Visual tracking of moving targets by freely flying honeybees

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Abstract

The ability of freely-flying honeybees to track moving targets was examined by training them to collect a reward on a target, and then videotaping their approach to the target while it was in motion. Training experiments were carried out with several groups of bees, using various colors for the target and the background. Computer-aided frame-by-frame analysis of video recordings was used to plot the instantaneous positions of the target, as well as the position and orientation of the approaching bee in three dimensions. The results show that bees are perfectly capable of tracking moving targets and landing on them. When the distance of the target is greater than 15 cm, approaching bees correct for angular deviations of the target from the midline, both in the horizontal and in the vertical plane. In either plane, the input variables that are important to the tracking system seem to be (1) the angular bearing of the target with respect to the midline, and (2) the angular velocity of the target with respect to the eye. The tracking control system tends to orient the bee such that the target is located frontally, at an angle of *ca.* 35 deg below the bee's long axis. The chromatic properties of tracking behavior were investigated by employing combinations of colors for the target and background such that the boundary between the target and the background presented a contrast that was visible either only to the green-sensitive receptors of the bee's eye, or only to the blue-sensitive receptors. The results of these experiments suggest that, in controlling tracking, the measurement of the angular velocity of the target is derived almost exclusively from signals from the green-sensitive receptors, as is the case with previously studied movement-sensitive behavior. However, the measurement of the angular bearing of the target is derived from the blue-sensitive receptors as well as the green-sensitive ones. When the target is closer than *ca.* 15 cm, approaching bees use translational maneuvers, in addition to rotational ones, to track the moving target. Translational target tracking appears to be driven primarily by signals from the green-sensitive receptors.

Keywords: Honeybee vision, Behavior, Target tracking, Color contrast

Introduction

When a foraging honeybee flies toward a flower to collect nectar, it obviously uses visual cues to guide its approach to the target, and to ensure a proper landing. What are the visual cues that the bee uses to "home in" on the flower, and ensure that the target is reached despite, say, a gust of wind that might displace the flower or blow the bee off course? In the present study, we investigate this question by filming and analyzing the flight paths of bees as they approach a moving target and alight on it.

Visual tracking of small objects has been studied in some detail in the fly, in the context of a male chasing a female (Land & Collett, 1974; Collett & Land, 1975; Buelthoff et al., 1980), or of a female tracking another fly (e.g. Wehrhahn et al., 1982;

Wagner, 1986). During tracking, the control of flight—measured as the turning rate of the tracking fly—seems to depend mainly on two parameters, namely, (i) the angular position and (ii) the angular velocity of the tracked fly with respect to the tracking fly. Although foraging honeybees do not show a marked tendency to chase or track each other, the fact that they can be trained to visit a stationary target and be highly motivated to collect a food reward from it, makes it reasonable to assume that the trained bees would attempt to approach the target and land on it even when it is in motion. In this paper, we use this paradigm to investigate the tracking control system of freely-flying bees, and to study its dynamical and chromatic properties.

Materials and methods

In each experiment, a group of 3–4 bees were individually marked and trained to visit the experimental apparatus, located in a laboratory 500 m away from the hive. The laboratory was

in a cottage in the Sleeping Buddha Temple Park in Beijing. The apparatus was placed near an open door, where the mean intensity of ambient light was *ca.* 2000 lux.

The apparatus consisted of a perspex box (33 cm × 45 cm × 33 cm high) with a 10-cm diameter hole in one wall through which the bees could enter and leave. The target, consisting of a 3.4-cm diameter disc, was placed on the floor of the box. During the training phase (which lasted until the bees had each completed *ca.* 20 rewarded visits), the target was stationary and offered a drop of sugar water. The position of the target on the floor was randomly varied between rewards.

In subsequent tests, the target carrying the reward was replaced by an identical, but fresh target (to eliminate olfactory cues), and the bees' approaches to the target were filmed in three dimensions by means of a video camera which was set up to view the flight trajectories in elevation (through one of the transparent lateral walls) and simultaneously in plan by means of a mirror, tilted at 45 deg to the horizontal, placed on top of the transparent lid of the box (Fig. 1).

In the tests, the target was either stationary or executed sinusoidal oscillatory motion along a straight line parallel to the X axis. The oscillation had an amplitude of 10 cm (peak to peak) and a frequency of 0.5 Hz or 1.0 Hz (corresponding to maximum target speeds of 15.7 cm/s and 31.4 cm/s, respec-
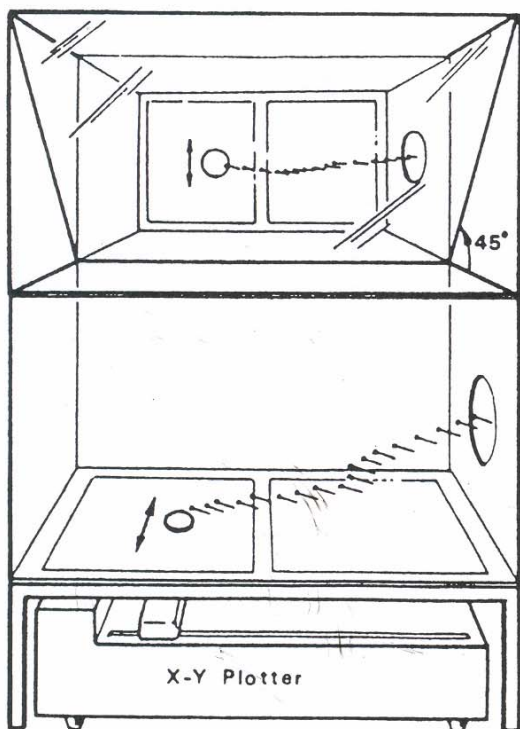

Fig. 1. Schematic of the experimental setup. The apparatus consisted of a perspex box (33 cm × 45 cm × 33 cm high) with a 10-cm diameter hole in one wall through which the bees could enter and leave. The target, consisting of a 3.4-cm diameter disc, was placed on the floor of the box, and was moved by means of a magnet carried on the arm of an X–Y recorder placed beneath the floor of the box. A mirror, tilted at 45 deg to the horizontal, was positioned on top of the transparent lid of the cage.

tively). The target was supported on the floor of the cage by means of a low-friction ballbearing, and was moved by means of a magnet carried on the arm of an X–Y recorder placed beneath the floor (Fig. 1). The X–Y recorder was driven by a Synthesizer Function Generator (HP 3325, Hewlett Packard, Palo Alto, CA).

The background consisted of a sheet of paper placed on the floor of the cage, under the target. The first series of experiments was carried out using a black target on a white background (abbreviated as B/W). The boundary between the target and the background offered a contrast of 82% for the blue receptors, and 83% for the green receptors. The contrast in the ultraviolet was not relevant, as there was negligible energy in the ambient light at wavelengths below 370 nm. Subsequent experiments were carried out using various colored papers for the target and background (paper manufacturers: Color-Vu, NY). In these experiments, the colors were chosen such that the target-background boundary offered a contrast exclusively to one spectral class of receptors. In one group of experiments, the colors (target: Color-Vu 122; background: Color-Vu 5) were such that the boundary offered a contrast of 44% to the green receptors, and 2% to the blue receptors. In another group of experiments, the colors (target: Color-Vu 122; background: Color-Vu 7) were such that the boundary offered a contrast of 67% to the blue receptors, and 2% to the green receptors. The calculation of contrast is described in detail in Srinivasan and Lehrer (1984, 1988); it is summarized briefly in this paper in a later section.

The instantaneous positions of the target, as well as trajectories of the approaching bees, were recorded on videotape at a frame rate of 25 Hz. A digitizing tablet, which projected a crosshair onto the video image, was used to enter this data frame-by-frame into a computer which calculated the true three-dimensional position and orientation of the bee by compensating for perspective-related distortions. The maximum positional error in the digitizing process was estimated to be ±3.5 mm, and the maximum angular error ±7 deg. Segments of approach flights, commencing when the bee was *ca.* 30 cm from the target, and concluding when the bee landed on it, were analyzed for each type of target and background.

Preliminary tests were carried out with the target either stationary or oscillating at various frequencies. In most of the later tests, however, the target oscillation frequency was kept constant at 1 Hz. These subsequent tests were used to investigate the effect of color on tracking behavior. From this data, scatter diagrams were plotted, and regression lines computed to evaluate the relationship between the following:

1. The horizontal bearing of the target Th and the horizontal component of the bee's angular velocity, Vh (i.e. yaw angular velocity). Th was defined as the angle, in the horizontal plane, between the target and the bee's long axis. It was reckoned positive to the right of the midline and negative to the left, as observed from above. Vh was reckoned positive for rotations toward the right, and negative for rotations toward the left. Roll motions of the bee (motions about the long axis), if any, could not be measured and were not taken into account.

2. The apparent angular velocity of the target in the horizontal plane dTh/dt and Vh. dTh/dt was evaluated as the difference between the horizontal bearings of the target in successive frames.

3. The angular elevation of the target Tv and the vertical component of the bee's angular velocity V_p (i.e. pitch angular velocity). Tv was defined as the angle, in the vertical plane, between the target and the bee's longitudinal axis, upward being reckoned as positive, and downward as negative.

4. The apparent angular velocity of the target in the vertical plane dTv/dt and Vp. dTv/dt was evaluated as the difference between angular elevations of the target in successive frames.

5. The X components of target position Tx and bee position Bx. (The X axis was defined as the direction along which the target oscillated.)

6. The X components of target velocity dTx/dt and bee velocity dBx/dt.

Items 5 and 6 were carried out only for "near" targets (target distances less than 15 cm).

In addition, histograms were drawn to describe the distribution of the horizontal (Th) and vertical (Tv) bearings of the target with respect to the bee's long axis.

The definition, measurement, and calculation of the contrasts offered by the various stimuli are described in detail in Srinivasan and Lehrer (1984, 1988); we give below a brief summary.

1. A spectrophotometer was used to measure the reflectance spectrum of each of the colored (as well as black and white) papers.

2. The quantal spectrum of the ambient light within the apparatus was measured.

3. Using the well-known spectral sensitivity curves of the three receptor types in the bee retina, the relative quantal excitation $P_{i,j}$ produced by a given paper i in the receptor type j ($j = UV$, blue or green) was then calculated using

$$P_{i,j} = \int_{\lambda=320 \text{ nm}}^{\lambda=600 \text{ nm}} R_i(\lambda)S_j(\lambda)E(\lambda)d\lambda,$$

where $R_i(\lambda)$ denotes the reflectance spectrum of paper i, $S_j(\lambda)$ the normalized spectral sensitivity function of receptor j, and $E(\lambda)$ the quantal spectrum of the ambient light within the apparatus.

4. The contrast produced in receptor type j at the boundary between two papers A and B was then calculated as $100[(P_{A,j} - P_{B,j})/(P_{A,j} + P_{B,j})] \%$.

Results

Control variables for angular tracking

A typical trajectory executed by a bee approaching a target along a direction approximately perpendicular to its axis of oscillation is shown in Fig. 2. The background is white, and the target is a black disc oscillating at 1 Hz. The upper panel depicts the trajectory as viewed from above (i.e. in the X–Y plane), and the lower one as viewed from the side (i.e. in the Y–Z plane). It is clear that the approaching bee follows the oscillatory motion of the target.
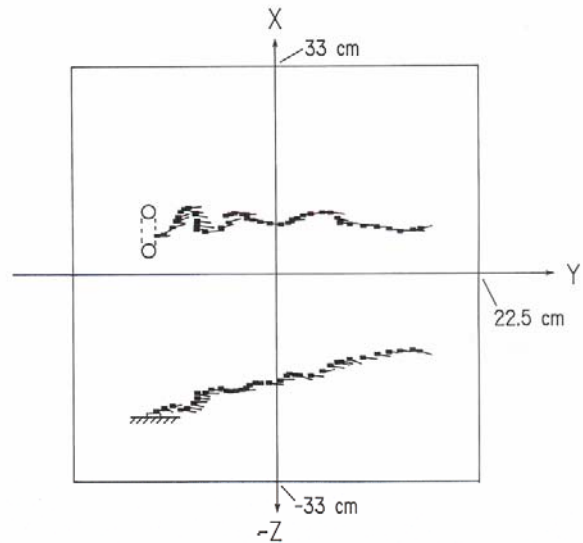

Fig. 2. A typical tracking trajectory. The background is white, and a black target oscillates sinusoidally at frequency of 1 Hz in a direction parallel to the X axis. The upper half of the figure is a view from the top in which the X axis is towards the camera. The lower half of the figure is a view from the front.

For the example shown in Fig. 2, the time courses of the various angular variables in the horizontal plane are shown in Fig. 3. These variables are defined in the top panel of Fig. 3. Starting from the topmost trace, they are as follows:

1. Target position Tp defined as the instantaneous position of the target along the X axis (see Fig. 2);

2. Target angular position Ta defined as the bearing of the target as seen from the bee's instantaneous position, measured relative to the negative direction of the Y axis (see Fig. 2);

3. Bee angular position Tb defined as the instantaneous direction of the bee's long axis, relative to the negative direction of the Y axis (see Fig. 2);

4. Horizontal bearing of target Th measured relative to the bee's long axis ($Th = Ta - Tb$);

5. Apparent angular velocity of the target in the horizontal plane dTh/dt; and

6. Yaw angular velocity of the bee Vh ($= dTb/dt$).

From the figure, it is clear that, although the motion of the target (Tp) is nearly sinusoidal, the angular tracking of it by the bee (Tb) is a very noisy sinusoid. As a result, neither Th nor dTh/dt are sinusoidal, and the main contribution to these signals comes from the noisiness in the bee's own angular movements. In order to investigate the extent to which the yaw angular velocity of the bee Vh is controlled by Th and/or dTh/dt, we have obtained scattergrams showing the relationship between Th and Vh, and between dTh/dt and Vh. These
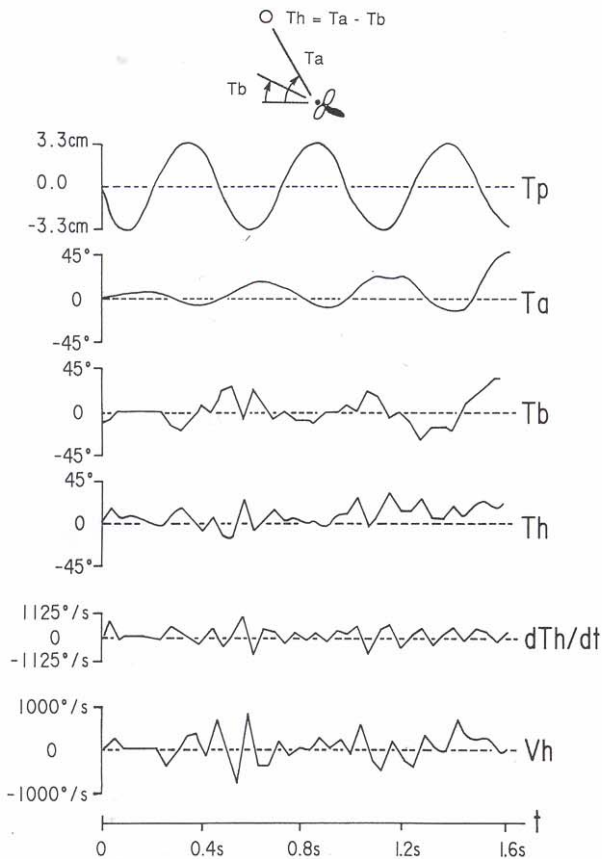
Fig. 3. The figure shows, for the trajectory of Fig. 2, the time courses of target position Tp, target angular position Ta, bee angular position Tb, horizontal target bearing Th, apparent angular velocity of target in the horizontal plane dTh/dt, and the yaw angular velocity of the bee Vh. These variables are defined in the top panel and in the text.

Fig. 4. Analysis of the horizontal angular adjustment for the approach trajectory documented in Figs. 2 and 3. (a) Scatter diagram and regression analysis for the horizontal component of angular velocity Vh vs. the horizontal error angle Th. The regression line is described by $Vh(t) = -486.84 + 56.31 \times Th(t-1)$ with $R = 0.50$ and $P < 0.01$. (b) Histogram of the horizontal error angle. (c) Scatter diagram and regression analysis for the horizontal component of angular velocity of the bee Vh vs. the horizontal angular velocity of the target dTh/dt. The regression line is described by $Vh(t) = 37.65 + 1.91 \times dTh/dt(t-1)$ with $R = 0.46$ and $P < 0.01$.

are shown in Fig. 4 for the trajectory of Fig. 2. Linear-regression analysis indicates a significant correlation in each case ($P < 0.01$; Fig. 4a and 4c), suggesting that the yaw angular velocity of the bee is controlled by the horizontal angular bearing of the target, as well as the angular velocity of the target with respect to the bee in the horizontal plane. In each case, the regression line intersects the abscissa close to the origin, suggesting that the "set point" for angular tracking in the horizontal plane is $Th = 0$, $dTh/dt = 0$. This is confirmed by the histogram showing the frequency distribution of Th (Fig. 4b), which reveals that the horizontal angular bearings of the target are tightly clustered around $Th = 0$.

Scattergrams showing the relationship between Tv and Vp, and between dTv/dt and Vp, are shown in Fig. 5 for the trajectory of Fig. 2. Linear-regression analysis (details in Fig. 5 legend) indicates a significant correlation in each case, suggesting that the pitch angular velocity of the bee is controlled by the vertical angular bearing of the target, as well as the angular velocity of the target with respect to the bee in the vertical plane. The regression line for Vp vs. Tv (Fig. 5a) intersects the abscissa at $Tv = -36$ deg, while that for Vp vs. dTv/dt intersects the abscissa near $dTv/dt = 0$ (Fig. 5c). This suggests that the "set point" for angular tracking in the vertical plane is $Tv = -36$ deg, $dTv/dt = 0$. This is confirmed by the histogram showing
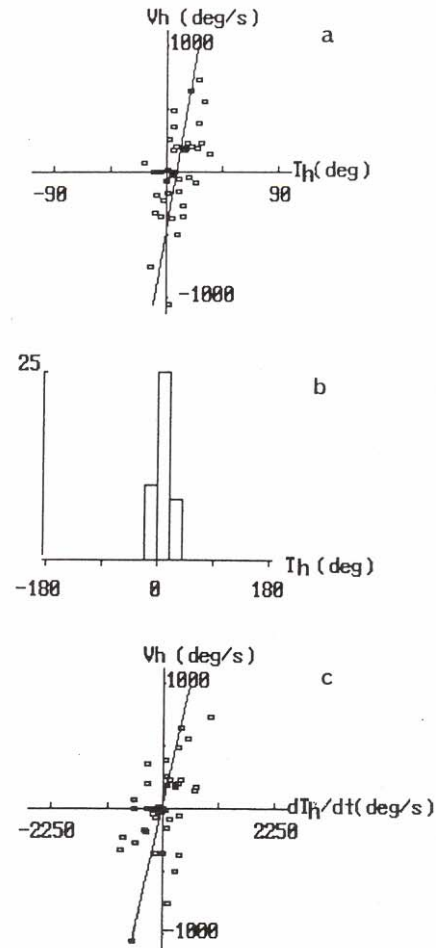
the frequency distribution of Tv (Fig. 5b), which reveals that the vertical angular bearings of the target are tightly clustered around $Tv = -35$ deg.

Dynamics of angular tracking

Scattergrams showing the relationship between Vh and Th, Vh and dTh/dt, Vp and Tv, and Vp and dTv/dt were plotted for a series of different time delays (measured in terms of number of video frames) interposed between the angular velocity of the bee (Vh or Vp) and the presumed control variable (Th, dTh/dt, Tv, or dTv/dt) (data not shown). Regression analysis of these scattergrams revealed that, in each case, the correlation coefficient was a maximum when the time delay was one interframe interval (40 ms). This suggests that the nervous system of the bee requires ca. 40 ms to acquire and process the relevant visual
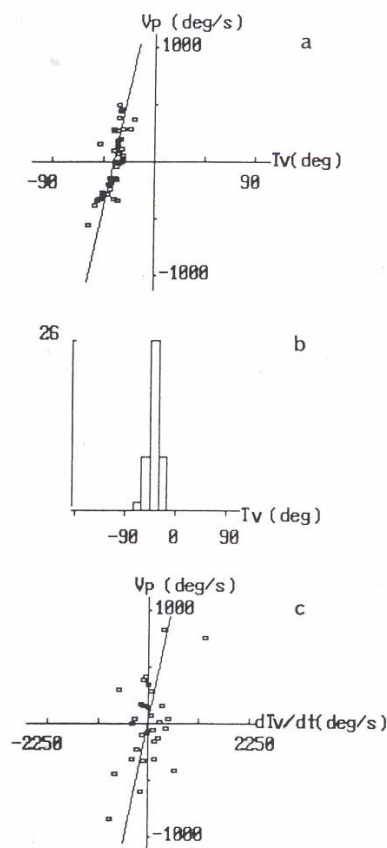
Fig. 5. Analysis of vertical angular adjustment for the approach trajectory shown in Fig. 2. (a) Scatter diagram and regression analysis for pitch component of angular velocity Vp *vs.* pitch error angle Tv. The regression line is described by $Vp(t) = 1643.95 + 45.59 \times Tv(t-1)$ with $R = 0.71$ and $P < 0.01$. (b) Histogram of pitch error angle. (c) Scatter diagrams and regression analysis for the pitch component of angular velocity of the bee Vp *vs.* pitch angular velocity of the target dTv/dt. The regression line is described by $Vp(t) = 71.79 + 2.32 \times dTv/dt(t-1)$ with $R = 0.38$ and $P < 0.01$.

Table 1. *Characteristics of angular target tracking for various color contrasts between the target and background*

Color contrast	Sample size	Position control			Velocity control		
		S_1	R_1	P	S_2	R_2	P
B/W	136	38.83	0.59	<0.01	1.37	0.54	<0.01
Green	164	45.2	0.39	<0.01	2.25	0.31	<0.01
Blue	144	22.31	0.45	<0.01	9.35	0.07	>0.30

S_1 is the slope of the regression line between the horizontal angular velocity Vh of the bee and the horizontal error angle Th of the target. R_1 is its correlation coefficient. S_2 is the slope of the regression line between the horizontal angular velocity Vh of the bee and the horizontal angular velocity dTh/dt of the target. R_2 is its correlation coefficient.

each case, we examined the relationship between Vh and Th, and between Vh and dTh/dt. The results are given in Table 1. Four trajectories were analyzed in the case of the black target on the white background, four in the case of the green-contrast color combination, and three in the case of the blue-contrast combination. All of these trajectories were analyzed after delaying the Vh data by one frame (40 ms). The slopes of the regression lines for Vh *vs.* Th and Vh *vs.* dTh/dt are given in Table 1, for each color combination. In the case of Vh *vs.* Th, the correlation coefficients are significant ($P < 0.01$) for the black/white, green-contrast, and blue-contrast conditions. However, the average slope of the regression line is lower in the blue-contrast situation, as compared to the others. In the case of Vh *vs.* dTh/dt, the correlation coefficients are significant for the black/white and green-contrast situations ($P < 0.01$), but not for the blue-contrast situation ($P > 0.3$). These findings, which will be discussed more fully later, suggest that tracking of the angular velocity of the target is mediated by a system that is sensitive only to green contrast, but that tracking of the angular *position* of the target is mediated by a subsystem that utilizes signals from the green as well as the blue receptors. The blue signals are, however, associated with a lower gain.

variables, and to translate them into tracking behavior. The accuracy of this estimate, is, of course, limited by the interframe interval (40 ms) associated with the video-recording process; our data only establishes that the true delay is less than 80 ms, and it is quite possible that the actual figure is similar to the 20-ms delay estimated by Land and Collett (1974) for chasing behavior in the housefly. All of the scattergrams in Figs. 4 and 5 are shown for the maximum-correlation case, i.e. that in which the variable shown on the ordinate is delayed by one frame with respect to that on the abscissa.

Chromatic properties of angular tracking

Tracking behavior was studied with a black target on a white background, as well as with combinations of colors that provided a contrast exclusively to the green receptors or exclusively to the blue receptors, at the target-background boundary. In

Translational tracking

When an approaching bee gets close enough to the target, it is often observed to track the target by adjusting its position, rather than its body orientation. This is clear in the example of Fig. 2, which is analyzed in Fig. 6 to show that, as the bee approaches the target ($D \to 0$), the oscillation of the target (target position: Tx), exerts a progressively greater influence on the bee's position Bx and velocity dBx/dt. Scattergrams of Bx *vs.* Tx and dBx/dt *vs.* dTx/dt for various delays interposed between the ordinate and the abscissa reveal that—as in the case of angular tracking—the correlation coefficient is a maximum when the ordinate is delayed by one frame interval relative to the abscissa (data not shown).

Scattergrams showing the relationship between Bx and Tx, and between dBx/dt and dTx/dt, are shown in Fig. 7 for a black target on a white background (Fig. 7a and 7b), and for targets offering green contrast (Fig. 7c and 7d) and blue contrast (Fig. 7e and 7f). One trajectory is analyzed in each case.
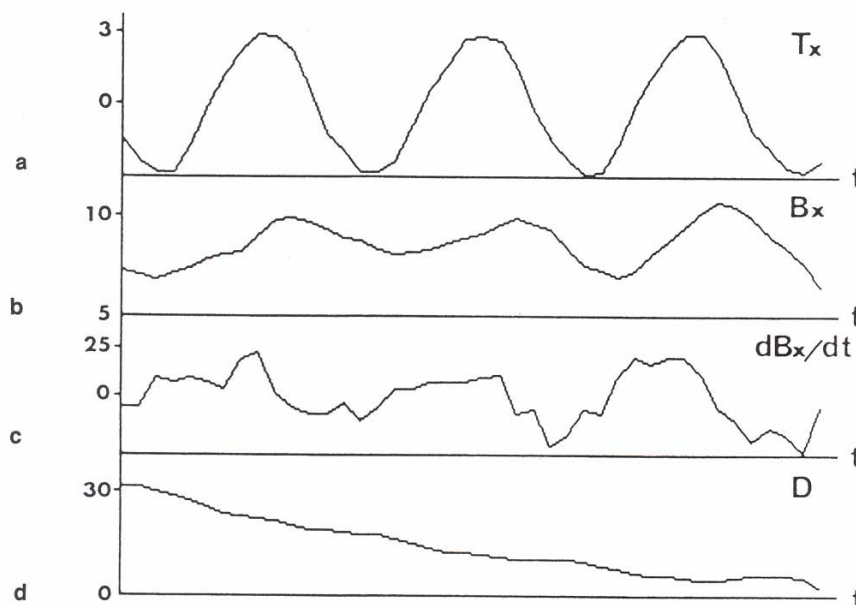
Fig. 6. Time course of translational tracking parameters associated with the approach trajectory illustrated in Fig. 2. (a) The time course of the instantaneous X component of the target position Tx. (b) The time course of the instantaneous X component of the honeybee's position Bx. (c) The time course of the instantaneous X component of the honeybee's velocity dBx/dt. (d) The time course of honeybee-target distance D during the approach.

For both Bx vs. Tx and dBx/dt vs. dTx/dt, the correlation coefficients of the regression lines are significant in the black-white and in the green-contrast situations, but not in the blue-contrast situation (details in Fig. 7 legend). These results indicate that translational tracking breaks down in the absence of green contrast.

Discussion

The results shown in Figs. 2–7 indicate clearly that honeybees are capable of tracking moving targets and landing on them. The scattergrams suggest that the angular position of the target as well as its angular velocity are input variables to the honeybee's tracking control system, both in the horizontal and in the vertical planes. The histograms of Figs. 4 and 5 indicate that this control system seeks to position the target frontally, about 35 deg below the bee's long axis. A similar tendency for ventral fixation has also been found in drones approaching the entrance to their hive (van Praagh et al., 1980).

With regard to tracking behavior in the horizontal plane, the data of Table 1 reveal that the correlation coefficient of the scattergrams relating Vh to Th are significant for the black/white, green-contrast, and blue-contrast situations, suggesting that the input variable corresponding to the horizontal *angular position* of the target Th uses information from the green as well as the blue channels (since there was very little ultraviolet in the ambient light in our experiments, the possibility of a contribution from the ultraviolet channel remains an open question).

The scattergrams relating the angular velocity of the bee Vh to the angular velocity of the target dTh/dt in the horizontal plane reveal that the correlation coefficient is high and significant ($P < 0.01$) in the black/white and green-contrast situations,

but low and not significant ($P > 0.30$, Student's t-test) in the blue-contrast situation (Table 1). This finding suggests that the input variable corresponding to horizontal *angular velocity* dTh/dt uses information from the green channel, but not from the blue channel. The possibility of a contribution from the ultraviolet channel again remains an open question, for the reason indicated above.

All of the previous work on motion perception in insects (which has been carried out mainly on flies and honeybees) suggests that motion-sensitive responses are "color-blind," being mediated by one spectral class of receptors, maximally sensitive in the green portion of the spectrum (review by Srinivasan, 1985). This holds for the optomotor response (bees: Kaiser, 1975; flies: Heisenberg & Buchner, 1977), the movement-avoidance response (Srinivasan & Lehrer, 1984), and visual scanning behavior (Lehrer et al., 1985). In the case of target tracking by bees, we seem to have, on the other hand, a response that is driven by two distinct components: one, corresponding to the *angular velocity* of the target, appears to be driven exclusively by signals from the green receptors, while the other, corresponding to the *angular bearing* of the target, uses information from the green as well as the blue receptors. We may conjecture that the neural substrate underlying target-tracking behavior comprises two pathways, one sensitive to target angular position and the other to target angular velocity, with chromatic properties as described above. A similar, dual-pathway organization has been proposed to account for target tracking in the fly (Land & Collett, 1974; Collett & Land, 1975; Wehrhahn et al., 1982). However, in that case, the chromatic properties of tracking behavior have not yet been examined. Parenthetically, it is of interest to note that evidence, albeit controversial, is accumulating to suggest that motion sensitivity is
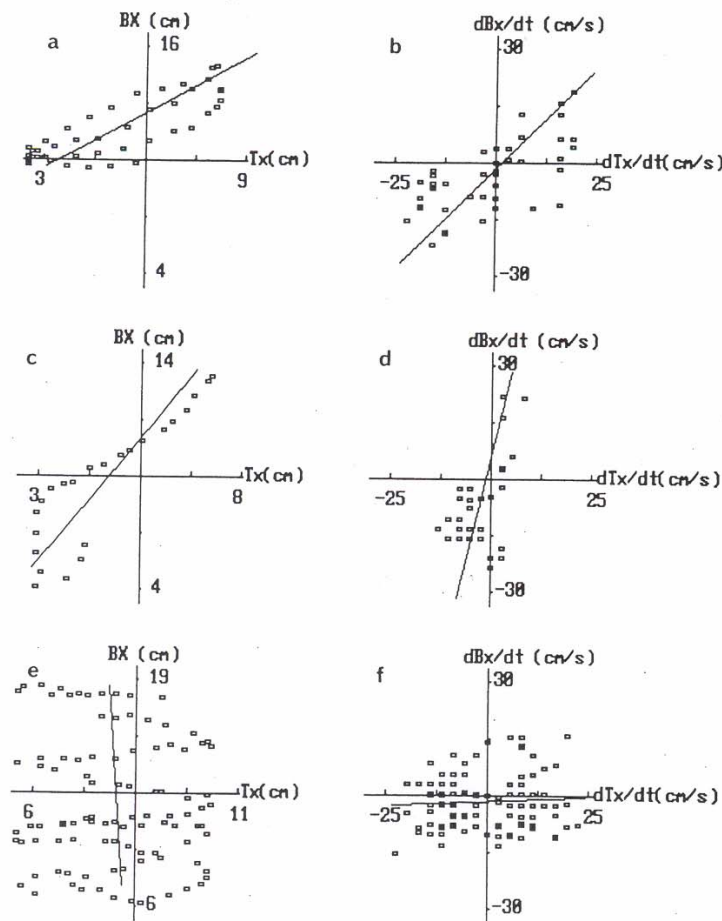
Fig. 7. Lateral position tracking and velocity tracking. (a) Lateral position tracking in the case of a B/W contrast target. The regression line is described by $Bx(t) = 2.23 + 0.88 \times Tx(t-1)$, with $R = 0.86$ and $P < 0.01$. (b) Lateral velocity tracking in the case of a B/W contrast target. The regression line is described by $dBx/dt(t) = -1.69 + 1.07 \times dTx/dt(t-1)$ with $R = 0.68$ and $P < 0.01$. (c) Lateral position tracking in the case of a green-contrast target. The regression line is described by $Bx(t) = -4.72 + 2.19 \times Tx(t-1)$ with $R = 0.88$ and $P < 0.01$. (d) Lateral velocity tracking in the case of a green-contrast target. The regression line is described by $dBx/dt(t) = 5.78 + 4.46 \times dTx/dt(t-1)$ with $R = 0.49$ and $P < 0.01$. (e) Lateral position tracking in the case of a blue-contrast target. The regression line is described by $Bx(t) = 297.82 - 31.85 \times Tx(t-1)$ with $R = 0.08$ and $P > 0.40$. (f) Lateral velocity tracking in the case of a blue-contrast target. The regression line is described by $dBx/dt(t) = -1.44 + 0.05 \times dTx/dt(t-1)$ with $R = 0.07$ and $P > 0.40$.

color-blind in humans as well, and is mediated by luminance signals (Livingstone & Hubel, 1987).

Bees, like flies (Wagner, 1986), are capable of controlling the lateral body position and velocity, in addition to angular orientation and velocity, while tracking a moving target (Figs. 6 and 7). Translational tracking is not very prominent at large target distances, but it appears to play an increasingly important role as the target is approached, i.e. as the distance between the bee and the target decreases (Fig. 6). In the case of a black target moving on a white background, there is a significant correlation between target position Tx and bee position Bx (Fig. 7a; $P < 0.01$), and between target velocity dTx/dt and bee velocity dBx/dt (Fig. 7b; $P < 0.01$). These correlations persist in the case of a green-contrast target (Fig. 7c,d; $P < 0.01$) but disappear in the case of a blue-contrast target (Fig. 7e,f; $P > 0.40$,

Student's t-test), suggesting that control of translational tracking is mediated by a system that is sensitive exclusively to signals from the green-sensitive receptors.

The existence of strong correlations between Tx and Bx, and between dTx/dt and dBx/dt in the black/white and green-contrast situations (Fig. 7a,b), does not necessarily imply that the linear target position and linear target velocity *per se* are the input signals to the control system that mediates translational tracking. Rather, the input signals must be related to angular bearing and its temporal derivatives, since locations and velocities in space can only be measured in terms of their angular projections on the eye. It is possible, in principle, to investigate this question by examining the relationship between Bx and Th, Bx and dTh/dt, and between dBx/dt and dTh/dt. However, we have not done this, because the procedure for deriving these

scattergrams is rather cumbersome. It is necessary to keep track of the polarity of the relationship between the position of the target and its angular bearing, which varies depending upon whether the bee approaches the target from a region to the left or to the right of the line along which the target oscillates. Thus, the analysis shown in Fig. 7 does not isolate the relevant input variables for translational tracking, but it does allow us to evaluate the chromatic properties of this performance.

Acknowledgments

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