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The control of optic flow during learning flights

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Abstract Hymenopteran insects perform systematic learning flights on departure from their nest, during which they acquire a visual representation of the nest environment. They back away from and pivot around the nest in a series of arcs while turning to view it in their fronto-lateral visual field. During the initial stages of the flights, turning rate and arc velocity relative to the nest are roughly constant at $100\text{--}200^\circ \text{ s}^{-1}$ and are independent of distance, since the insects increase their flight speed as they back away from the pivoting centre. In this paper I analyse how solitary wasps control their flight by having them perform learning flights inside a rotating striped drum.

The wasps' turning velocity is under visual control. When the insects fly inside a drum that rotates around the nest as a centre, their average turning rate is faster than normal when they fly an arc into the direction of drum rotation and slower when they fly in the opposite direction. The average slip speed they experience lies within $100\text{--}200^\circ \text{ s}^{-1}$. The wasps also adjust their flight speed depending on the rotation of the drum. They modulate their distance from the pivoting centre accordingly and presumably also their height above ground, so that maximal ground slip is on average 200° s^{-1} . The insects move along arcs by short pulses of translation, followed by rapid body turns to correct for the change in retinal position of the nest entrance. Saccadic body turns follow pulses of translation with a delay of 80–120 ms. The optomotor response is active during these turns.

The control of pivoting flight most likely involves three position servos, to control the retinal position of

both the azimuth and the altitude of nest and the direction of flight relative to it, and two velocity servos, one constituting the optomotor reflex and the other one serving to clamp ground slip at about 200° s^{-1} . The control of ground slip is the prime source of the dynamic constancy of learning flights, which may help wasps to scale the pivoting parallax field they produce during these flights. Constant pivoting rate may in addition be important for the acquisition of a regular sequence of snapshots and in scanning for compass cues.

Key words Wasps · Learning flights · Optomotor response · Optic flow · Visual control of flight

Introduction

Wasps and bees acquire a visual representation of a goal's environment during learning flights on departure. The insects move in very distinct ways during these flights [ground-nesting wasps and bees: Zeil and Kelber (1991); Zeil (1993a); social wasps: Collett and Lehrer (1993); Collett (1995); honey bees: Lehrer (1991, 1993); Lehrer and Collett (1994); reviewed by Zeil et al. (1996)]; after lift-off from the nest or a newly discovered feeding dish, the insects turn to face the goal and then back away while flying along ever increasing arcs that are roughly centred on the goal. Ground-nesting *Cerceris* wasps steadily increase both their horizontal distance from the nest and their height above ground, to the effect that the nest is viewed at a fairly constant altitude below the horizon. While flying along these arcs, the wasps match arc velocity and turning velocity to view the nest entrance in the lateral visual field between 30 and 70° away from the midline. Mean rate of turning and arc velocity lie between 100 and 200 s^{-1} independent of distance from the nest. The insects thus move through equal angles in equal time relative to the nest by increasing flight speed in proportion to distance (Zeil 1993a).

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In this paper I investigate how solitary wasps (*Cerceris rybyensis*) control their learning flights. My aim is twofold: since the significance of the distinct flight manoeuvres during learning flights is by no means clear, a better understanding of the flight control mechanisms involved might help us to find adequate functional interpretations. Beyond their role in learning, these flights are an interesting case of visually guided, but actively modified behaviour in insects that seems to be composed of more than just stabilising reflexes. On the phenomenological level we would ideally need a set of instructions and guidance mechanisms to simulate these flights. With this goal in mind I concentrate here on three elements of flight control during learning flights: the control of turning rate, of arc velocity and the fine structure of flight.

Materials and methods

Cerceris rybyensis wasps (Sphecidae, Hymenoptera) were studied during the summer months in a little-used quarry near Andelfingen, Switzerland. Females dig vertical burrows into horizontally exposed layers of sand and provision the nests with immobilised solitary bees. Wasps perform learning flights on their first departure in the morning and whenever they had been forced to search for the nest during their previous return (Iersel and Assem 1964; Zeil 1993a). The learning flights were filmed from above with a video camera and the films were later analysed frame by frame to determine animal positions and the orientation of their longitudinal body axis.

The control of turning rate was examined by centering a large Perspex cylinder (45 cm diameter, 30 cm height) over the nest entrance. The inside of the drum carried a black and white stripe pattern (stripe width 3.9 cm). Viewed from the nest, the pattern had a spatial wavelength of approximately 20° . The striped drum was suspended from the centre of the camera tripod by three pieces of nylon thread that were fastened to the drum at three equally spaced points along its upper rim. It could be turned around the nest entrance by hand. Wasps often do not like the drum when they first see it and procrastinate their learning flight. The procedure I therefore adopted was to allow wasps to perform their first learning flight in the presence of the tripod and a single small cylindrical landmark (2.2 cm diameter, 6.3 cm height) close to the nest. I then closed the nest entrance and had the returning wasp search for up to 5 min before allowing her to find the nest. The subsequent updating or re-orientation flight was then performed inside the stationary drum. On her next return, the wasp searched for her nest inside the drum. She subsequently tolerated the rotating drum both during her search and her learning flights.

Results

A typical learning flight of a *C. rybyensis* wasp is shown in Fig. 1a [for a more detailed account see Zeil (1993a)]. While flying along an arc around the nest, the wasp's mean rate of turning $\dot{\theta}$ (the slope of the fat line in Fig. 1b) is constant and matches the arc velocity $\dot{\beta}$, which can be visualised as the change of orientation of a line connecting the wasp to the nest (slope of the thin dotted line in Fig. 1b). As a result, the wasp views the nest at fronto-lateral positions in her visual field. The situation is rather similar when the same wasp performs her learning

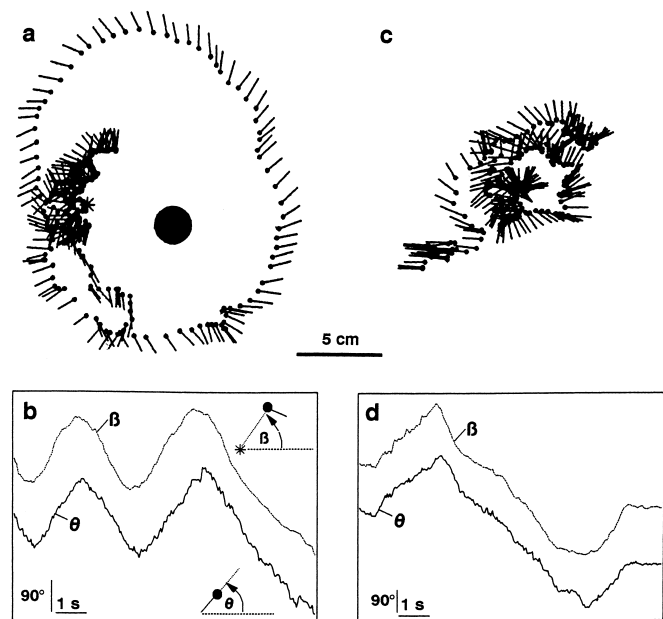


Fig. 1a,c Two segments of learning flights by a *Cerceris* wasp as viewed from above. The position of the head of the wasp is marked by a dot and the orientation of her longitudinal body axis by a line attached to it. Positions are shown every 40 ms. The two examples show in (a) 10 s of flight in the normal environment with a landmark (black circle) placed close to the nest entrance (star) and in (c) another flight by the same wasp inside a stationary striped drum. **b,d** Time-course of the orientation (θ) of the wasp and her bearing relative to the nest entrance (β) for the sequences shown on top

flight inside a stationary striped drum (Fig. 1c,d). Although the radius of arcs is smaller, the wasp still turns and moves relative to the nest at a fairly constant rate. These dynamic aspects of learning flights are surprisingly constrained: they are rather invariant, regardless of

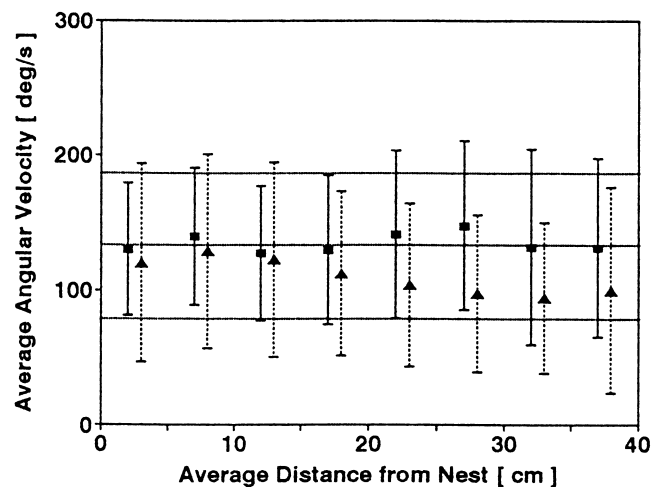


Fig. 2 The average angular velocity of wasps as a function of their distance from the nest entrance, during 22 learning flights. Squares denote mean turning velocities ($\dot{\theta}$) and triangles mean arc velocities ($\dot{\beta}$). Vertical lines depict the standard deviations of the mean values. Angular velocities were determined from 400 ms running averages and sorted into 5 cm bins. Data from six wasps

whether one compares the flights of an individual, those of different individuals, or even those of wasps and bees belonging to different species, whereby some species of bees and wasps tend to turn faster at $200\text{--}300^\circ\text{ s}^{-1}$ (Zeil and Kelber 1991; Collett 1995). Figure 2 shows the average turning rate ($\dot{\theta}$) and the average arc velocity ($\dot{\beta}$) as a function of distance from the nest for 22 learning flights of six *Cerceris* wasps. Turning rate is practically independent of the radius of an arc up to a distance of 40 cm from the nest. The arc velocity becomes somewhat smaller with distance which indicates that the wasps at larger distances do not pivot exactly about the nest entrance.

Learning flights in a rotating drum

I tested the hypothesis that turning speed is under visual control by having wasps perform learning flights inside a rotating striped drum. *Cerceris* wasps tolerate this interference and are able to turn both into and against the direction of drum rotation (Fig. 3a,c). The insects translate and turn faster than normal when they fly along an arc in the direction of drum rotation, and slower than normal when they fly in the direction opposite to the drum rotation (Fig. 3b,d). The left and right panels in Fig. 4 illustrate this finding for two learning flights of a wasp during counter-clockwise and clockwise rotation of the drum. In Fig. 4b,e the dotted line shows the temporal fine structure of the wasp's turning speed as determined over consecutive 80 ms. The continuous line is the running average of turning speed over 400 ms which smoothes the peaks that result from the wasps' saccadic way of turning (Zeil 1993a). The arc velocity is plotted in Fig. 4c,f. The rotating drum has the

effect of shifting both the rate of turning and the arc velocity of wasps towards higher and lower values that lie symmetrically around the drum speed. As far as turning rate is concerned, the rotating drum may influence either the amplitude or the frequency of the wasps' saccadic turns. A rough count by eye produced saccade frequency values of $4.24 \pm 0.64\text{ Hz}$ for arcs flown in drum direction ($n = 42$) and of $4.15 \pm 0.68\text{ Hz}$ for arcs flown against the drum ($n = 33$).

While the frequency of turns does not differ significantly between sections of flight in and against the direction of drum rotation, the drum clearly influences the turning speed and amplitude of the saccadic turns (Fig. 5a,b). The histogram in Fig. 5 shows the frequency distribution of angular velocities determined in 80-ms intervals for arcs flown against drum rotation (grey-shaded area), in the direction of drum rotation (fat line) and for arcs flown before the drum started moving (thin line). The optomotor response is operating both during the body saccades and during the short periods of 'fixation' marked by dots in the orientation trace in Fig. 5a, as indicated in the exploded view of the trace.

The shift induced by the rotating drum is demonstrated for all of the wasps tested, by the frequency histograms in Fig. 6. Since the wasps alternate between pivoting with and against the direction of drum rotation, the histograms show a two-peaked distribution of angular velocities $\dot{\theta}$ (thick line) and of arc velocities $\dot{\beta}$ (thin line) for counter-clockwise (positive sign, Fig. 6a) and clockwise drum rotation (negative sign, Fig. 6b). The whole distribution is shifted into the direction of drum rotation. As a result, the distribution of slip speeds between the wasps' turning rate and the drum rotation shows two peaks between 100 and 200° s^{-1} clockwise and counter-clockwise (Fig. 6c), which are centred on approximately the same image velocities wasps produce when flying inside a stationary drum (Fig. 6d) or with unimpeded view of the natural scene around their nest (Fig. 6e). The wasps thus adjust their turning velocity and their arc velocity such as to keep large-scale image velocity constant during learning flights. The insects seem to be able to do this adjustment regardless of pattern properties, that is regardless of whether they fly inside a striped drum (Fig. 6d) or with full view of the natural panorama (Fig. 6e). It is not only during learning that the wasps regulate the image flow in their visual field. When they return to search inside a striped drum for the hidden nest, they sometimes also move to generate similar image speeds, regardless of whether the drum is stationary or rotating (Fig 6f).

Wasps not only adjust their turning rate but also their translational velocity depending on drum rotation, as is indicated by the thin line histograms in Fig. 6a–c which represent the frequency distributions of arc velocity $\dot{\beta}$. The arcs are flown faster when the wasps fly into the direction of drum rotation, and slower when they fly into the opposite direction (thin line histograms in Fig. 6a and b). The effect for arcs in drum direction is comparatively weak partly because the insects modulate

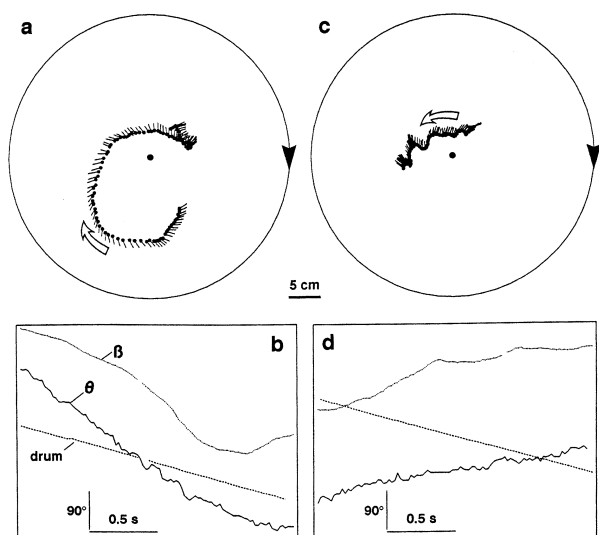


Fig. 3a–d 2 s sections from a learning flight of a wasp inside a striped drum rotating clockwise. *Open arrow* shows the direction of movement of the wasp. Positions are shown every 20 ms. **b,d** Orientation (θ) and bearing (β) of the wasp over time during the same sequences

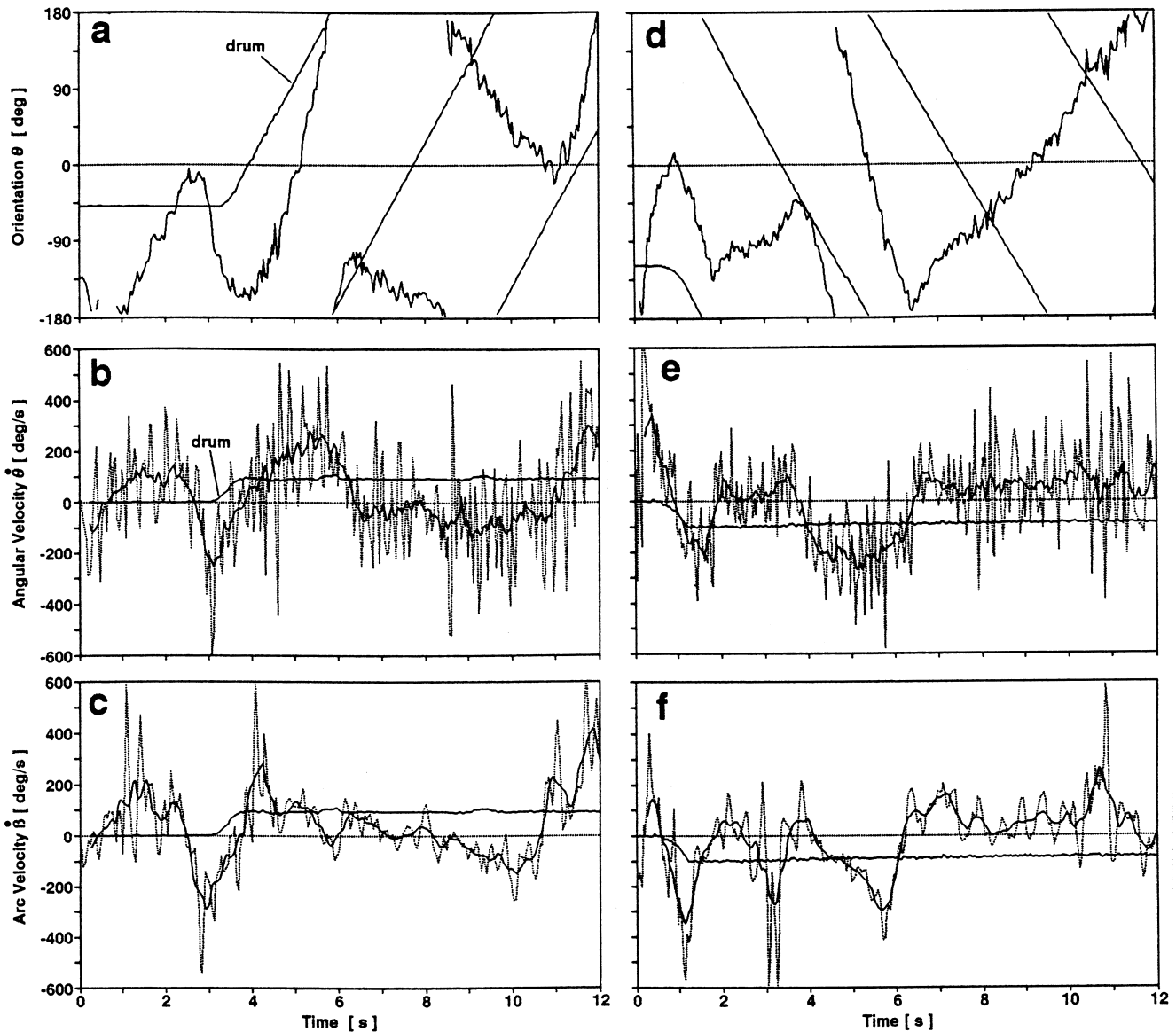


Fig. 4a–f Orientation and angular velocities during two learning flights of a wasp in a drum that rotated counter-clockwise (*left panels*) and clockwise (*right panels*): **a,d**: arbitrary drum orientation and the orientation of the wasp over time; **b,e**: angular velocity of drum (*continuous line*) and turning velocity ($\dot{\theta}$) of the wasp (*fat continuous*

line: running average over 400 ms; *dotted line*: velocity determined over 80 ms); **c,f**: angular velocity of the drum (*continuous line*) and arc velocity ($\dot{\beta}$) of the wasp (*fat continuous line*: running average over 400 ms; *dotted line*: velocity determined over 80 ms)

their distance from the pivoting centre, in addition to their flight speed (see below). However, as in the case of rotational slip, translational slip lies in the range 100° – $200^{\circ} \text{ s}^{-1}$ (Fig. 6c).

The histograms shown in Fig. 6 do not reveal how accurately the wasps control their turning rate and arc velocity during individual arcs. In order to gain a measure of accuracy, I determined the slope of the regression line through the values of body axis orientation θ and of the bearing relative to the nest β for each arc segment separately (see θ -trace in Fig. 7a,b). Figure 7c,d shows these slopes as a function of the average speed of drum rotation with filled dots marking values measured for arcs flown in the direction of drum rotation and open

dots those for arcs flown against it. If the wasps were simply moving and turning to compensate for the image flow generated by the rotating drum, all the values would lie on the line of equality (fat dashed line in Fig. 7c,d). If they ignored the drum, values would lie scattered in two broad bands parallel to the x -axis, within the range indicated by the open squares and the standard deviation bars at zero drum velocity. The scatter of the data is large, but the wasps do seem to pivot and turn in such a way as to generate a slip speed of 100° – $200^{\circ} \text{ s}^{-1}$ (thin dashed lines in Fig. 7c,d). Interestingly, the insects virtually stop pivoting and turning when moving against the direction of a drum spinning at their favourite speed and in a few cases even turn with

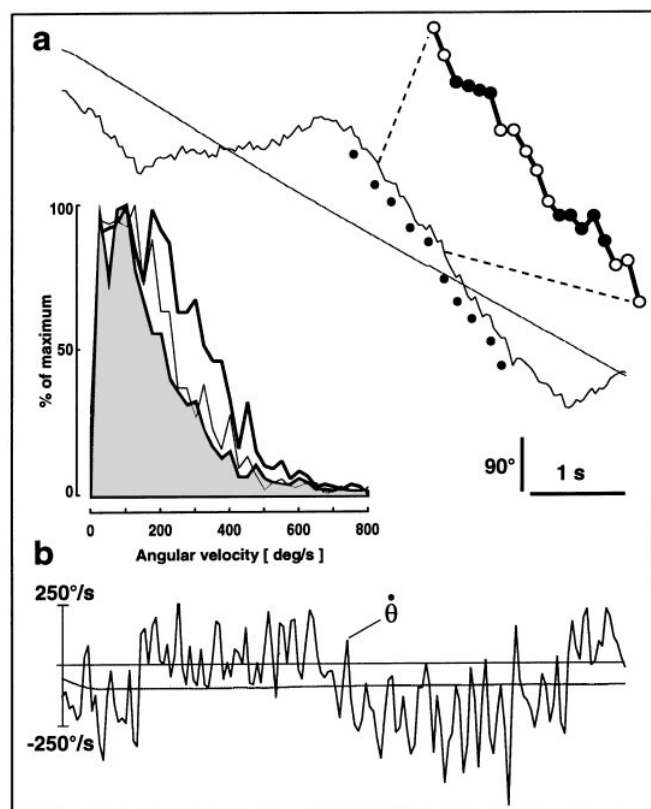


Fig. 5a Time-course of the orientation (θ) of a wasp performing her learning flight in a striped drum that rotated clockwise. The *dots* mark short periods of 'fixation' during a section where the wasp turns into the same direction as the drum (see also *filled circles* in the exploded view). Note the increased turning speed during the saccadic turns. **b** Angular velocity of wasp and drum as a function of time for the same sequence. The histogram in the centre shows the frequency distribution of angular velocities determined over 80-ms intervals for arcs flown against the direction of drum rotation (*grey-shaded area*), in the direction of drum rotation (*fat line*) and before the drum started moving (*thin line*)

the drum, as during the segment marked by an arrow in Fig. 7a.

The control of flight

In their study of visual behaviour in hoverflies, Collett and Land (1975) suggested three ways in which circling flight could be achieved: the arc velocity of a pivoting insect may be controlled by the error angle of the pivoting centre at the retina, by an internal adjustment of velocity, assuming that the insect knows the distance to the pivoting centre, or by a mixture of both. Collett and Land (1975, see also Land 1993) used the ratio of the mean error angle to the mean arc velocity during circling to distinguish between these three possibilities, their argument being that this ratio should be close to zero for all distances, if circling was achieved by internal adjustment of velocity, and some constant positive value, if it was due to tracking alone. A combination of both mechanisms would yield an inverse relationship between

this ratio and distance. The data from hoverflies clearly indicate that tracking is of minor importance, since the ratio between the error angle and the arc velocity is close to zero over a range of distances. For the wasps, in contrast, it is a constant 0.2 over distance, suggesting that tracking is involved. In line with this conclusion are two aspects that clearly differ when comparing the circling flight of male hoverflies around a female sitting on a flower and the pivoting flight of learning wasps: firstly, hoverflies point at the female during circling with practically no retinal position error while the equivalent error angle during learning flights is quite large, and secondly, wasps hold their arc velocity constant, while hoverflies vary it depending on distance.

If pivoting flight was due to tracking, one would expect variations of the wasps' arc velocity to be driven by, and thus to lag behind, variations in the retinal position of the nest entrance. However, a detailed analysis of the fine structure of normal learning flights reveals that the reverse is true: variations in retinal position are a consequence of variations in arc velocity. The wasps fly along arcs by first translating into a direction approximately 90° to the direction of regard of the nest entrance (Zeil 1993a) and then correcting the resulting retinal position error of the nest entrance by a rapid turn. To demonstrate this causal chain of events, I plotted in Fig. 8a the time-course of arc velocity (β), turning velocity ($\dot{\theta}$) and the retinal position of the nest entrance (ϕ_n) for a section of a normal, unimpeded learning flight. Variations in ϕ_n clearly follow those of β and precede variations in $\dot{\theta}$. For the sequence shown, the delay between these variables is in the range of 80 ms to 120 ms (Fig. 8b,c), which is a regular feature of learning flights. Figure 9 shows the results of a correlation analysis for five learning flights each of two wasps: maximal correlation between ϕ_n and β occurs when ϕ_n is shifted backward in time by 80 ms relative to β (Fig. 9a,c). The correlation between θ and ϕ_n is maximal when θ is shifted 40 ms backward in time relative ϕ_n (Fig. 9 b and d). So it seems that wasps pivot about the nest by exerting sideways thrust and by subsequently compensating for the shifted retinal position of the nest entrance by saccadic body turns. Even inside a rotating drum, this position servo is fairly successful in keeping the nest entrance in the fronto-lateral visual field of the wasps (Fig. 10a), although compared to the situation in a stationary drum or with unimpeded view (Fig. 10b), lateral fixation is not as pronounced. The rotating drum seems to have the effect of shifting the retinal image of the nest both towards the midline and towards more lateral directions of view. This shift should depend on whether wasps move with or against the drum rotation, towards the midline in the former and away from it in the latter case. There is, however, no clear indication of such a specific difference in the two histograms in Fig. 10a.

The correlation analysis tells us that the corrective turns serve to compensate for changes in the retinal position of the nest entrance, and the experiments with rotating drums show that the optomotor response is not

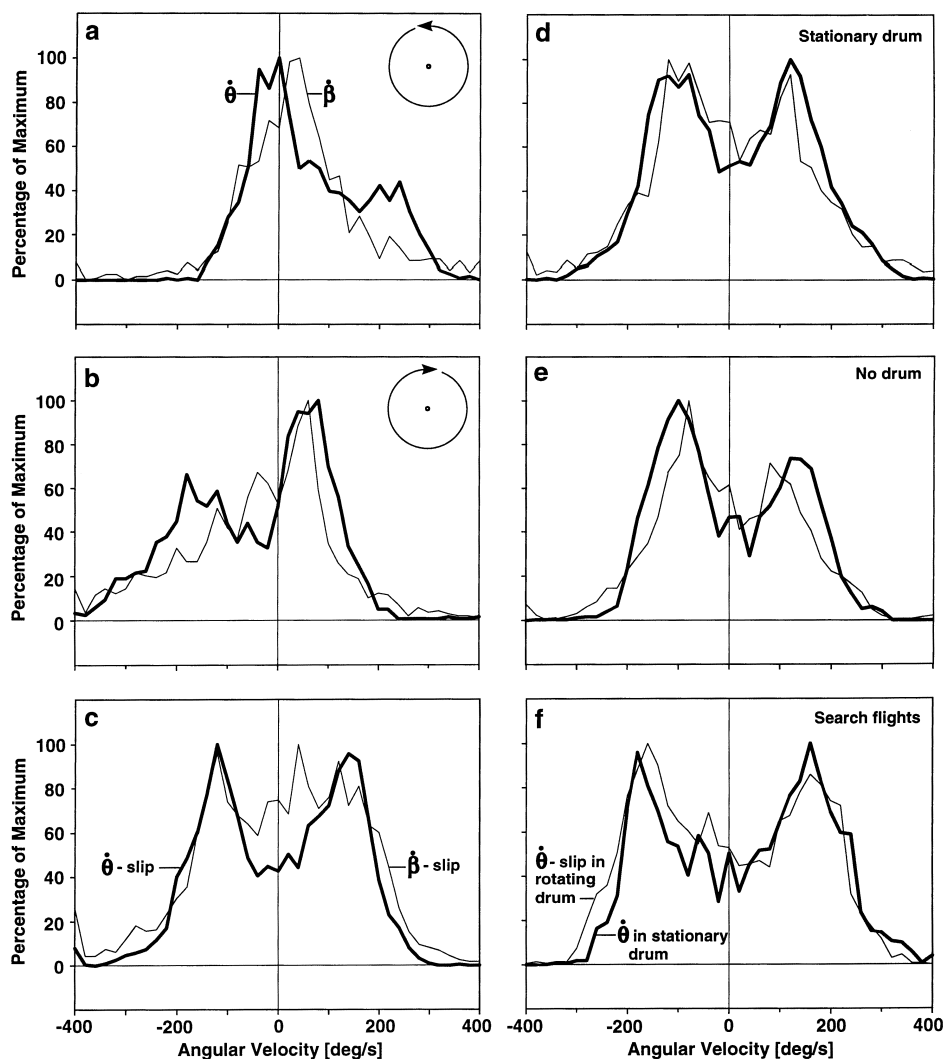


Fig. 6a–f Frequency distributions of turning velocities $\dot{\theta}$ (*thick lines*) and arc velocities $\dot{\beta}$ (*thin lines*) of wasps performing their learning flights in a drum that rotated counter-clockwise (**a**) or clockwise (**b**). Sign convention: counter-clockwise positive, clockwise negative. The frequency distribution of the slip speeds experienced by the wasps in both situations is shown in (**c**). (**d**) Histogram of turning velocities and arc velocities during flights in a stationary striped drum. (**e**) Same for learning flights with normal unimpeded view. (**f**) Histogram of angular

velocities of returning wasps searching for their hidden nest inside a stationary drum (*thick line*, 1.5-min search) and of the slip speeds they produced when searching inside a rotating drum (*thin line*, 1.5-min search). Angular velocities were sampled as 400 ms running averages. Sample size: (a) 4 wasps, 5 learning flights; (b) 4 wasps, 7 learning flights; (c) 4 wasps, 12 learning flights; (d) 7 wasps, 13 learning flights; (e) 6 wasps, 11 learning flights; (f) 2 wasps, 6 search flights

switched off during their execution. The angular velocity of the wasps flying in a rotating drum may thus be simply a consequence of the interaction between the optomotor response and the tracking system that is driven by the retinal position of the nest entrance. In this respect, learning flights share similarities with the tracking behaviour of flies (Virsik and Reichardt 1976; Collett 1980) with the exception that in the case of learning flights, the insects do not track a moving target but pivot around a stationary one, like male hoverflies during circling. In contrast to hoverflies, however, wasps maintain a rather constant arc velocity over a large range of distances from the pivoting centre by increasing their flight speed as they move away from the nest (Zeil 1993a). It remains to be explained, what cues the wasps

may use to adjust their flight speed, and through this, their arc velocity appropriately. There would seem to be two obvious possibilities: (i) the wasps know their distance from the nest entrance and increase their flight speed proportionally, or (ii) they keep the retinal elevation of the nest constant and modulate flight speed in such a way as to generate a constant maximal ground slip, that is image motion emanating from texture on the ground directly below. The problem with the first scheme is that one would need to show that the wasps do indeed have a measure of distance to the nest. Although they might derive it by comparing the retinal size of nest-associated contours during flight to the size they had at lift-off, the data at hand favour the second scheme. In the normal situation, the wasps match their height above

Fig. 7a,b Orientation θ and bearing β of a wasp as a function of time during learning flights in a drum rotating clockwise (**a**) and counter-clockwise (**b**). For θ , a regression line is fitted to each arc segment, to gain a quantitative measure of the mean turning velocity during each arc. Thick sections in the β -trace mark arcs flown against the direction of drum rotation. **c** Average turning velocity $\dot{\theta}$ of wasps as a function of the average drum velocity. Each data point represents the slope of a regression line fitted to the orientation of wasps for each arc segment separately, *open circles* denoting arcs flown against and *filled circles* arcs flown in the direction of drum rotation. *Open squares* with standard deviation bars are the mean velocities of those arcs that were flown before the drum started rotating. **d** Same for the average arc velocity β . Conventions as in (**a**). Data from 5 wasps, 15 learning flights

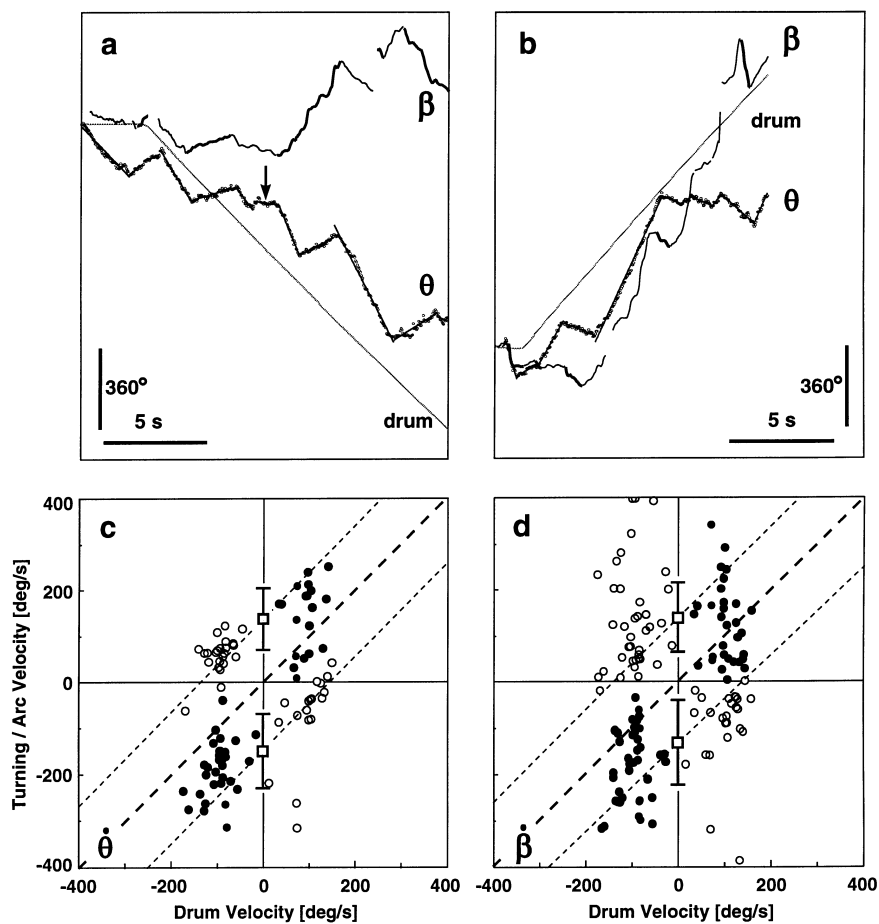


Fig. 8 a The time-course of arc velocity β (*continuous line*), turning velocity $\dot{\theta}$ (*dotted line*) and retinal position of nest entrance ϕ_n (*dashed line*) for a 6-s section of learning flight. **b** ϕ_n versus β with a delay of 120 ms for the same learning flight. *Y*-intercept: 1.54. Inset shows the correlation coefficient for different time shifts of ϕ_n versus β . Sampling rate: 25 Hz. **c** $\dot{\theta}$ versus ϕ_n with a delay of 80 ms. *Y*-intercept: -4.9. Inset shows the correlation coefficient for different time shifts of $\dot{\theta}$ versus ϕ_n

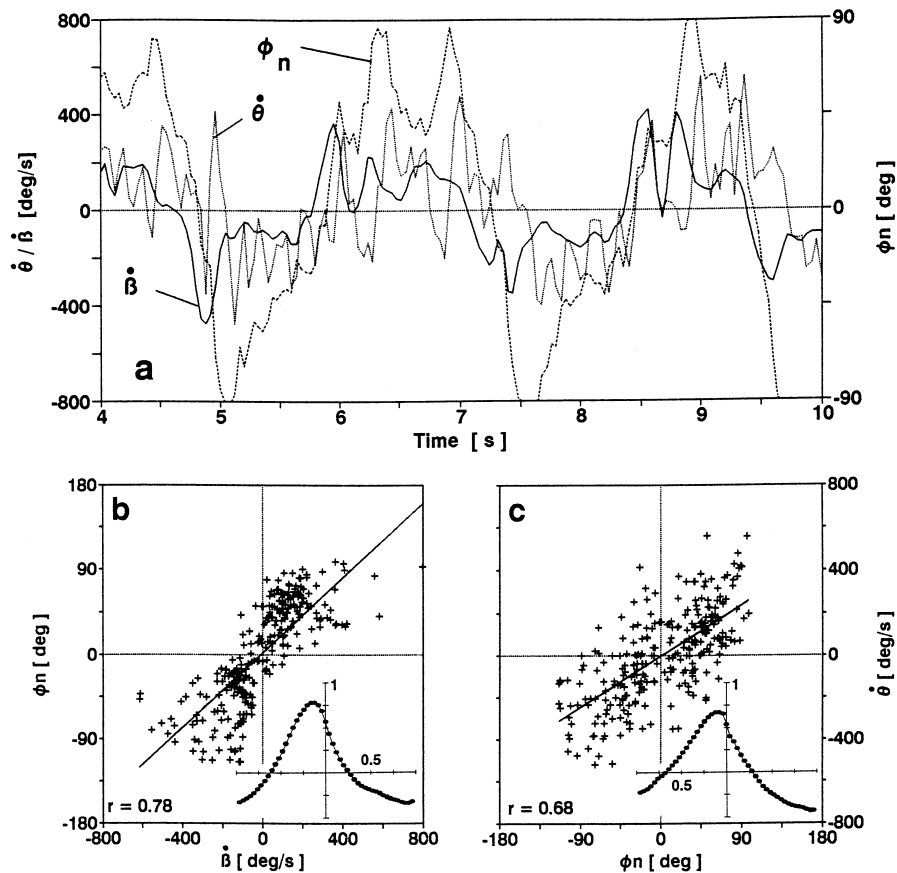


Fig. 9a-d Correlation coefficient for different time shifts of ϕ_n versus $\dot{\beta}$ (a and c) and $\dot{\theta}$ versus ϕ_n (b and d) for five learning flights each of two wasps (*top and bottom*). The figures show the mean (dotted line) and standard deviations (thin continuous lines) of the correlation coefficients calculated for each learning flight separately. Sampling rate: 25 Hz

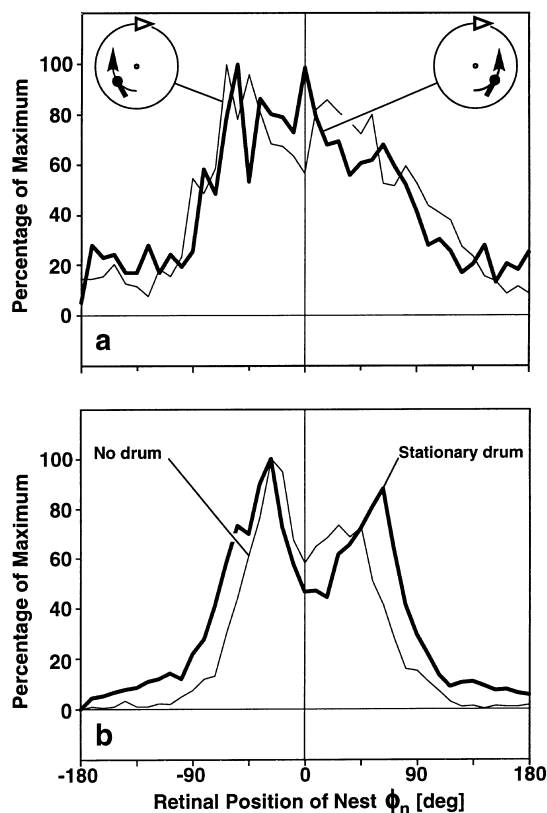
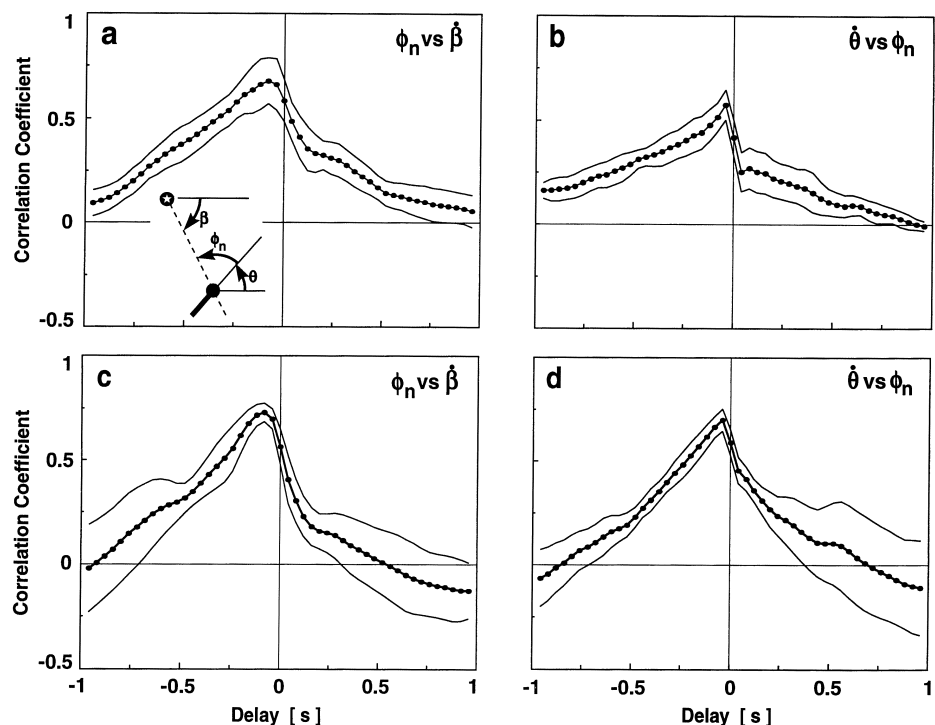


Fig. 10 a Frequency distributions of the retinal azimuth position of the nest entrance ϕ_n for learning flights in rotating striped drums. Data are plotted depending on whether wasps flew against (*thick line*) or in the direction of drum rotation (*thin line*). **b** Retinal positions during flights inside a stationary drum (*thick line*) and with open view to the panorama (*thin line*). Sample size: (a) 5 wasps, 15 learning flights; (b) stationary drum: 7 wasps, 13 learning flights; no drum: 6 wasps, 12 learning flights

ground to their horizontal distance from the nest and therefore view it at a rather constant elevation in the ventral visual field. The distribution of ground slips $\dot{\phi}_{gr}$ they experience has a maximum at 200° s^{-1} (bar histogram in Fig. 11b), suggesting that their flight speed is matched to their distance from the nest.

If the wasps adjust their flight speed to keep ground slip constant, how would a rotating drum interfere with this control system? Imagine a wasp flying against the direction of drum rotation. The optomotor response works against the fixation of the nest in this case and would cause its image to shift away from the animal's midline. The resulting position error can only be corrected by a turn against the direction of drum rotation. The situation is different in the second case: when the wasp flies in the direction of drum rotation the optomotor response assists fixation but shifts the retinal position of the nest towards the midline, a position error which can either be corrected by a turn against the direction of drum rotation or by an increase in pivoting velocity. Pivoting with the drum, wasps do indeed almost always increase their flight speed, as in the example shown in Fig. 11a. At the same time, however, they also tend to increase their distance from the nest, which lessens the effect increased flight speed has on the image motion of the nest. Provided the wasps in these experiments approximately matched their height above ground and their horizontal distance from the nest as they normally do, this last observation suggests that they try to maintain a constant ground slip even inside a spinning drum. It was difficult to determine the wasps' height above ground inside the drum, so that it is impossible to get a measure of the ground slip they maintained in these experiments. However, assuming height and distance are

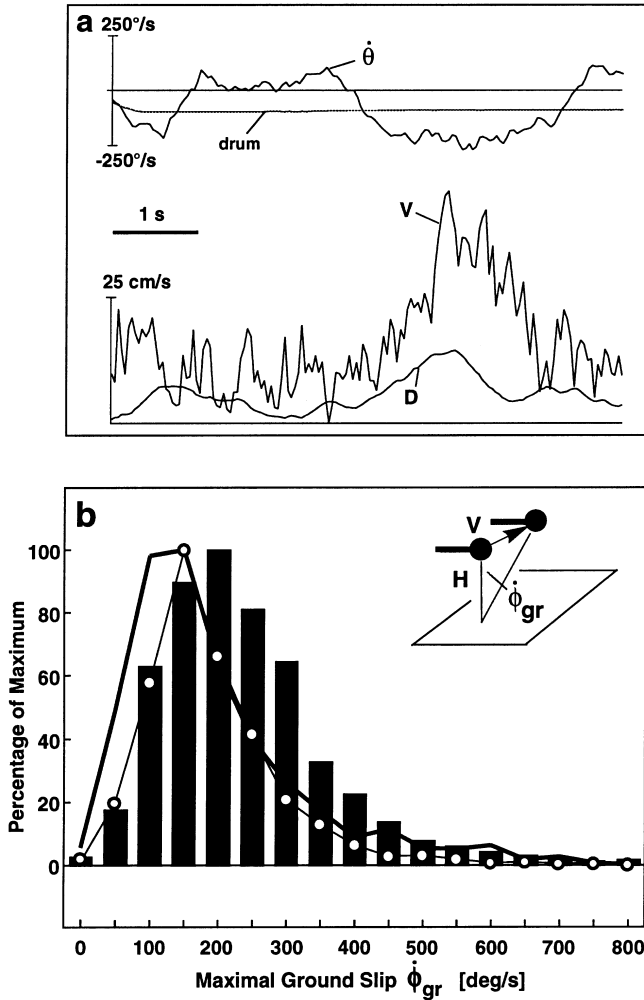


Fig. 11 **a** Angular velocity $\dot{\theta}$, flight speed V and the distance from the nest D for the same episode. Drum speed is also shown. **b** Bars: frequency distribution of maximal ground slips $\dot{\phi}_{gr}$ during four normal learning flights (of the same wasp) that have been reconstructed in three dimensions. *Thin line and open dots*: frequency distribution for the same four flights but ground slip was approximated by dividing V by the horizontal distance D from the nest entrance. *Thick line*: frequency distribution of approximated ground slips during four learning flights of two wasps inside a rotating drum

approximately equal, dividing flight speed V by the horizontal distance from the nest D , provides a rough estimate. The frequency distribution of ground slips determined in this way is shown in Fig. 11b for four learning flights inside a spinning drum (thick line) and four unimpeded flights without a drum (thin line and open dots). The distribution of ground slips generated by the wasps inside the drum is slightly broader than normal, but its maximum at $100\text{--}150^\circ\text{ s}^{-1}$ coincides quite exactly with that of normal, unimpeded learning flights.

Thus, in the rotating drum, the wasps are confronted with a conflicting situation: moving with the drum, the optomotor system shifts the nest entrance forward in the visual field, which the wasps try to compensate for by accelerating. The increasing flight speed in turn increases ground slip which possibly triggers an adjustment of

height above ground. The resulting increase in the elevation at which the nest is seen may then lead to the move away from the pivoting point that often accompanies an increase of flight speed in the drum experiments. The last manoeuvre, however, reduces the arc velocity $\dot{\beta}$, and makes it difficult for the wasp to catch up with the image of the nest moving forward in the visual field. When wasps fly against the direction of drum rotation, the optomotor response pulls the nest entrance backwards in the visual field which should trigger body turns against the direction of drum rotation and decrease flight speed. The problem for the wasps in this situation may be that the ground slip should be increased while the movements of the nest entrance call for a decrease in flight speed or an increase in distance from the pivoting centre.

Discussion

The present paper demonstrates that wasps during their learning flights generate a specific pattern of image motion by visually controlling the slip speed that results from their own rotational and translational movements. The wasps move to generate rather constant maximal image motion on the ground while their angular velocity is driven by the retinal position of the nest and by the optomotor response to rotational disturbance. The large field rotational slip speed the insects experience is similar, regardless of whether they fly inside rotating striped drums, still drums or with unimpeded view of the natural panorama. Learning flights are thus an exquisite example for an active vision procedure, whereby animals move in specific ways to aid visual information processing. What then are the necessary ingredients of flight control and what is the functional significance of the dynamic constancy during learning flights?

Flight control

The diagrams in Fig. 12 summarise the geometry of pivoting flight and the control systems likely to be involved. A wasp's flight speed $V(\Delta s/\Delta t)$ translates into an arc velocity $\dot{\beta}(\Delta\beta/\Delta t)$ by

$$\dot{\beta} = V \sin(\alpha_{\phi_n}) / (D - V \cos(\alpha_{\phi_n})) [\text{rad s}^{-1}] \quad (1)$$

depending on $D = D' + D_v$, the wasp's horizontal distance from the nest (see Fig. 12a,b) and on α_{ϕ_n} , the flight direction relative to the line connecting the wasp and the nest, because the following relations hold: $\cos(\alpha_{\phi_n}) = D_v/\Delta s$; $\sin(\alpha_{\phi_n}) = \Delta s'/\Delta s$ and $\Delta\beta = \Delta s'/D'$.

The relationship between the arc velocity $\dot{\beta}$ and the maximal ground slip $\dot{\phi}_{gr}(\Delta\phi_{gr}/\Delta t)$ can be found by substituting V in Eq. 1 by $V = D\dot{\phi}_{gr}\tan(\phi_{e1})$, with $\dot{\phi}_{gr} = V/H$ and $\tan(\phi_{e1}) = H/D$ (see Fig. 12a):

$$\dot{\beta} = \dot{\phi}_{\text{gr}} \tan(\phi_{\text{el}}) \sin(\alpha_{\phi_n}) / (1 - \phi_{\text{gr}} \tan(\phi_{\text{el}}) \cos(\alpha_{\phi_n})) \text{ [rad s}^{-1}\text{]} \quad (2)$$

The geometry of pivoting flight now forms the basis for the tentative signal flow diagram in Fig. 12c. The input variables are highlighted by the small hatched boxes and the numbers above the boxes indicate the setpoints of the input variables. I have labelled the different control loops with large boxes and gave them the abbreviated names vs 1, vs 2 or ps 1–3, depending on whether I consider them to be velocity or position servos. The box on the top left shows the control loop vs 1 which keeps the maximal ground slip $\dot{\phi}_{\text{gr}}$ constant at about 200° s^{-1} by varying linear acceleration and through this horizontal flight speed V_h (with $\dot{\phi}_{\text{gr}} = V/H$). When the nest is held at a retinal elevation ϕ_{el} of 45° and when the flight direction α_{ϕ_n} is 90° , this velocity servo will generate an arc velocity $\dot{\beta} = \dot{\phi}_{\text{gr}} = V/D$ (cf. Eq. 1) which in turn influences the retinal position of the nest entrance ϕ_n . The right part of the flow diagram shows the position servo ps 1 which clamps the nest entrance at lateral azimuth positions by generating a turning velocity $\dot{\theta}$. Although not explicitly shown in the diagram, I assume that an efference copy of the position servo output prevents the optomotor control loop vs 2 in the centre from being activated (cf. Collett 1980; Varjú 1990). The output of the optomotor system counteracts any rotational disturbance as it is generated for instance by the drum velocity $\dot{\phi}_d$ in my experiments. The retinal azimuth position of the nest entrance is also used to clamp the direction of thrust at about 90° relative to the retinal position of the nest (ps 2). The third position servo (ps 3) on the bottom left of the flow diagram serves to clamp the nest entrance at a certain elevation in the visual field. The input to ps 3 would be vertical retinal position and its output a thrust vector that lies in the vertical plane through the direction of regard to the nest and that points perpendicular to this direction, upward and forward if the elevation is smaller than the setpoint (closer to the eye equator) and downward and backward if it is larger (further away from the eye equator).

The rotating drum influences not only the angular velocity of the wasps, but also modulates their flight speed (Figs. 7d, 11a). In the flow diagram I indicated in the grey-shaded branch one possible way how this could happen. The tangential movements of a pivoting wasp always shift the image of the pivoting centre from front to back in the visual field, so that the position of the nest entrance or its direction of movement could be a cue that controls flight speed and that is modified by the drum: when the drum shifts the nest entrance forward, flight speed should be increased, when the drum shifts the nest image backwards, like in the case of a wasp pivoting against the direction of drum rotation, flight speed should decrease. The nest entrance azimuth position or image velocity of the nest are not likely to influence the flight speed directly, since the ground slip

velocity servo would counteract this input. The modulation of flight speed in a rotating drum thus indicates that the wasps either change the setpoint of the ground slip servo, or their height above ground and their distance from the nest. It seems to be this conflict between the control of retinal position of the nest in both azimuth and elevation, and the control of ground slip which causes the wasps to increase their distance and possibly their height above ground when they pivot with the drum.

The flow diagram in Fig. 12c is incomplete in that it neither addresses the saccadic nature of pivoting and compensatory turns nor the delays in the system. Pivoting flight control needs to be simulated in order to assess the importance of delays. All that can be said at present is that the saccadic structure of the flights is likely to be generated by a sampled data control system rather than a normal position servo. The observation that turn frequency is unaffected by the drum excludes both continuously operating position servos and those of the kind found in waterstriders, which work discontinuously because of limits in resolving power of the eye or some other threshold (Junger 1991).

In this tentative scheme, the wasps' pivoting flight thus involves five feedback loops. The centre core is formed by three position servos that clamp the retinal position of the nest in both azimuth and elevation and the direction of thrust relative to that position. One of the velocity servos is the classical optomotor system that counteracts rotational disturbances around the yaw axis and the second one modifies the flight speed of the wasps to generate a constant maximal ground slip. It is this ground slip velocity servo which, according to this scheme, is the prime source of the dynamic constancy of learning flights, driving the wasps' arc velocity and, through the servo controlling the retinal position of the nest, also their rate of turning.

The functional significance of dynamic constancy

Why are learning flights structured in this particular way? The movements of the insects during these flights differs in one fundamental aspect from most other cases of peering or scanning movements in insects. During learning flights the insects do not move in a way to create a translational egocentric, but a pivoting, geocentric parallax field that is centred on a point in space. The parallax field generated by an animal during pure translation is characterised by a velocity gradient decreasing with the distance of contours at directions of view that lie perpendicular to the direction of translation. The rotational parallax field produced by wasps during learning flights by circling a fixation point differs from the translational field in that contours close to the fixation point will move little at the insect's retina while distant contours beyond the fixation point move at the animal's own turning speed (but in opposite direction). The velocity gradient is thus reversed: it increases with

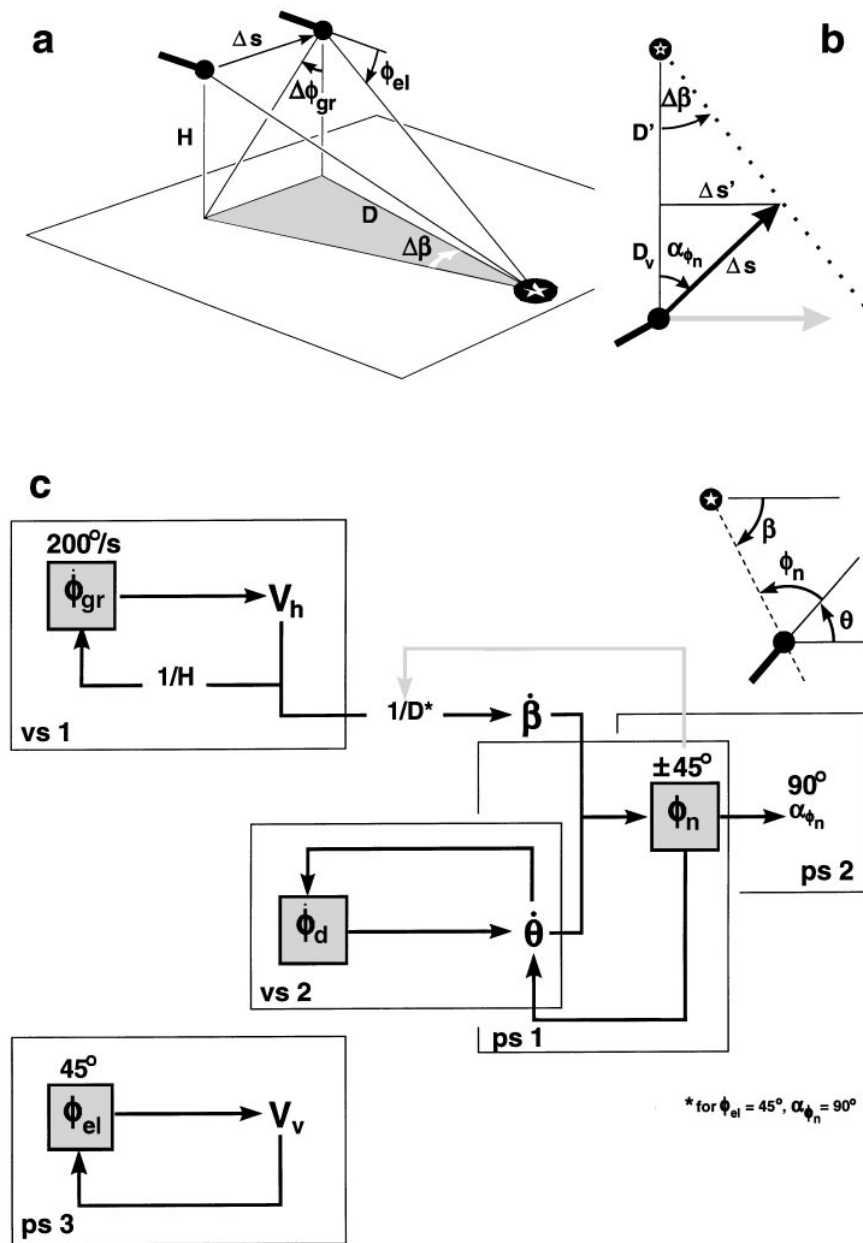


Fig. 12a–c The geometry of pivoting flight and a tentative signal flow diagram: **a** the drawing shows a wasp moving sideways above the ground plane. The nest is marked by a star. Definition of parameters: H : height above ground (cm); Δs : the distance flown (cm); ϕ_{el} : retinal elevation of nest; $\Delta\phi_{gr}$: ground slip (deg); $\Delta\beta$: change of bearing relative to the nest (deg); **b** the wasp is seen from above and is supposed to be moving in the direction of the straight black arrow. The horizontal distance D to the nest is broken down into the two components D' and D_v . How much a given movement of the wasp with velocity V ($\Delta s/\Delta t$) changes her bearing $\Delta\beta$ relative to the nest is determined by the direction of flight α_{ϕ_n} relative to the retinal azimuth position at which the nest is seen; **c** sketch of the systems likely to be involved in the control of pivoting flight (see inset, and **a** and **b** for definition of parameters). The input variables are highlighted by the small hatched boxes and the numbers above the boxes indicate their setpoints. The different control loops are boxed and labelled *vs 1*, *vs 2* or *ps 1–3*, depending on whether they are considered to be velocity or

position servos. *vs 1*: control loop to clamp the maximal ground slip $\dot{\phi}_{gr}$ at about 200° s^{-1} by varying linear acceleration and through this horizontal flight speed V_h (with $\dot{\phi}_{gr} = V/H$). For $\phi_{el} = 45^\circ$ and $\alpha_{\phi_n} = 90^\circ$, this velocity servo will generate an arc velocity $\dot{\beta} = V/D$ (cf. Eq. 1) which in turn influences the retinal position of the nest entrance ϕ_n . *ps 1*: position servo which clamps the nest entrance at $\pm 45^\circ$ in the lateral visual field by generating a turning velocity $\dot{\theta}$. *vs 2*: the optomotor system that counteracts any external rotational disturbance like the drum velocity $\dot{\phi}_d$. *ps 2*: position servo with ϕ_n as input to fix the direction of thrust at about 90° relative to the direction of regard of the nest. *ps 3*: position servo that serves to clamp the retinal position of the nest entrance at 45° below the horizon in the visual field. The output of *ps 3* modifies the vertical flight speed component V_v . The grey-shaded branch indicates one possible way how the rotating drum could influence the flight speed of wasps (cf. Fig. 11a). See text for discussion and further details

* for $\phi_{el} = 45^\circ$, $\alpha_{\phi_n} = 90^\circ$

the distance of contours from the pivoting centre. The dynamic constancy of learning flights has the specific consequence that the place-centred parallax field is scaled to the insect's own distance from the pivoting centre (Zeil 1993a): contours, for instance, that a wasp perceives to move at half her own turning speed will always be double the wasp's own distance from the nest away from her.

Scaling the pivoting parallax field relative to turning speed would be sufficient if the insects were using image motion for foreground-background segmentation and for the identification of three-dimensional objects. As the insects back away from the goal this segmentation may allow them to select a sequence of objects at successively larger distances from the goal that could later guide the different stages of their return flight. However, bees and wasps are also able to pick up absolute depth information during their learning flights (Brünnert et al. 1994; Lehrer and Collett 1994; Zeil 1993b) and this observation raises the question whether there is a possibility for them to scale the optic flow they produce in absolute terms.

The geometry of pivoting flight is such that the retinal position of the nest entrance ϕ_n is given by the wasp's orientation θ and her bearing relative to the nest β by $\phi_n = 180^\circ - (\theta - \beta)$ (see inset Fig. 12c). Through differentiation we arrive at $\dot{\phi}_n = \dot{\beta} - \dot{\theta}$ for the retinal velocity of the nest entrance at the eye of a pivoting wasp. The angular velocity $\dot{\theta}$ of the wasp produces rotational image flow $\dot{\phi}_r$ in the opposite direction so that $\dot{\theta} = -\dot{\phi}_r$. During the phases of fixation, $\dot{\phi}_n$ equals zero because $\dot{\beta} = -\dot{\phi}_r$. The arc velocity $\dot{\beta}$ depends on the flight speed V , the flight direction relative to the retinal position of the nest entrance α_{ϕ_n} , and the horizontal distance to the nest D (see Eq.1). For $\alpha_{\phi_n} = 90^\circ$, Eq. 1 simplifies to $\dot{\beta} = V/D$ so that the distance D to the pivoting centre is given by $D = V/\dot{\beta} = V/\dot{\phi}_{gr} = V/\dot{\phi}_r$. With constant average ground slip and arc velocity, distance D is directly proportional to the flight speed V of the wasp. Knowing this distance, the wasps could in principle scale the rest of the parallax field and extract absolute distance information from it. In the presence of wind drift, however, the insects would need to calibrate their flight speed or their height above ground, independently from optic flow. It is hard to be sure at present whether such a calibration is at all possible for a flying wasp. Interestingly, all relevant flight parameters are pulsed, including flight speed: the insects alternate between linear accelerations and zero thrust and also bob up and down while flying along an arc. They may have a chance of calibrating their flight speed or their height above ground by looking at the ground during the appropriate phases of thrust production (Srinivasan 1993). This possibility can be tested and it will be interesting to see, how the wasps use the image motion emanating from texture on the ground to achieve the dynamic constancy of their learning flights and to extract visual information from the pivoting parallax field.

There may be additional reasons why learning wasps control their turning and arc velocity so accurately. They acquire a visual representation of the nest environment during their learning flights and it has been suggested that they may do this in the form of snapshots taken at the end of arcs. In some insects, the ends of arcs lie on lines radiating from the goal (Collett and Lehrer 1993), which hints at some spatial constraint on where snapshots should be taken. A similarity analysis between the flight-paths during learning and those during subsequent search for the goal equally highlights the second part of arcs as the segments where learning is likely to take place (Zeil et al. 1996). In addition to this spatial constraint, the dynamic constancy of learning flights may also reflect a temporal constraint on learning. Wasps may need to control their rate of turning and their arc velocity to link the different views of a scene in a regular temporal sequence.

Yet another possible function of constant turning rate is suggested by a puzzling feature in the histograms of Fig. 6a,b. The different size of the peaks in the bimodal distributions means that the wasps spent more time turning against the direction of drum rotation than with drum rotation. The wasps seem to take note of some drum-independent, external cue while flying along an arc. A possibility is that they record their change of orientation relative to sky or earth-based compass cues like the sun, the pattern of skylight polarisation or the magnetic field (Collett and Baron 1994; Frier et al. 1996). In order to move through a given angle relative to these compass cues inside a spinning drum they would have to fly longer against the direction of drum rotation than with drum rotation.

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