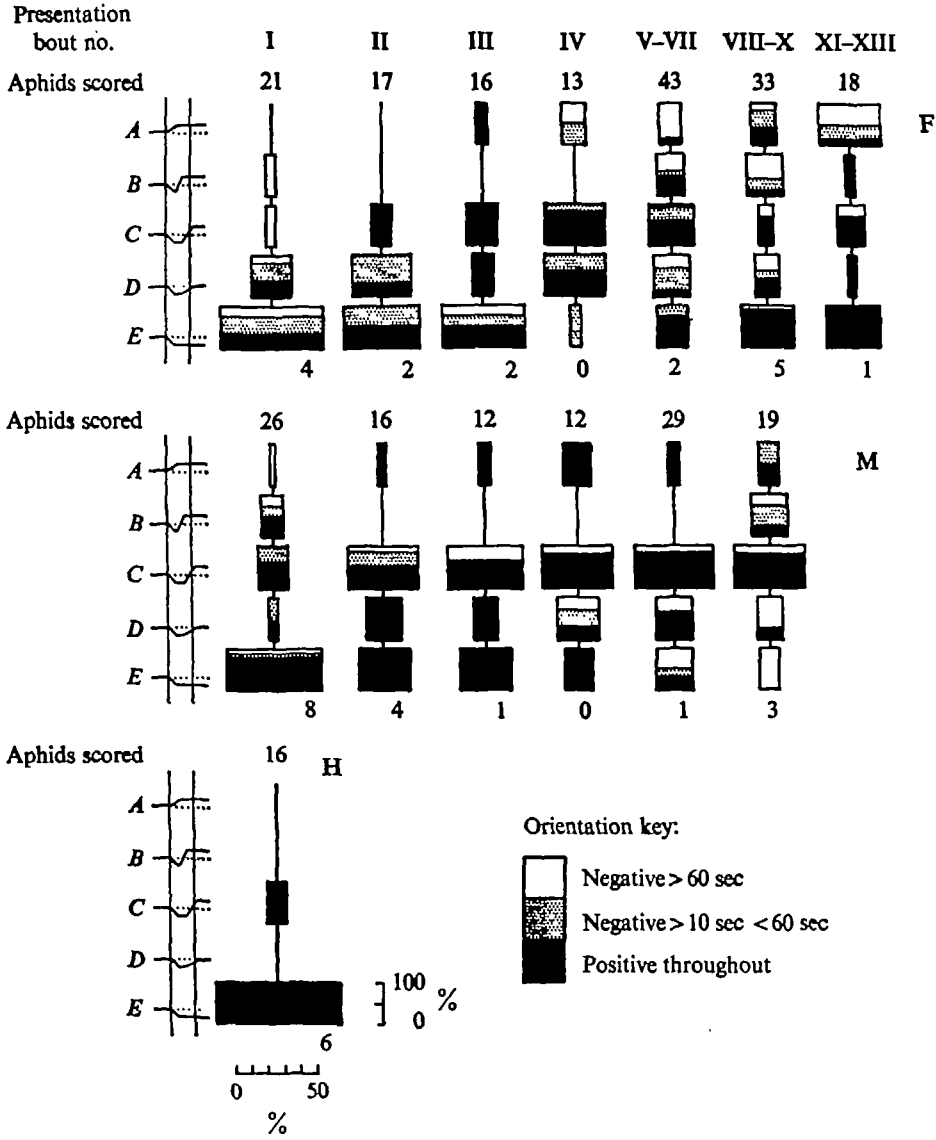


Fig. 6. Incidence of the five commonest types of sequence of change in the rate of climb that were induced by successive 200-300-sec bouts of target presentation, together with the incidence of positive and negative orientation to the target, under Treatments F, M and H. The rate-of-climb sequences are shown schematically at left (representing types A-E in Fig. 4) where the vertical lines mark the start and finish of the target presentation. Width of each block proportional to the percentage of aphids (horizontal scale at lower left) that followed the sequence indicated. Depth of layers within each block proportional to the percentage of aphids (vertical scale at lower left) that spent their time orientating to or avoiding the target according to the key at lower right. Aphids 'ranging out' are included in sequence type E but given separately in the figure below each column.

test) and fewer turned toward the target ($P < 0.001$), after 90 sec than after 600 sec of prior flight.

Thus, when migratory flight had only begun, target presentation commonly failed to induce oriented approaches and sometimes actually strengthened the migratory flight as measured by the rate of climb; but with lengthening periods of prior migratory flight the target increasingly induced homing-in and depression of the rate of climb: there was a 'priming' of the targeted flight response. The illustrative examples given in Figs. 3 and 4 of the various patterns of change in the rate of climb that are induced by target presentation have therefore been arranged in an order that corresponds with the shift in their relative frequency that occurs as priming proceeds. When there had been very little prior flight, sequences of types *A* and *B* in Fig. 4 predominated, but as the prior flight was increased in length the most frequent type shifted downwards through *C* to *D* and *E*. The effects of 10-sec presentation-bouts shifted similarly downwards through Fig. 3.

A clearly cumulative, depressing effect was often observed during the aphid's repeated circling under the roof window in the presence of the on- or off-course target. Thus the depression often did not reach its maximum with the first few such cycles of stimulation and response, but deepened irregularly over 10–20 cycles as illustrated in Fig. 4*D* and 4*E*. Consequently, when the first presentation bout lasted only 10 sec (2–4 stimulation cycles: Treatments J and K), the rate of climb was much less depressed than when it lasted 200 sec or more (Treatments M and L: see Fig. 7). When the rate of climb decreased in this progressive fashion, the outcome was sometimes 'ranging out' to the dark wall at zero rate of climb. But more often the rate of climb began to rise again within the same presentation bout (Fig. 4, *D* and *E*), if the prior flight had not been too long.

Effects of serial target-presentation bouts

Within presentation bouts

Consider first the effects on the rate of climb of Treatments M and F, where the presentation bouts were long enough (200 and 300 sec, respectively) and far enough apart (400 and 300 sec, respectively) for the detailed sequence of events to be followed bout by bout in a large number of aphids (Table 1). The five most common types of sequence of change in the rate of climb, during and just after a presentation bout, were those illustrated in Fig. 4; together these five made up 99 % of the recorded sequences under Treatment M and 91 % under Treatment F. The order in which the sequences were arranged in Fig. 4, it may be recalled, corresponds with the process of 'priming' of the targeted flight response during uninterrupted flight, wherein the most frequent type of sequence shifts in the direction away from type *A* toward type *E*. The same order is used again in Fig. 6 in setting out the relative frequencies of these different sequence types during serial presentation bouts. This makes it plain that the effect of the serial bouts was indeed to counteract and even to reverse the priming of targeted flight. The serial presentation bouts caused a shift in the opposite direction, away from type *E* toward type *A*, that is toward less depression of the rate of climb and more boosting of it after the presentation bout or even during it.

The sixth presentation bout under Treatment M came after the same length of

prior flight (57 min), lasted for the same time and used the same mode of target presentation as the first presentation bout under Treatment H, the effects of which are shown for comparison in Fig. 6. When the two resulting sequence-frequency distributions were compared by Mann-Whitney U test (after each recorded sequence had been scored on an arbitrary ordinal scale corresponding to the order in Figs. 4 and 6), they were found to differ significantly ($P = 0.02$).

The lesser depression shown by the M than by the H aphids at that time was not due to earlier elimination of the more readily depressed members of the M group. More fliers had, indeed, 'ranged out' before the 57th minute under Treatment M (13 out of 25, or 52 %) than H (6 out of 23, or 26 %); and more did range out during the ensuing first presentation under H (6 out of 16, or 38 %) than during the ensuing sixth presentation under M (0 out of 13). But, even if all the aphids that ranged out during the first presentation under Treatment H are excluded from the comparison, as in Fig. 7, the depression of the rate of climb recorded in the remainder is significantly greater than that recorded during the same minutes under Treatment M (Mann-Whitney U test, $P = 0.02$). Similarly, the shift in Fig. 6 toward increasingly frequent boosting of the rate of climb by succeeding target-presentation bouts under Treatments M and F was not solely due to the more readily depressed aphids dropping out early. This was ascertained from block diagrams constructed like Fig. 6 but showing only the behaviour of the same individuals throughout, by excluding short-fliers. These diagrams incorporated the results from the eleven individuals that continued flying through seven presentation bouts (70 min) under Treatment M, and the five individuals that did so through fourteen presentation bouts (140 min) under Treatment F. Both diagrams closely resembled those in Fig. 6.

The continuously frontal presentations of Treatment F caused more depression of the rate of climb than did the off-course presentations of Treatment M, throughout the series of bouts (Fig. 6). Accordingly, the opposite, boosting effect was slower to develop through the series of bouts under Treatment F. Once developed, however, it went further, and bouts when boosting occurred both during and after the presentations (types *A* and *B*) eventually became more frequent under F than under M. An association between depression and boosting of the rate of climb, now within the effects of a single presentation bout, is also seen when Treatments H and M are compared (Figs. 5 and 7). The depression caused by the late, first presentation bout of H was deeper than that caused by any presentation bout of M, and the rate of climb took longer to recover after that H bout. But the eventual rebound of H was then greater than after all presentation bouts of M.

Serial presentation bouts also affected the orientation response, counteracting the trend toward increased readiness to home in on the target that had been observed with increase in the duration of the prior flight (p. 183). Thus Fig. 6 reveals no such trend under Treatments F and M, and there is some indication of an opposite trend: sustained avoidance of the target for 60 sec or more became commoner during the later presentation bouts.

No matter how much boosting of the rate of climb and avoidance of the target the fliers had displayed during the serial presentation bouts, all fliers sooner or later (if allowed to continue flying) began again to home in on the target persistently and to be solely depressed by it, and then 'ranged out' toward the dark. This behaviour

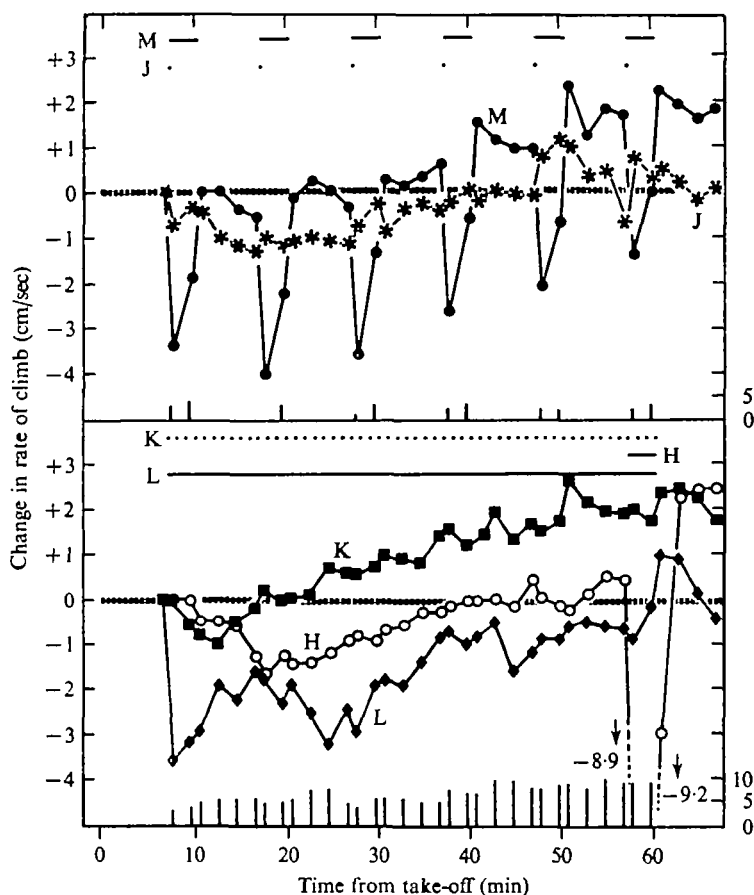


Fig. 7. Progressive changes in the rate of climb (averaged over 60 sec) under Treatments H, J, K, L and M. Lines and dots at top of each frame mark the periods when the target was present. Each point represents the mean difference ($n = 10$, except for Treatment K when $n = 9$) between an aphid's rate of climb at that time, and at 7 min from take-off (reference level, marked by heavy broken line). Vertical bars on base lines show (according to scale at right) the number of aphids that failed to home in on the target for at least 10 sec during the 60 sec when the rate of climb was measured, under Treatment M above and L below. Other treatments produced negligibly few such target avoidances.

reversion as 'range-out' became imminent is illustrated with 60-sec presentation bouts in Fig. 9A. The whole sequence of changes in responsiveness recalls the initial weakening and eventual strengthening of the settling responses observed in previous experiments (Kennedy & Booth, 1963b).

Block diagrams incorporating the results of Treatments A, B, B', D and J and constructed in the same way as those in Fig. 6 showed a similar overall pattern, first an increase and eventually a decrease in the boosting effect of the target and in the incidence of target avoidance.

Overall trends

The effects of the single presentation bouts could not be measured separately under Treatment K as they were under the other treatments above, because the K bouts

were less than 60 sec apart. However, all the treatments of Expt II including K could be compared in terms of the general trend in the rate of climb that each produced. These trends (Fig. 7) were obtained by plotting, for each treatment, the mean difference between each individual's original rate of climb between 340 and 400 sec from take-off (i.e. for 60 sec just before any target presentation began), and its rate of climb at each of a succession of measured minutes up to 60 min later (67 min from take-off). To make the measurements comparable throughout this time, the curves refer only to those aphids that completed the standard 67 min of flight. The aphids under Treatment H ceased to serve as unstimulated controls when they received their first target presentation (the results of which have already been discussed) after 57 min of flight.

Under Treatment J the presentation bouts were brief and infrequent and not unexpectedly the rate-of-climb curve follows the H curve closely except for the brief rebound after each presentation. Both curves fall initially but then turn upwards at around 20 min from take-off or 13 min from the first presentation. With the interval between equally brief (10-sec) presentation bouts reduced to 50 sec under Treatment K, the curve turns upwards distinctly earlier, at about 6 min after the presentation began, and remains above H, J and L thereafter. The mean rates of climb of groups K and H over the period from 10 to 50 min after the presentations began were compared by Wilcoxon matched-pairs, signed-ranks Test, and proved to be significantly different at $P < 0.001$.

However, when the intervals between presentation bouts were eliminated altogether (Treatment L) so that the aphid was subjected to an unbroken succession of 3-4-sec stimulation cycles on its circular flight path (p. 178), this did not boost the rate of climb still further. On the contrary, the mean rate of climb was deeply depressed within the first 60 sec of target presentation and remained lower than the H, J and K curves throughout ($P < 0.001$). The L curve eventually rises slowly like the others, but this common rise cannot be attributed to a cumulative effect of the target presentations, since the aphids under Treatment H showed a parallel rise in their mean rate of climb from about 20 min after take-off onwards (Fig. 7), although they were not presented with any target until 37 min later. Nevertheless, the H aphids were then far more depressed by the target than were the L aphids at the same time (Fig. 7), so there must have been some cumulative, adaptation-like loss of responsiveness under the prolonged target presentation of Treatment L. Note that when at last the target was withdrawn from the L aphids, at 60 min from take-off, their mean rate of climb did not rebound to as high a level as that attained by the H aphids at the same time after their presentation bout also came to an end.

The orientation records, also, show a cumulative effect of the L presentations. Among the sixteen H aphids, given their first presentation bout at 57 min, only one failed to home in on the target for as long as 10 sec; whereas nine out of the ten L aphids that continued flying for that length of time then failed to home in for at least 10 sec. Indeed, there was a cumulative increase in the frequency of target avoidance throughout the L Treatment as Fig. 7 shows.

Treatment M provided another form of intermittent stimulation for comparison with the continuous stimulation of Treatment L. Fig. 7 shows that each M presentation bout, after the first, depressed the rate of climb more than did the same target at the same times in the course of Treatment L (modified Mann-Whitney U test).

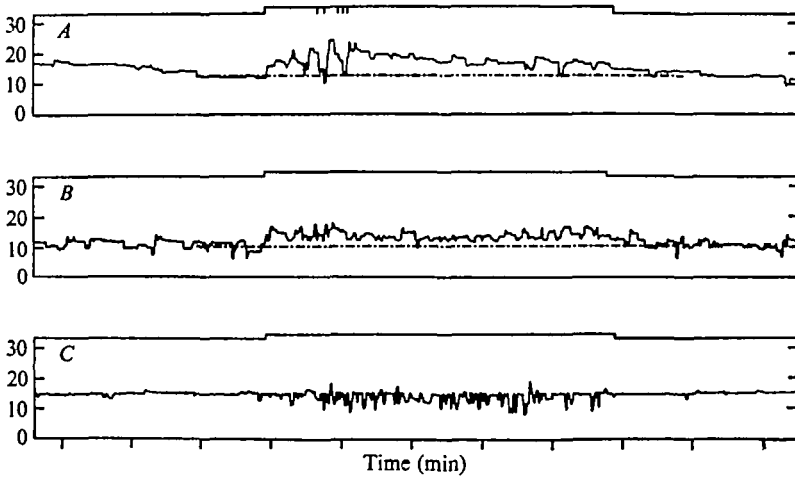


Fig. 8. Examples of rate-of-climb changes in the presence of an on-course target during repeated avoidance of it. Particulars as for Fig. 4. *A*, rate of climb increased except for several brief decreases associated with a period of homing in on the target; *B*, rate of climb increased during unbroken target avoidance; *C*, rate of climb decreased during unbroken target avoidance.

$P = 0.004$); correspondingly, Treatment M produced less avoidance of the target than did Treatment L. But the mean rate of climb of the M aphids showed lasting rebound after each of those five presentation bouts (see also Fig. 6), and the result (Fig. 7) was that during the intervals between presentation bouts the curve for the M aphids rose above all the other curves at 10–12 min from take-off and remained above all the others, except K, thereafter.

Thus intermittent bouts of target presentation boosted the rate of climb more than did continuous presentations, and this appears to have been due in part to the fact that boosting occurred mostly as rebound after target withdrawal. On the other hand, failure to orient toward the target and recoiling from it were promoted by continuous rather than intermittent presentations.

Relation between vertical and horizontal responses to the target

During the majority of presentation bouts the aphids both oriented repeatedly toward the target in the horizontal or yawing plane, and showed some net depression of their rate of climb toward the overhead light. These two effects both increased significantly with increase in the duration of prior uninterrupted flight, and some correlation between them was also discernible in the opposite sense through the serial presentation bouts, as described earlier. On closer examination it was found that during the F and M measurements, for instance, the rate of climb was significantly less depressed and more often boosted during those presentation bouts wherein the aphid was consistently avoiding the target than in those wherein it consistently homed in on the target ($P < 0.002$ for F, < 0.0034 for M: Mann-Whitney U tests). Fig. 8B is an extreme case of this when the aphid's response to the presence of an on-course target was to increase its rate of climb while dodging the target on every circuit for 5 min succession. Furthermore, in many records it was possible to see a gross association

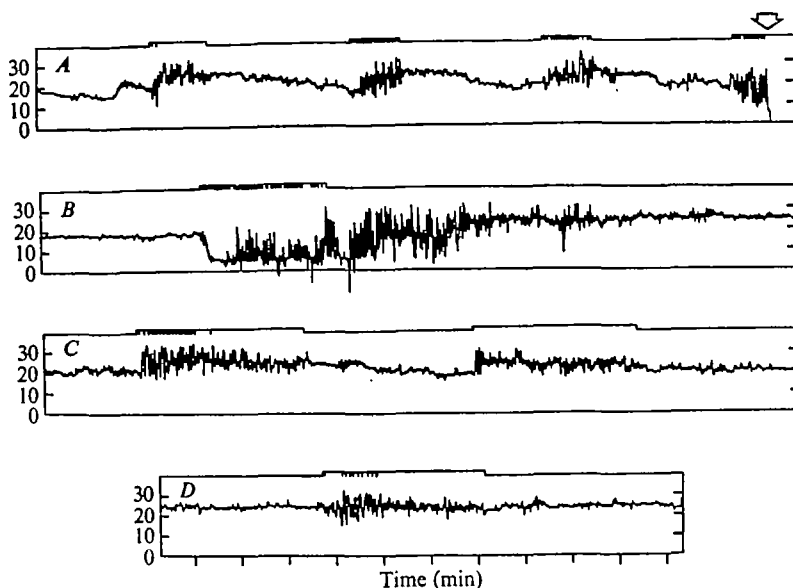


Fig. 9. Examples of rate-of-climb responses to the presence of an off-course target, with and without avoidance of it. Particulars as for Fig. 4. *A*, final 15 min of a long flight punctuated by target presentations, showing the eventual re-appearance of regular homing in on the target after previous avoidance of it, then the re-appearance of depression of the rate of climb after previous boosting, and finally 'ranging out' at zero rate of climb (arrow); *B*, first bout of target presentation after 57 min of uninterrupted flight (Treatment H), showing long-lasting oscillation and net depression of the rate of climb but eventual rebound; *C*, continuation of record in Fig. 4*A*, showing target-induced oscillation with net boosting of the rate of climb, both when homing in on and when avoiding the target; *D*, target-induced oscillation without net increase or decrease of the rate of climb, during both homing in and avoidance.

between positive orientation responses to the target and drops in the rate of climb within a single bout of presentations, as illustrated in Fig. 8*A*. In this particular case the target again boosted the rate of climb throughout the presentation bout but there were several pronounced drops in the rate, and these were associated with the short period when the aphid was orienting positively to the target. This was common; and sometimes the rate of climb decreased and increased again cyclically in perfect synchronization with the aphid's circuits under the window and thus with its once-per-circuit oriented approaches to the target.

However, such synchronization was more often lacking, as in Figs. 3, 4, 8 and 9. Inspection of Fig. 8*A*, for example, does not show a one-to-one relationship between the drops in the rate of climb and the approaches to the target; and the first drop occurred before the approaches began. The correlation between the orientation and rate-of-climb effects of the target was poor between presentation bouts, also. Figs. 4 and 8 illustrate how both continuous boosting and continuous depression of the rate of climb could occur both with persistent homing in on the target (Fig. 4*A* and *E*) and with persistent avoidance of it (Fig. 8*B* and *C*). Between these extremes all types of intermediate combination also occurred: Fig. 6 gives some idea of their relative frequencies under Treatments F, H and M.

The results thus suggest that, although the target stimulated both horizontal a

critical responses and these had a definite tendency to vary and change sign together, nevertheless they did so because the treatment affected both types of responsiveness in parallel and not because the effect on one was a consequence of the effect on the other.

Much the most consistent effect of target presentations was the induction of rapid fluctuations in the rate of climb. Relative to the pre-presentation level these fluctuations were made up of falls and recoveries, or of rises and recoveries, or of both falls and rises alternately, as shown in Figs. 3, 4, 8 and 9. Nearly all records showed such induced oscillations when the target was present, whether there was also a net increase in the rate of climb, a net decrease, or both, or for that matter no net change at all as in Fig. 9*D*, and whether the aphid was homing in on or avoiding the target. Sometimes the induced oscillations ceased abruptly when the target was withdrawn (e.g. Figs. 3*A*–*C*, 4*A*, 8*C* and 9*C*) but sometimes they continued for some time thereafter, damping out gradually (e.g. Figs. 3*D*, 4*B* and *C* and notably 9*B*).

The incidence of the horizontal orientation response to the target was better correlated with the intensity of the rate-of-climb oscillation than it was with any net change in the rate. Whether there was a net decrease or a net increase or neither, the amplitude of the oscillations was usually greater when the aphid was homing in on the target than when it was avoiding it. This may be illustrated from Figs. 4*A* and 9*C*, which are consecutive extracts from the same flight record covering three successive bouts of presentation of the off-course target. The greatest amplitude, 10–15 cm/sec, occurs in each period when the aphid is repeatedly homing in on the target, that is during the first part of the first and of the second presentation bouts. Intermediate amplitudes prevail whenever the target is present but the aphid is avoiding it, that is during the second part of the same bouts and during all of the third; while in each target-free interval between bouts the aphid reverts to a minimal or 'basal' amplitude of 3–5 cm/sec.

Induction other than rebound

The post-inhibitory rebound (antagonistic induction) of the rate of climb that was often recorded upon re-take-off after landing in the previous experiments (Kennedy, 1965) was paralleled in the present ones by many instances of a rise in the rate of climb after the target that had been depressing it was withdrawn (Figs. 3*A*–*B*, *B*–*C* and 9*B*). But there was of course no previous parallel for the rises recorded in the present experiments while the target was still present, and the records were therefore scrutinized to determine how often such rises had occurred without prior depression.

During the 10-sec presentation bouts with the off-course target under Treatment J, a rise in the rate of climb of 2 cm/sec or more above the maximum recorded over the previous minute was recorded only once without any prior fall. During the more extended series of 10-sec presentation bouts with the on-course target under Treatment D, such rises not preceded by a fall were recorded during 13 % of the grand total of 281 bouts. They became commoner later on in these series of bouts, occurring in 9 % of the 126 bouts at and after the tenth (100 min from take-off) compared with only 8 % before this, a difference which is significant at $P < 0.001$ using the χ^2 test. In analysing the rate-of-climb changes during the 200–300-sec presentation bouts

Table 3. *Incidence of rises in the 60 sec mean rate of climb without a prior fall, during 200–300 sec bouts of target presentation. Percentages in brackets*

	Target-presentation mode		
	On-course	Off-course	Continuous frontal
Total bouts recorded	280	375	259
Bouts including a 60 sec mean rise without a prior 60 sec mean fall	80 (29)	59 (16)	32 (12)
Bouts including a 60 sec mean rise with no trace of prior fall	40 (14)	20 (5)	7 (3)

of Treatments A, B, B', F and M, so far, a rise or fall was scored whenever the rate of climb, as averaged over 60 sec, was measurably higher or lower, respectively, than the average during the 60 sec just before the target presentation began. On this criterion a rise was recorded with no prior fall many times, as shown in Table 3, line 2. However, if some change was inevitable in most presentation bouts (less than 2 % showed no measurable change at all) one would expect by chance that about 50 % of initial responses would be a rise. The observed percentage was 19 over all treatments. Thus the overall figures give evidence only of the depressing effects of the target.

However, the distribution of initial rises was not random: they occurred predominantly late in the flights of a few long-flying aphids, and then seemed too frequent to be explained by chance. This hypothesis was tested by a χ^2 test on the presentation bouts immediately following each presentation bout in which the initial response was a rise (see Statistical Appendix). The observed data differed markedly from those predicted from the null hypothesis that rises and falls were equally likely. There were 57 rises following the 94 rises shown by the eleven longest-flying aphids (expected = 47, $P < 0.05$, χ^2 test).

Thus there appear to be phases, particularly late in the flight, when rises without previous falls occur in response to the target more often than expected by chance, and these are presumably due to some independent boosting process. However, an average rise over 60 sec could conceal some initial depression of the rate of climb before the rise developed. Therefore a stricter criterion was applied to the same records. If either before or at the beginning of such a 60-sec average rise, the record showed any perceptible fall, even a momentary one, to a level below the *minimum* that had been reached during the last 60 sec before the presentations began (as for example in Fig. 4A), that case was discarded. Also discarded was any case where the rate of climb during the presentation bout, but before the rise, remained below any given level for longer than it had in the 60 sec before the presentation began.

The cases that were left after these eliminations were cases of pure boosting of the rate of climb by the target stimulus with no trace of any prior depressing effect (as in Figs. 8A and 9C). Such cases were relatively few (Table 3, line 3) but they came from the records of eighteen different aphids and were in all too many to be ignored. They totalled 67 cases and became commoner later in the flights, occurring in 16 % of the 330 presentation bouts after the eighth (at least an hour from take-off) but in only

■% of the 584 bouts before then, a difference which is significant at $P < 0.001$ using the χ^2 test.

DISCUSSION

Antagonistic induction and depression. The question first posed was whether the interaction between migratory flight and targeted flight would resemble the interaction between migratory flight and settling behaviour, in showing antagonistic induction and antagonistic depression. In the event similar effects have been found, and such after-effects may participate in many other behavioural sequences which are similarly labile and not 'fixed action patterns' (Kennedy, 1974).

For example, eliciting migratory flight had the effect of 'priming' the settling responses to a surface that was landed upon (Kennedy and Booth, 1963*b*); likewise, eliciting migratory flight primed the orientation response to a visible target. Inhibiting migratory flight briefly but repeatedly, by eliciting serial landings, served to counteract the priming of settling (Kennedy & Booth, 1964); likewise, exerting an inhibitory influence on migratory flight briefly but repeatedly, by eliciting serial targeted flights, counteracted the priming of targeted flight. In both sets of experiments, the after-effect of such repeated inhibition of migratory flight could be either to 'boost' it or to depress it, as measured by the rate of climb, and this depended loosely on the strength, duration and frequency of the inhibition and on the duration of the prior flight. But if flight was continued for long enough, then in spite of the continuing counteracting effect of interruptions, the priming of targeted flight or settling eventually re-asserted itself and became dominant.

The occurrence of rebound of flight, after a target had been presented but no landing had been permitted, strengthens the earlier conclusion (Kennedy, 1966 *et ante*) that, even when a landing has been permitted, rebound of flight is a central nervous process and not due to some peripheral one such as fuel mobilization while at rest.

Oscillations. The after-effects of inhibiting flight by eliciting settling always seemed to be compounded of both boosting and depressing effects on the rate of climb, in varying proportions (Kennedy, 1965, 1966). Immediately after each take-off the rate of climb typically oscillated rapidly from one to the other. Merely presenting the visible target acted in the same way (p. 191). Even in the absence of any visible target the rate of climb of almost all fliers fluctuated on a time-scale of seconds, in both sets of experiments. This fluctuation varied greatly in waveform, amplitude and frequency from aphid to aphid, each specimen having a characteristic and remarkably persistent 'signature' waveform. There was even an occasional sharp drop in the rate of climb followed by rebound. But the fluctuations were almost always conspicuously greater when a visible target was present. Presentation of the target always appeared, not to cause a simple change in the rate of climb, but rather to increase the amplitude and frequency of pre-existing fluctuations and usually to give them a bias upward or downward. As suggested elsewhere (Kennedy, 1974) further analysis of such irregular central oscillators might throw light on the regular type usually studied.

Induction without prior depression. The present experiments provided continuous information on the excitability of migratory flight as measured by the rate of climb, ■ether the visible target was present or not. In the previous experiments no informa-

tion on flight excitability was available during the landings, and the after-effects on landings on the rate of climb were naturally seen as post-inhibitory effects. It turned out that, in the great majority of presentation bouts without landings in the present experiments, the first effect of the target was again to inhibit flight, judging by the depressed rate of climb. If that had always been so then any subsequent boosting of the rate could still have been regarded as post-inhibitory rebound. But there was a minority of cases in which the first effect of presenting the target was to boost the rate of climb, with no trace of prior depression (p. 192). Boosting of migratory flight by a visible target is therefore not necessarily an after-effect of inhibition. 'Post inhibitory rebound' appears to be compounded of two separate effects of the stimulus, one excitatory and the other inhibitory.

This situation would not be an entirely novel one neurophysiologically. It would fit a model such as Willows, Dorsett & Hoyle (1973) have proposed for the central co-ordination of escape swimming by the nudibranch mollusc, *Tritonia diomedea*. The dorsal and ventral flexion neurones in the pedal ganglia are reciprocally inhibitory but they also excite one another, more slowly, through their common connexions with 'general excitatory' neurones. An analogous situation was described by D. Kennedy (1960) in a photoreceptive neurone of the lamellibranch mollusc, *Spisula solidissima*. The pattern of this unit's activity depends on two pigments with overlapping absorption spectra that mediate opposite responses. The excitatory response has a higher threshold but is longer-lasting than the inhibitory one, so it is masked during illumination but appears as an off-response, thus giving the impression that it is an after-effect, only, like post-inhibitory rebound.

Coupling and uncoupling. The co-ordination of different activities in the aphid contrasts with that of those single, fixed-action systems in the molluscs in that the time relations of the opposite effects of the target stimulus on the aphid were not fixed but varied greatly. More important, this timing was evidently under the influence of antecedent behaviour. For example, boosting of the rate of climb while the target was present, rather than after it had been withdrawn, was more likely if there had been a series of previous bouts of target presentation (Fig. 6 and p. 186). This labile situation implies a further type of change of responsiveness that is governed by antecedent reflex activity, beyond the antagonistic induction and depression so far considered.

Landing on a surface invariably had some inhibitory effect on flight and some excitatory effect on settling, and prolonging migratory flight served simply to strengthen both these effects of mechanical contact with a surface. By contrast, the visual stimulus from the target did not always have an inhibitory effect on migratory flight nor did it always excite orientation toward the target. When migratory flight had just started, and again later if there had been intervening target presentations, the aphid's rate of climb often increased instead of decreasing in the presence of the target; and at these same times, although not always on the same occasions, the aphid often failed to home in on the target and instead turned away from it toward the lit central window. When the target stimulus had these effects it was clearly promoting migratory flight jointly with the overhead light, instead of working antagonistically.

At such times the aphids' responses to the target were in fact highly variable in their interrelations as well as in their strength. An aphid homing in on the target might show an increase or decrease in its rate of climb, and so might an aphid that

Missing the target (Figs. 8 and 9). However, if migratory flight was allowed to continue undisturbed for many minutes before any target presentation, then the responses made to the target, both horizontally in orientation towards the target and vertically in depression of the rate of climb, became consistently and strongly antagonistic to migratory flight.

Antecedent reflex activity not only strengthened some reflex systems relative to others; it also strengthened some interconnexions among them relative to others. Thus, the effect of a long undisturbed bout of migratory flight was to yoke firmly together orientation towards the target and depression of the rate of climb, and at the same time to strengthen both of them as responses to the target in place of antagonistic, migratory flight responses to it. But those now-exclusive couplings of stimulus to response and of response to response could be loosened again by interruptions of migratory flight.

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STATISTICAL APPENDIX

by A. R. Ludlow

In considering the rises or 'boosts' in rate of climb which occurred in the presence of the target the following hypotheses were examined:

H₁, that the presentation of the target had no effect on the rate of climb;

H_2 , that the presentation of the target had a depressing effect on the rate of climb which remained constant throughout the flight;

H_3 , that the presentation of the target had a depressing effect which varied with time of flight and between aphids, but which never became a boosting effect;

H_4 , that the target normally has a depressing effect, but that at times in the flight of some aphids the target has a boosting effect. For the purposes of these hypotheses a depressing effect is postulated whenever the observed depressions were significantly more frequent than expected, and a boosting effect whenever observed boosts were significantly more frequent than expected boosts.

H_1 may be rejected by standard statistical methods. For example among 914 presentation bouts from all treatments, the initial change in the presence of the target (averaged over 60 sec) was a depression in 80% and a rise in only 19% of cases ($\chi^2 = 347.7$, 1 d.f.). Thus we reject H_1 and postulate a depressing effect.

Similarly H_2 may be rejected by a runs test which shows that in the 914 presentation bouts from all treatments there were significantly fewer, and therefore longer, runs than expected ($P < 0.001$). The significant result in the runs test could have been brought about by variations between aphids, some being more prone to depression than others, or by changes in responsiveness during the flight of individual aphids. Either could cause varying probability of depression and thus significantly long runs. The occurrence of boosts was largely confined to the later part of the flight of a few long-flying aphids (p. 192) which suggests that both of those effects were operating. Thus it is extremely improbable that the relative probabilities of depressions and boosts remained constant throughout the flight.

While the runs test indicates that the relative probability of boosts varied, it does not indicate whether the probability of boosts ever became greater than that of depressions, or in other words, whether the target ever had a boosting effect. Thus the runs test does not provide a way of distinguishing between H_3 and H_4 . The problem, which must arise commonly, is that when one effect is observed in the majority of cases, any process which might be causing the opposite effect will usually be masked.

An effort was made to unmask any minority effect by examining the probability of boosts entirely within those phases of the flight when boosts were occurring. This could be done without unfairly selecting the data by examining the next presentation bout after each one that gave a rise. This does of course select the bouts to be examined, but the rise which caused the bout to be selected is not included. We might for example measure the proportion of 'heads' and 'tails' in the whole series of coin tosses, or we might include only those tosses which followed a 'head'. We should expect similar results in the two cases, although in one we are selecting tosses while in the other we are not.

Applying this method to the aphid data we find that the 94 boosts shown by the eleven longest-flying aphids are followed by 57 rises. If boosts and depressions were equally probable we would expect about half the boosts (47) to be followed by a boost. A χ^2 test shows that the observed boosts were significantly more frequent than expected ($P < 0.05$). Hence we reject H_3 in favour of H_4 and postulate that the target normally has a depressing effect, but that at times in the flight of some aphids it has a boosting effect.