

Honeybee navigation: properties of the visually driven 'odometer'

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Summary

Recent work has revealed that honeybees determine distance flown by gauging the extent to which the image of the environment moves in the eye as they fly toward their destination. Here we examine the properties of this visually driven 'odometer', by training bees to fly to a feeder in a tunnel lined with a range of different visual patterns, and analysing their dances when they return to the hive. We find that the odometric signal is relatively unaffected by variations in the contrast and spatial frequency content of the patterns. Furthermore, a strong

signal is generated even when the walls or the floor of the tunnel provide only weak optic-flow cues. Thus, distance flown is measured by a visually driven odometer that is surprisingly robust to variations in the texture or sparseness of the visual environment through which the bee flies.

Key words: visual pattern, odometric signal, honeybee, navigation, optic flow.

Introduction

When a scout honeybee discovers an attractive patch of flowers, she performs the famous 'waggle dance' that advertises the location of the food source to her nestmates (von Frisch, 1993). The dance consists of a series of alternating left-hand and right-hand loops, interspersed by a segment in which the bee waggles her abdomen from side to side. The duration of this 'waggle phase' conveys to the potential recruits the distance of the food source from the hive: the longer the duration of the waggle, the greater the distance (von Frisch, 1993). This information is used by the recruited bees to locate the food source. Clearly, then, the scout, as well as the recruits, is able to gauge how far she has flown in search of food.

Early studies concluded that bees estimate distance flown by gauging the amount of energy they expend to reach the destination (for a review, see von Frisch, 1993). More recent studies, however, are providing increasing evidence that this 'energy hypothesis' is incorrect, at least for moderate distances of a few hundred meters (Neese, 1988; Esch et al., 1994, 2001; Esch and Burns, 1995; Srinivasan et al., 1996, 1997, 2000). Over these distances, bees appear to gauge distance flown in terms of the extent to which the image of the environment moves in the eye (Esch and Burns, 1995, 1996; Srinivasan et al., 1996, 1997, 2000; Esch et al., 2001). In other words, the optic flow experienced by the eye (that is, the speed of motion of the image of the environment) is integrated over time to obtain an estimate of distance traveled. The most compelling evidence for this was obtained in a study in which bees were trained to fly to a feeder placed inside a short, narrow tunnel, the walls and floor of which were lined with a random visual

texture. When bees returned to the hive from the tunnel, they performed a waggle dance in which they indicated a feeder distance as large as 200 m, despite the fact that they had only flown a distance of 6 m (Srinivasan et al., 2000). Evidently, the proximity of the walls and floor of the tunnel greatly amplified the magnitude of the optic flow that they experienced, in comparison with the situation during outdoor flight in a natural environment. On the other hand, when the same tunnel was lined with axial stripes – so that a bee flying through it would experience very little optic flow, because the stripes were parallel to the flight direction – the bees signaled a very small distance, even though they had flown the same physical distance as in the previous condition (Srinivasan et al., 2000). This experiment indicated that distance flown was being measured in terms of integrated optic flow, and not in terms of physical distance flown or energy consumed.

If bees do indeed gauge distance traveled by measuring optic flow and integrating it over time, it is pertinent to enquire into the properties of their visually driven 'odometer'. Given that the environment through which a bee flies can vary substantially in terms of its visual properties, such as contrast, texture and the distribution of objects, it is important to know whether, and to what extent, the bee's perception of distance flown is affected by these environmental variables. In other words, how 'robust' is the honeybee's odometer?

The tunnel experiment described above (Srinivasan et al., 2000) offers a convenient means of exploring this question under controlled laboratory conditions, since outdoor flights of a few hundred meters can be simulated in the laboratory by

flying bees through narrow tunnels a few meters long. Thus, one can investigate the effects of varying the contrast, texture or other attributes of the environment by varying the properties of the visual patterns that line the walls and floor of the tunnel, and analysing the resulting dances.

Materials and methods

Bees (*Apis mellifera* L.) from an observation hive were trained to fly to a tunnel placed outdoors with its entrance at a distance of 35 m from the hive. The walls of the hive were made of clear Perspex sheets, which facilitated the viewing and filming of bee dances. The tunnel was oriented with its entrance facing the hive. It was 11 cm wide, 20 cm high and 6 m long in all experiments except one, in which it was 2 m, 4 m or 8 m long. A strip of black insect screen cloth formed the roof of the tunnel, allowing the observation of bees within. Bees were trained to fly to a feeder containing sugar solution placed at the far end of the tunnel, which was kept closed, so that bees could only enter and leave the tunnel through the near end. Up to 20 bees were marked at the feeder for each experimental condition. Dances performed by marked bees returning from the tunnel were filmed at the hive using a digital video camera, and later analysed.

Tunnel patterns

The side walls and floor of the tunnel were lined with various black-and-white patterns and gratings. In the first series of experiments, the walls and floor of the tunnel were lined with a checkerboard pattern of squares 3.2 cm², or with axial stripes at 8 cm intervals. In the second series, a randomly textured Julesz pattern with a pixel size of 1 cm and a pattern of axial stripes were used in various combinations. As controls, bees were made to fly to feeders placed at either 35 m or 41 m from the hive entrance. In a third experimental series, the side walls and floor of the tunnel were lined with vertical square-wave gratings at 3.6 cm intervals and contrasts ranging from 20% to 92%. In a fourth series, the patterns were sinusoidal gratings of medium contrast and varying spatial periods (values given in Results).

In the latter two series of experiments the checkerboard pattern was used to provide a baseline against which to compare data obtained from the other experimental conditions. The axial pattern was used to create a condition in which the optic flow experienced by bees flying through the tunnel was very weak, because flight in the direction of the stripes produced very little apparent motion of the images of the walls and floor in the eyes.

The patterns were printed on a laser printer using a computer running a graphics program. The contrasts of the patterns were measured by using a photodiode that had a linear intensity–response function and a visual field considerably narrower than the smallest pixel or stripe width that was used.

Dance analysis

For each experimental condition, we analysed the dances

performed by the marked bees upon their return to the hive. A dance typically consisted of a number of loops, alternating between the clockwise and counterclockwise senses. Some of these loops displayed a waggle component, whereas others did not. For each dance, we measured three parameters: (i) the percentage of waggle loops; (ii) the mean duration of the ‘pure’ waggle component (considering only the waggle loops and disregarding loops that contained no waggle) and (iii) the mean duration of the waggle component over the entire dance, assigning a waggle duration of zero to each loop that had no waggle. The Fisher’s Least-Significant-Difference Test was used to test for statistically significant differences between the mean waggle durations obtained for different conditions.

Results

Dances of bees returning from tunnels

We began by training bees to fly to a feeder placed inside a tunnel in which the walls and floor were lined with a checkerboard pattern. We filmed the dances of marked bees returning from the tunnel with the feeder placed at distances of 2 m, 4 m, 6 m and 8 m from the tunnel entrance.

The dances observed (see Materials and methods) were typically somewhat different from the dances that are elicited by long flights in natural outdoor environments, where almost every loop contains a waggle (A. Si, M. V. Srinivasan and S. Zhang, unpublished observations). Both measurements of waggle duration increased systematically with distance flown (Fig. 1), as did the percentage of waggle loops (Fig. 2). At a distance of 8 m into the tunnel, the mean waggle duration was approx. 250 ms (Fig. 1). This waggle duration is comparable to that exhibited by bees that return from distances as large as 100–200 m in a natural outdoor environment (Srinivasan et al., 2000; Esch et al., 2001). Evidently, the proximity of the walls and the floor of the tunnel greatly amplify the magnitude of the optic flow in comparison with what the bees would normally experience during outdoor flight in a natural environment. On the other hand, when the tunnel was lined with axial stripes, the mean waggle duration was very low (approx. 80 ms) regardless of whether the tunnel was 4 m or 8 m long (Fig. 1). Under these conditions the percentage of waggle loops was also at its lowest level, approximately 40% (Fig. 2).

These data support the conclusions of earlier studies (Srinivasan et al., 2000; Esch et al., 2001) that honeybees gauge distance flown in terms of the amount of image motion that is experienced by the eyes *en route* to the food source. The present results extend those findings by showing that the odometric signal increases with distance flown in the tunnel, just as it does in the case of outdoor flight in a natural environment. The difference is that in the tunnel the odometric signal increases at a higher rate than during outdoor flight. The tunnel can thus be used as a convenient experimental device in which to ‘simulate’, for the bee, outdoor flights of a few hundred meters, and to study the effects of varying the contrast, texture and other properties of the visual environment on the odometric signal.

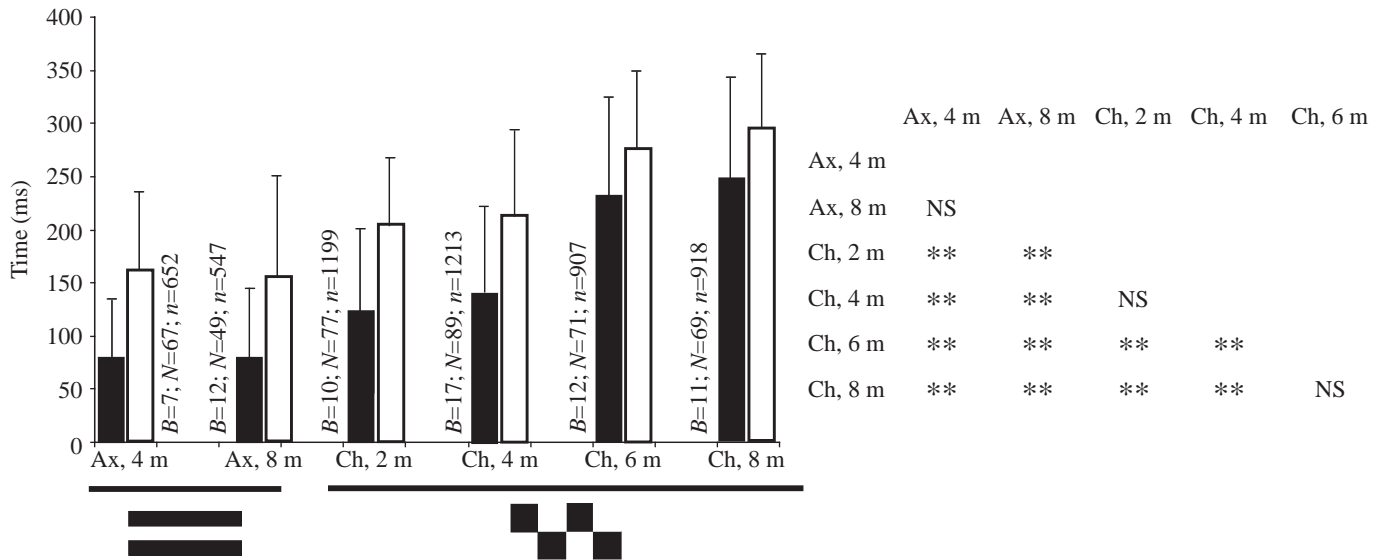


Fig. 1. The effect of varying tunnel length on the mean waggle duration (black bars) and the mean pure waggle duration (white bars) of bees returning to the hive after being rewarded inside the tunnel. Values are means \pm s.d. for each experimental condition; in this and all figures, *B* denotes the number of bees, *N* the number of dances analysed, and *n* the total number of loops (waggle + non-waggle) analysed. The walls and floor of the tunnel (length 2, 4, 6 or 8 m) were lined with a checkerboard pattern in all but two cases, where axial stripes were used instead. The table on the right of the histogram shows the results of a pair-wise Fisher's Least Significant Difference Test for differences in the values of mean waggle duration; * $P < 0.05$; ** $P < 0.01$; NS, no significant difference ($P > 0.05$). Ax, axial; Ch, checkerboard.

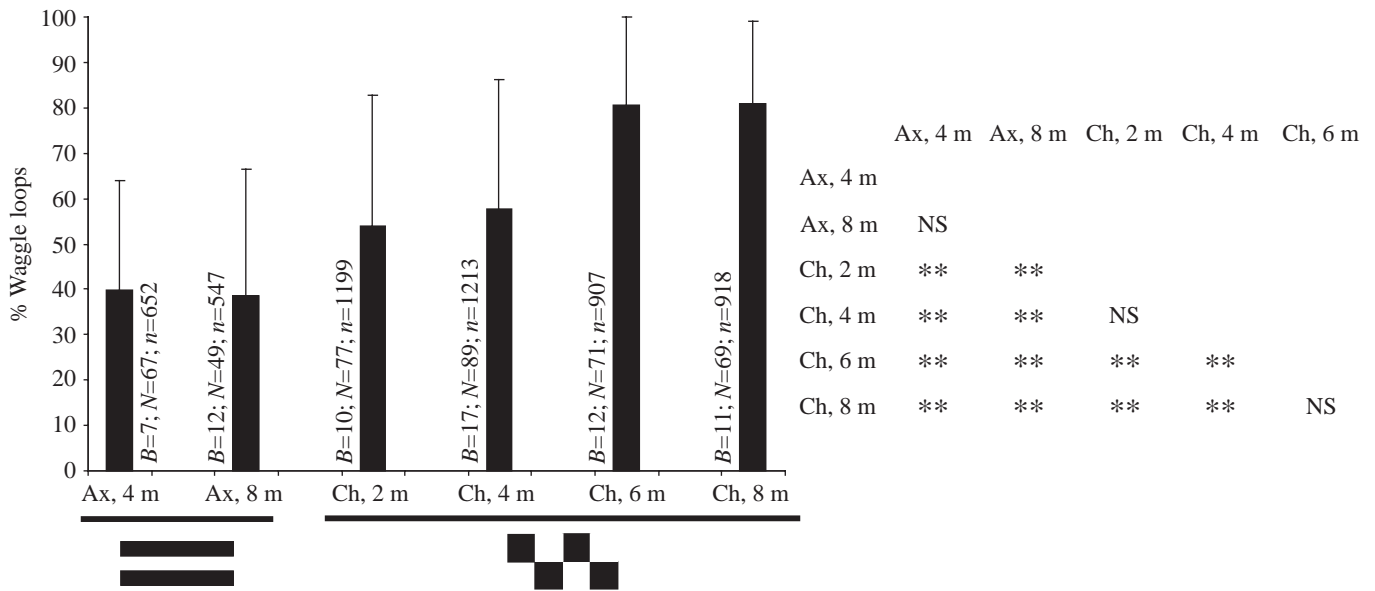


Fig. 2. The effect of varying tunnel length on the proportion of waggle loops. Other details as in Fig. 1.

We did not experiment with tunnels longer than 8 m, because it is difficult to coax bees to fly through long, narrow tunnels and dance upon their return. However, there is every indication that the mean waggle duration would have continued to increase with tunnels longer than 8 m, because other experiments in our laboratory have revealed that mean waggle duration can be increased beyond that at maximum tunnel length by moving the pattern on the wall backwards, against

the bee's flight, thereby increasing the magnitude of the integrated optic flow (H. Esch, S. Zhang and M. V. Srinivasan, unpublished observations).

In another set of experiments we examined the effect of varying tunnel width. For a tunnel of a fixed length, increasing the width should decrease the magnitude of the integrated optic flow that is experienced by the bees, because the walls are then more distant from them. In an 8 m long, 11 cm wide tunnel

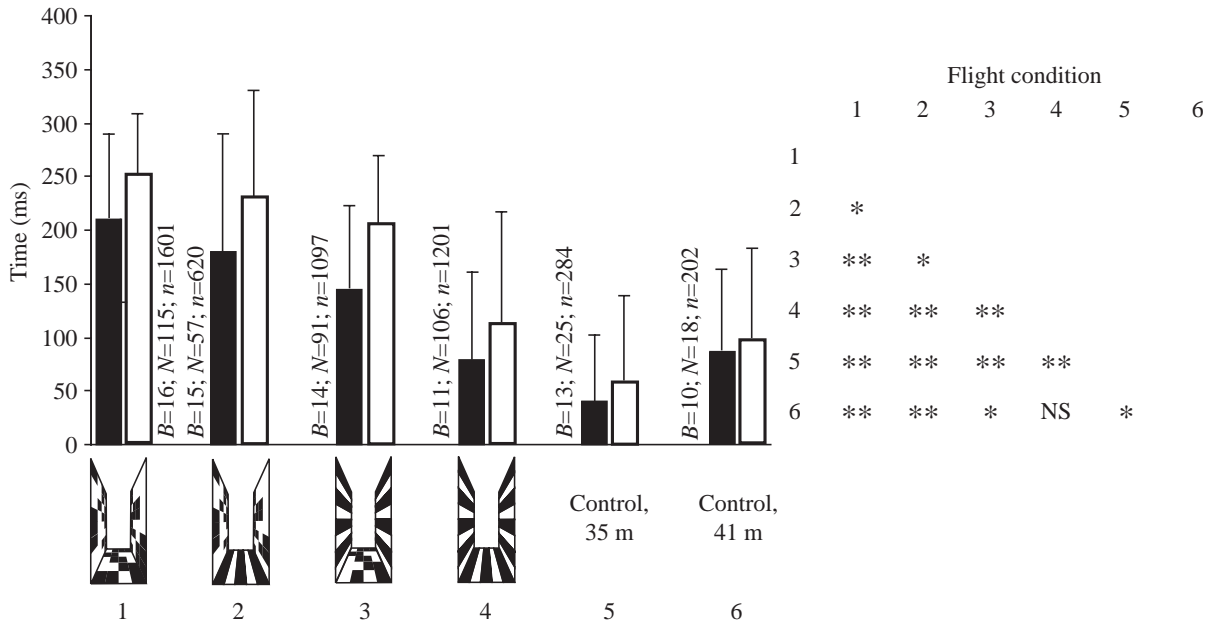


Fig. 3. The contribution of the lateral and ventral visual fields to odometry. Variation in mean waggle duration (black bars) and the mean pure waggle duration (white bars) of bees after flying in a tunnel with different surfaces providing optic flow (random Julesz pattern) or no optic flow (axial stripes) (indicated below). Controls, behaviour after outdoor flight to the tunnel entrance; see text for details. Other details as in Fig. 1.

lined with the checkerboard pattern, the mean waggle duration was 373 ms and the mean pure waggle duration was 401 ms (33 dances, 406 total loops). (These figures are higher than those shown in Fig. 1 because the new set of experiments was performed in a different year, using a different colony of bees). When the width of the tunnel was increased to 22 cm, the corresponding figures were 260 ms and 295 ms, respectively (30 dances, 366 total loops). Both mean waggle duration and mean pure waggle duration were significantly lower when the tunnel was wider ($P < 0.001$). Thus, the dances show a clear dependence on tunnel width, as one might expect if travel distance were gauged in terms of the optic flow experienced *en route*.

Contribution of lateral and ventral visual fields to odometry

We next asked which region or regions of the eye are involved in the measurement of the optic flow that is used by bees to assess distance traveled, and how sensitive the calibration of the honeybee’s visual odometer is to deprivation of optic flow in specific regions of the visual field.

Bees were made to fly through a tunnel whose floor, or side walls, or all surfaces, were lined with a random black-and-white Julesz pattern to provide motion cues. The remaining surface(s) were lined with an axial striped pattern, and thus provided very weak optic flow cues.

The results revealed that when the tunnel provided optic flow on all surfaces (walls as well as floor), the mean waggle duration was approx. 210 ms (Fig. 3). This was the experimental condition that elicited the largest mean waggle duration and the largest mean pure waggle duration (Fig. 3),

as well as the largest percentage of waggle loops (82%, Fig. 4). When the walls of the tunnel provided optic flow, but not the floor, the mean waggle duration and the mean pure waggle duration decreased slightly (Fig. 3). The percentage of waggle loops also displayed a slight decrease (Fig. 4). When the floor contributed optic flow, but not the walls, both measures of waggle duration decreased by further, small amounts (Fig. 3), which was mirrored by a further, small decrease in the percentage of waggle loops (Fig. 4). Comparing the data in the second and third columns of Fig. 3, we see that the walls of the tunnel make a slightly, but significantly greater contribution to the odometric signal than does the floor. The striking feature of the dances that were elicited by these three conditions, however, lies not in their slight differences, but in their similarity. Thus, even when optic flow cues were restricted to the floor (and the floor comprised only 20% of the tunnel’s interior surface area), the mean waggle duration and the mean pure waggle duration were still approximately 70% of the value that was observed when all of the surfaces provided optic flow. The percentage of waggle loops also exhibited a relatively modest variation between these two rather extreme conditions. These findings indicate that the honeybee’s odometer is remarkably robust to deprivation of optic flow information in large sections of the visual field, regardless of whether this deprivation occurs in the lateral or the ventral field of the eyes.

When all of the interior surfaces of the tunnel were lined with axial stripes, both measurements of waggle duration dropped further (Fig. 3), as did the percentage of waggle loops (to 38%, Fig. 4). However, even under this highly

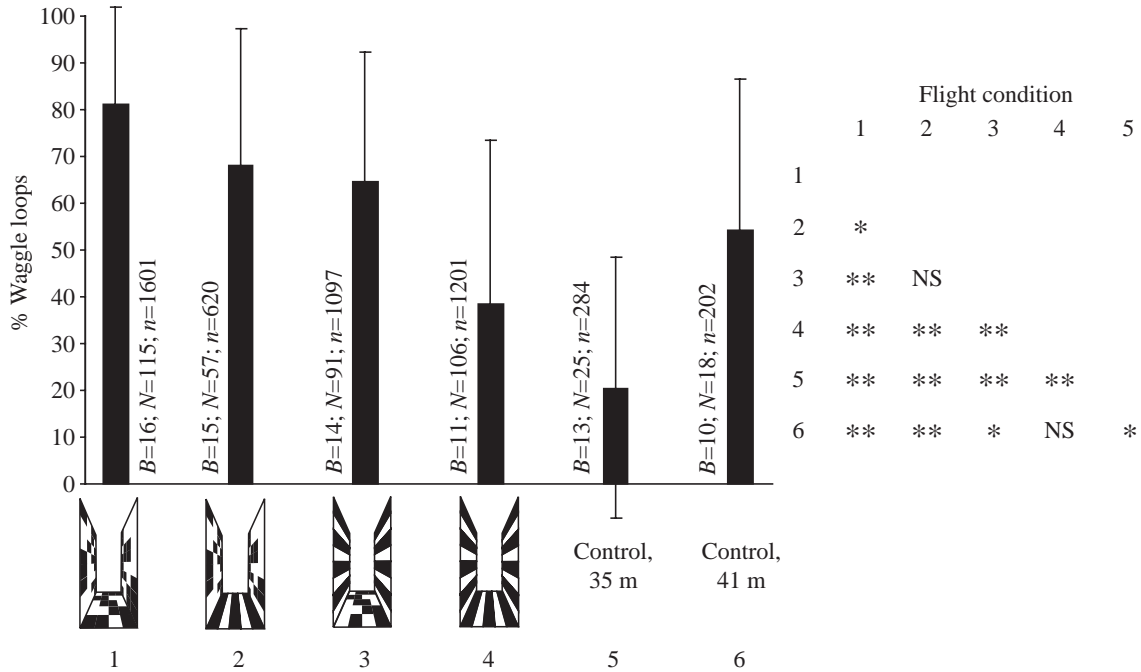


Fig. 4. The contribution of the lateral and ventral visual fields to odometry. The histogram shows the variation of the proportion of waggle loops. Other details as in Fig. 3.

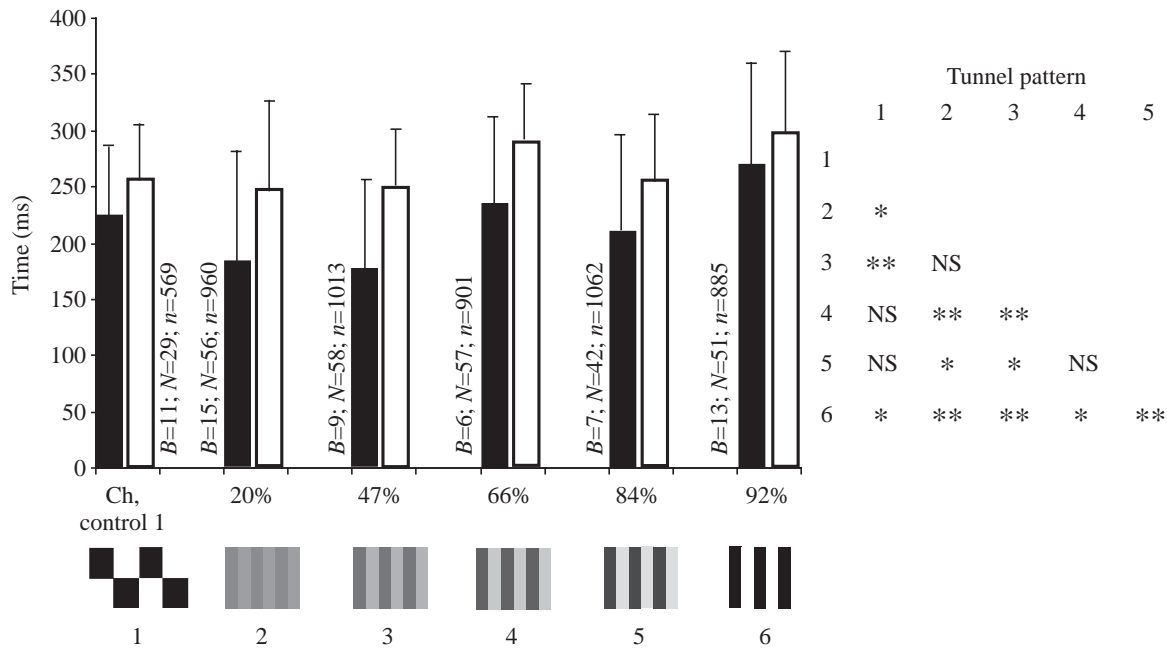


Fig. 5. The effect of contrast on mean waggle duration (black bars) and the mean pure waggle duration (white bars). The walls and floor of the tunnel were lined with square-wave gratings of various % contrasts, as shown. A 92% contrast checkerboard (Ch) pattern was used as a control to provide a baseline value. Other details as in Fig. 1.

impoverished condition, the bees signaled a distance that was greater than that corresponding to the outdoor flight of 35 m to the tunnel entrance (which elicited 18% waggle loops and a mean waggle duration of 40 ms). Evidently, small imperfections in the construction and laying of the axial stripe pattern in the tunnel (and, possibly, stray shadow edges)

produced small, residual optic flow cues that were registered by the odometer.

Finally, when the bees returned from an outdoor feeder positioned 41 m from the tunnel entrance, they exhibited 55% waggle loops and a mean waggle duration of 80 ms. These values represent a flight distance that is slightly larger than that

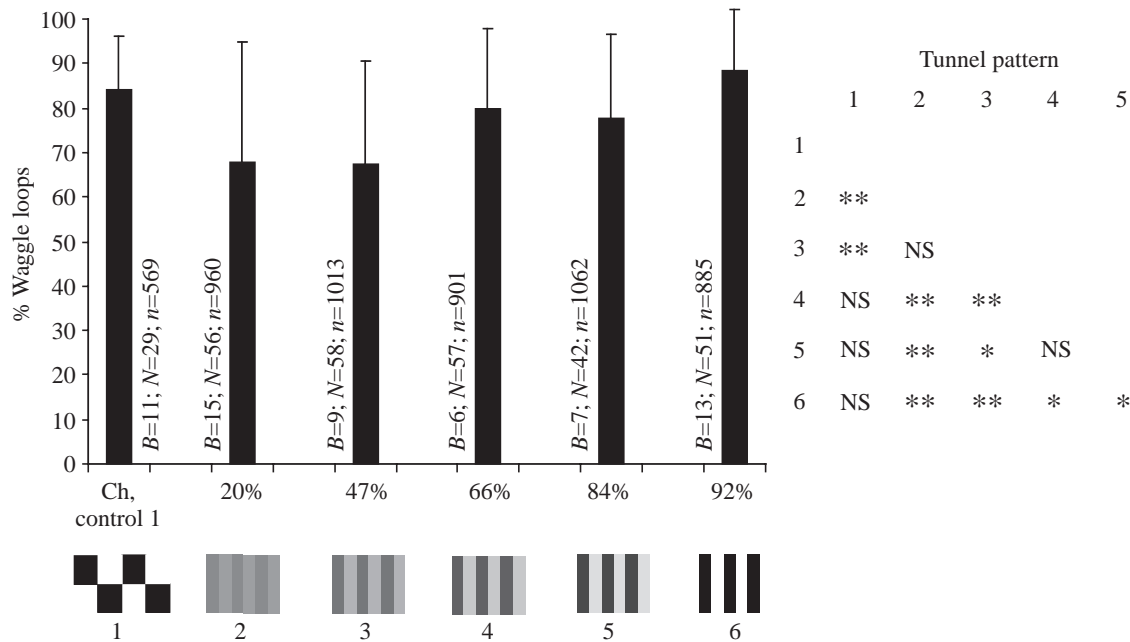


Fig. 6. The effect of contrast on the proportion of waggle loops. Other details as in Fig. 5.

corresponding to an outdoor flight of 35 m, but lower than the distances that were signaled after flights within the tunnel when some or all of the surfaces provided optic flow cues. This is despite the fact that the bees flew the same distance from the hive to the feeder in the tunnel (35 m + 6 m) as they did when they flew to the outdoor feeder at 41 m. Clearly, then, the larger magnitude of the optic flow that bees experience in the tunnel – due to the proximity of the walls and the floor compared to outdoor flight in a natural environment – caused the bees to signal a greater distance when they flew in the tunnel, provided at least one of the surfaces generated optic flow cues.

Effect of contrast on the odometric signal

Next, we investigated the influence of the contrast of the visual environment on the perception of distance flown. In a series of experiments, bees were made to fly a constant distance (6 m) into a tunnel in which the walls and floors were lined with square-wave gratings of constant period, but with contrasts ranging from 20% to 92%.

Analysis of the dances of bees returning from this tunnel revealed that the odometric signal is rather insensitive to variation of contrast (Fig. 5). When the contrast was decreased from 92% to 20% (a 78% reduction), the mean waggle duration decreased from 270 ms to 180 ms (a reduction of only 33%). The 180 ms waggle duration elicited by the 20% contrast grating was more than twice as large as the waggle duration elicited by a tunnel lined with axial stripes (compare with Fig. 1). Evidently, even small contrasts generate sufficient optic flow information to produce an odometric signal of nearly normal strength. There was no significant decrease in the mean waggle duration when the contrast was reduced from 85% to 66%, or from 47% to 20% ($P > 0.05$). The mean pure waggle duration exhibited a similar insensitivity to variation of

contrast (Fig. 5), as did the percentage of waggle loops in the dances (Fig. 6). These findings indicate that the odometric signal is rather insensitive to variations of contrast in the environment.

Effect of spatial frequency content of the environment on the odometric signal

In another series of experiments, bees were made to fly a constant distance (6 m) into a tunnel in which the walls and floor were lined with sinusoidal gratings of fixed contrast (mean contrast, 58%) but with varying spatial periods of 1.8 cm, 3.6 cm and 7.2 cm. (For a bee flying along the axis of the tunnel, the spatial frequencies of these gratings as seen by the lateral field of the eye would range from 0.03 to 0.10 cycles deg^{-1}). The results (Fig. 7) revealed that the mean waggle duration does not vary significantly with a twofold increase in spatial period from 1.8 cm to 3.6 cm. There was only a slight, but significant decrease in mean waggle duration with an increase in spatial period from 3.6 cm to 7.2 cm. There was, however, no significant difference between the mean waggle durations for any of the spatial periods and those obtained in the conditions in which the walls and floor of the tunnel were lined with a checkerboard pattern (Fig. 7; $P > 0.05$), but all of these mean waggle durations were significantly higher than that corresponding to the axial-stripe condition, in which there was very weak optic flow (Fig. 7). The mean pure waggle duration showed a similar behaviour (Fig. 7). Overall, these results indicate that the calibration of the odometer is quite insensitive to variations in the spatial texture of the environment through which the bee flies, provided that the texture is capable of generating optic flow information. A similar conclusion is reached when the waggle loop percentages are analysed for these various conditions (Fig. 8).

Fig. 7. The effect of spatial period on mean waggle duration (black bars) and the mean pure waggle duration (white bars). The walls and floor of the tunnel were lined with sinusoidal gratings of spatial periods 1.8 cm, 3.6 cm and 7.2 cm, as shown. A 92% contrast checkerboard pattern (Control 1) and axial stripes (Control 2) were used as controls. Other details as in Fig. 1.

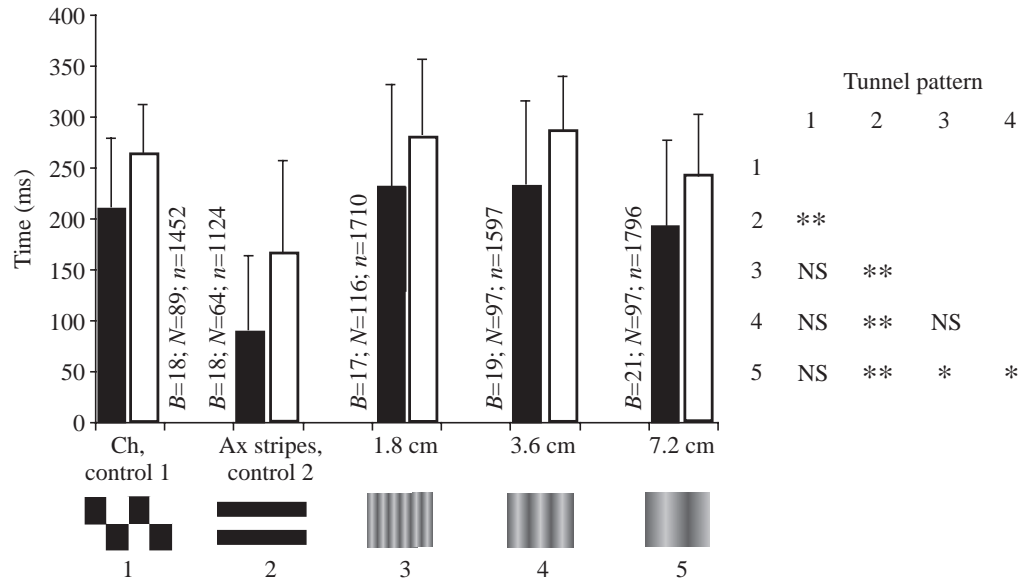
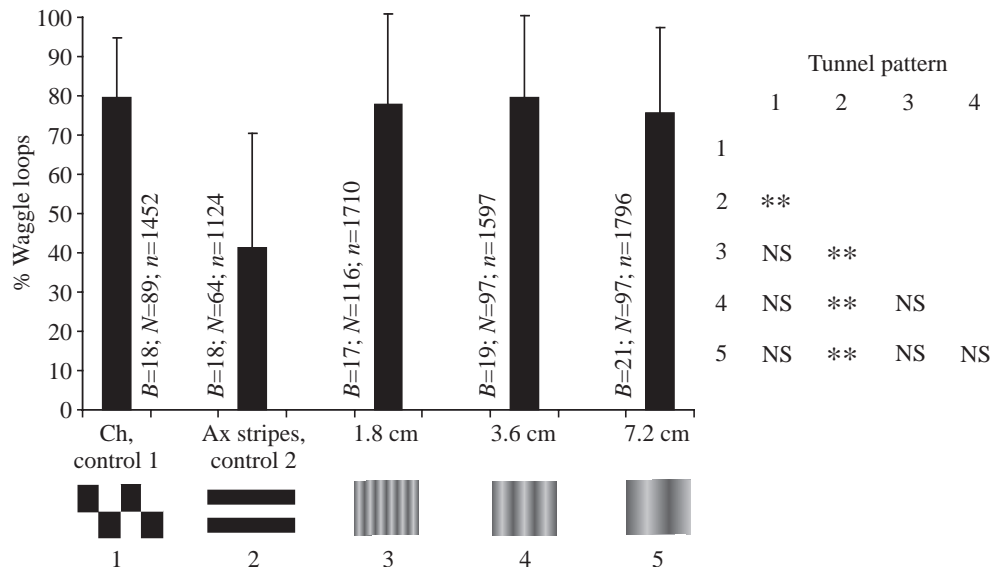


Fig. 8. The effect of spatial period on the proportion of waggle loops. Other details as in Fig. 7.



There were no statistically significant differences between the waggle loop percentages for the three different spatial periods ($P > 0.05$).

Discussion

The results of this study indicate that the honeybee's odometer is remarkably robust in its performance. The odometric signal continues to be strong even when the optic flow is restricted to the walls or the floor of the tunnel. It is striking that the contributions of the floor and the wall are approximately equal, despite the fact that the floor occupies only about 25% of the area of the walls. If bees were to fly axially through the centre of the cross section of the tunnel, which is roughly what they tend to do (A. Si, M. V. Srinivasan and S. Zhang, unpublished observations), then the two walls

would together cover approx. 244° of the visual field, whereas the floor would subtend only approx. 58° . Thus, the odometer appears to be able to use optic flow effectively even if flow is restricted to a small region of the visual field. Such robustness would be advantageous, given that bees forage in a variety of environments that may have extremely different visual properties. This kind of robustness is also evident from the study of Esch and Burns (1995), where bees flew in an open meadow and experienced image motion only in the ventral field. Exactly how this robustness is achieved at the neural level remains to be discovered. This finding diverges somewhat from that of Srinivasan et al. (1997), who reported that bees could locate the position of a feeder in a tunnel more accurately if optic flow cues were provided by the walls instead of the floor. The reason for this discrepancy remains to be explained. One possibility might be that the odometric

mechanisms that control the search for a food source are different from those that drive the dance behaviour.

Our findings also indicate that the odometric signal is rather insensitive to variations of scene contrast. The dances elicited by visual contrasts in the range 66–92% are remarkably similar in their properties (Figs 5, 6), although with 92% contrast the mean waggle duration and waggle loop percentage elicited by the grating (Figs 5, 6) were slightly, but significantly greater than those elicited by the checkerboard (Figs 5, 7) or the random texture (Figs 1–4; $P < 0.05$). When the contrast is reduced to below 50%, there is a slight decrease in the mean waggle duration, mean pure waggle duration and waggle loop percentage, but these values continue to be high even at a contrast as low as 20%. This robustness to contrast variations should be of considerable advantage, since the contrast of natural scenes can vary widely and it would be important to have access to a strong and reliable odometric signal even when the contrast in the environment is low. von Frisch noted that bees returning from a feeder on a lake signaled almost the same distance in their dances as bees that had flown a comparable distance on land (von Frisch, 1993, pp. 111–113). Given that the surface of the lake offered very low optical contrast, he concluded (from this and other evidence) that bees use energy consumption, rather than visual information, to estimate how far they have flown. Recently, however, considerable evidence has been mounting against this so-called ‘energy’ hypothesis, and in favour of a visually driven odometer (Neese, 1988; Esch et al., 1994, 2001; Esch and Burns, 1995, 1996; Srinivasan et al., 1996, 1997, 2000; and our present results). In the light of these recent findings, we reinterpret von Frisch’s results as implying that the odometer is indeed visually driven, and that it generates a substantial signal even at the low contrasts that are characteristic of water surfaces. Indeed, our finding that there is a measurable odometric signal even in the axial-striped tunnel suggests that very weak motion cues are sufficient to drive the odometer.

Substantial sensitivity to motion of low-contrast images has also been observed in the so-called ‘centring response’ – another visually mediated behaviour in honeybees (Srinivasan et al., 1991). Bees fly through the centre of narrow gaps or corridors by balancing the speed of image motion in the lateral fields of the two eyes. The visual subsystem that mediates this behaviour appears to measure image speed accurately even at low contrasts: bees will fly through the middle of a corridor even when one wall carries a 60% contrast pattern and the other a pattern with a contrast as low as 15% (Srinivasan et al., 1991). Exactly how the visual system accurately registers motion of very low contrast images remains to be unraveled. It is clear, however, that neurons in the peripheral stages of the insect visual pathway display some degree of contrast invariance and show substantial responses to low contrast images (Laughlin, 1981, 1989).

Our findings indicate that the odometer is also robust to variation in the spatial texture of the visual environment through which the bee flies, provided the texture is capable of providing optic flow information. When the tunnel is lined with

vertical gratings, a fourfold change in spatial period produces only modest variations in either measurement of waggle duration, and no variation at all in the waggle loop percentage (Figs 7, 8). A similar insensitivity to variations in spatial period was observed in an earlier study, which investigated the ability of bees to use odometric information to locate a feeder placed at a fixed position inside a tunnel (Srinivasan et al., 1997). There, the bees’ accuracy in pinpointing the feeder location was unaffected when the spatial period of the gratings lining the tunnel walls and floor was varied over a fourfold range (Srinivasan et al., 1997). This robustness to variation of spatial texture is also mirrored in the centring response: bees will fly down the middle of a corridor even when the spatial periods of the gratings on the two walls differ by a factor of four (Srinivasan et al., 1991).

It is interesting, however, to note that the dances elicited by the tunnel are somewhat different from those performed by bees flying in a natural environment to a distant feeder/food source. The proportion of non-waggle loops, when compared to the tunnel dances, is often much reduced or completely absent in dances performed by bees flying in the open (A. Si, M. V. Srinivasan and S. Zhang, unpublished data). This suggests that the dance performed by the tunnel bees is actually a modified form of the classical waggle dance, possibly arising from the result of a conflict between the bees’ normal odometric signal derived from optic flow, and the ‘true’ distance based on the bees’ previously acquired knowledge of the environment external to the tunnel. These bees were likely to have a very good knowledge of the environment in the vicinity of the hive. Thus, when they were made to fly into the tunnel with a clear ceiling through which the outside environment was partly visible, there was likely to have been a strong conflict between their position as gauged by external landmarks, as opposed to optic flow.

Our results reveal that, while both the mean and pure waggle durations increase with distance flown in the tunnel (Fig. 1), the variability in these durations (measured as standard deviation) remains rather constant, and independent of this distance. This finding is at some variance with the study of Srinivasan et al. (1997), where it was observed that the accuracy with which bees search for a feeder in a tunnel deteriorates with increasing distance. While there could be many reasons for the discrepancy, one possibility may be that the variability in the dance behaviour is much larger than the errors associated with odometry, and swamps the latter. Indeed, detailed examination of our dance data reveals considerable variability, not only across bees, but also across dances of a given individual, as has been observed in classical studies of the waggle dance (von Frisch, 1993, pp. 70–74). Further investigation is needed, however, to test this hypothesis.

Our present study, as well as the others mentioned above, indicate that there are pathways in the honeybee visual system that are capable of measuring image speed rather independently of contrast and spatial texture. Most motion-detecting neurons that have been studied so far in the insect visual system

(Egelhaaf and Borst, 1993), and the well-known model of visual motion detection in insects – the autocorrelation model (Hassenstein and Reichardt, 1956) – do not exhibit this property. However, there are several neurophysiologically realistic ways in which robust measurement of image speed can be carried out, at least in principle (for a review of such models, see, for example, Srinivasan et al., 1999). A recent study has reported the existence of velocity-sensitive motion-detecting neurons in the honeybee (Ibbotson, 2001). More studies at the neurophysiological level are required to explore how image velocity is computed in a robust fashion.

The honeybees' odometer does not appear to be robust to variations in the height at which the bee flies above the ground (Esch and Burns, 1995, 1996), or to variations in the distances to vertical surfaces (Srinivasan et al., 1996, 1997; note also the data in the present paper investigating the effect of tunnel width). This is what causes the bees to signal an aberrantly large distance when they fly in our narrow experimental tunnels. Thus, outdoor flight at a low altitude, for example, would increase the magnitude of the optic flow that is experienced by the ventral field of view, and therefore generate a larger odometric signal, than flight at a high altitude. Indeed, studies of bees flying in outdoor environments indicate that the mean waggle duration in the dance is shorter when bees are forced to fly a given distance at a greater altitude (Esch and Brown, 1996). It would therefore be of interest to investigate whether bees foraging under natural conditions tend to fly at a more or less constant height, or to correct the odometric signal for height variations in some as yet unknown way.

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