

**Bush crickets**

Bush cricket wing morphologies were recorded (100% accuracy for *M. roeselii*; 98.25% for *C. discolor*, on the basis of detailed morphological measurements of a sample of 286 *C. discolor* specimens) in the field, from August to October 2000. The sexes did not differ in morphology frequencies. The year of the first record from each bush cricket population was obtained from refs 7–9 (also from J. Widgery, personal communication).

Received 18 January; accepted 6 March 2001.

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**Acknowledgements**

We thank D. Blakeley, H. Burton, C. Dytham, K. Ericson, P. Ewin, R. Fox, C. Gardener, S. Glencross, A. Goodhand, S. Hanna, I. Hanski, S. Hartley, J. Hill, C. Holloway, P. Hoskin, W. Kunin, R. Leaper, G. Jeffcoate, J. Lennon, J. Mellings, A. Moilanen, C. Parmesan, G. Parris, M. Rosenzweig, D. Sazer, J. Silvertown, M. Singer, D. Taneyhill, J. Thomas, J. Travis, J. Widgery, K. Wilson and I. Wynne for discussions, assistance and/or comments on the manuscript. Maps were produced in DMap. This work was funded by The UK Natural Environment Research Council, EU TMR FRAGLAND and English Nature. We also thank English Nature, the National Trust and other landowners for permission to carry out the research, and the amateur butterfly and Orthoptera recorders who recorded 10-km distributions.

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**Honeybee dances communicate distances measured by optic flow**

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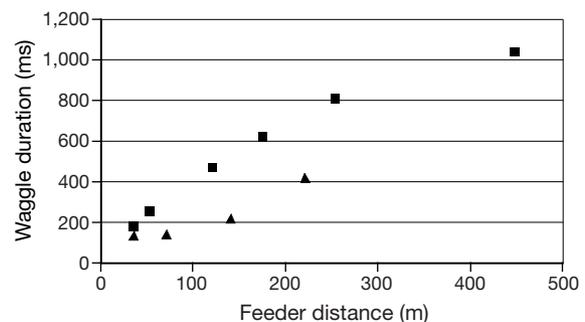
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In honeybees, employed foragers recruit unemployed hive mates to food sources by dances from which a human observer can read the distance and direction of the food source<sup>1</sup>. When foragers collect food in a short, narrow tunnel, they dance as if the food source were much farther away. Dancers gauge distance by retinal image flow on the way to their destination. Their visually driven odometer misreads distance because the close tunnel walls increase optic flow<sup>2</sup>. We examined how hive mates interpret these dances. Here we show that recruited bees search outside in the direction of the tunnel at exaggerated distances and not inside the tunnel where the foragers come from. Thus, dances must convey information about the direction of the food source and the total amount of image motion *en route* to the food source, but they do not convey information about absolute distances. We also found that perceived distances on various outdoor routes from the same hive could be considerably different. Navigational errors are avoided as recruits and dancers tend to fly in the same direction. Reported racial differences in honeybee dances<sup>1</sup> could have arisen merely from differences in the environments in which these bees flew.

We began by setting up an 8-m tunnel pointing southwards, with its entrance 3 m from the hive. A fresh set of ten marked bees was trained to forage from a feeder placed at the far end of the tunnel (feeder distance 11 m). The mean waggle duration of tunnel dancers was 358 ms (Table 1). We then determined which distance corresponds to a waggle duration of 358 ms in bees that fly outdoors, outside the tunnel, to a feeder in the southern direction. Ten marked foragers were trained to fly to a feeder positioned successively at various distances due south, up to a maximum of 450 m. Several hundred dances of marked individuals returning from the feeder were videotaped at each position. The calibration curve relating waggle duration to feeder distance is shown in Fig. 1 (details in Table 1). According to this calibration, tunnel bees that waggle for 358 ms indicate an outdoor feeder 72 m south of the hive.



**Figure 1** Distance calibration. Variation of waggle duration with feeder distance for an outdoor feeder positioned at various distances from the hive in the southern (squares) and northwestern direction (triangles).

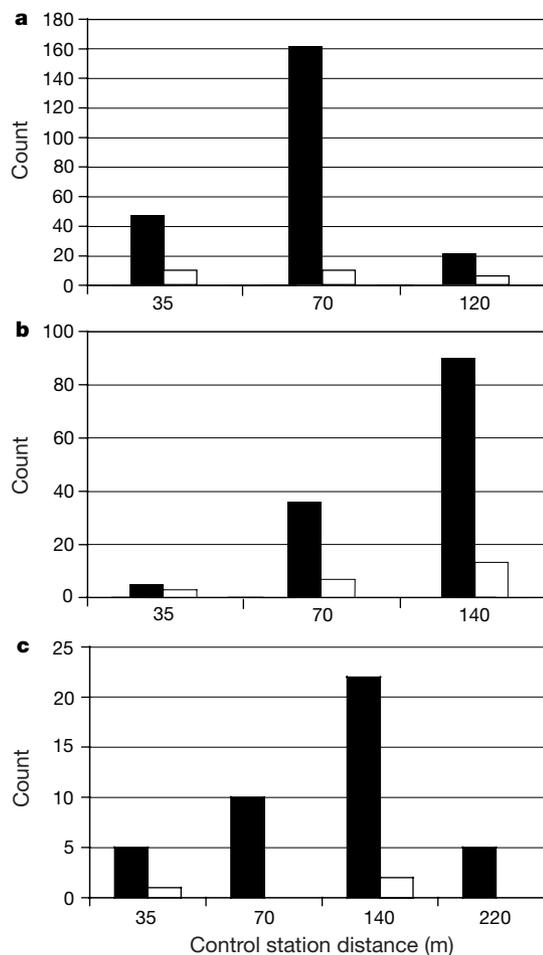
Next, we examined how recruits interpret tunnel dances. Control stations were set up at 35, 70 and 140 m in the southern direction along the axis of the tunnel. In the first 30 min of each experiment, tunnel bees were prevented from entering the tunnel by closing its entrance. No dances occurred, and no recruits were observed at control stations.

Tunnel bees began to dance when the tunnel was opened. Newcomers appeared near control sites about 10 min thereafter. Observers at each control station counted the number of individuals searching persistently within a radius of 1 m from the control feeder. Recruits searched for a short time and disappeared. Their arrivals were spread over the whole observation period. We did not use scent, and newcomers were not rewarded in any way (see Methods); thus they had no obvious reason to stay around. If they returned, their persistence showed that they must have had information about feeder distance. Bees that alighted on control station feeders were caught and put into alcohol. This ensured that a tunnel bee had recruited each visiting bee and not a forager that had found a control station previously. Control sites were monitored for 2 h 30 min. The search distribution is shown in Fig. 2a. Most recruits appeared at the 70-m site. No recruits were observed at the tunnel feeder. Recruits must have read tunnel bee dances and interpreted them to represent a distance of 70 m—much greater than the 11 m the tunnel bees had actually flown (3 m outdoors and 8 m in the tunnel). Seventy metres is very close to the distance a human observer reads from tunnel dances (72 m). Thus, it would seem that most recruits read the objective distance information given by dancing tunnel bees and responded accordingly.

We repeated the above series of experiments with a 6-m-long tunnel pointing in the northwestern direction. In this case, bees that returned from the tunnel showed a mean waggle duration of 270 ms (Table 1). This duration is predicted by the results of the southerly tunnel, in which an 8-m flight elicited a mean waggle duration of 358 ms. That is, the waggle duration is proportional to the distance flown in the tunnel. From the calibration curve for the southern direction (Fig. 1), a waggle duration of 270 ms translates to an outdoor flight of 52 m.

To check whether recruited bees searched at the predicted distance, control sites were set up in the northwestern direction, as in the southern experiment. When the tunnel was closed for 30 min, no recruits appeared at the control sites. The tunnel was then opened and the control sites were monitored for 2 h 50 min. Surprisingly, most of the recruits searched at 140 m (Fig. 2b). In a second experiment, an additional control site was set up at 220 m, and recruits were monitored for 1 h 30 min. Most of the recruits again searched near 140 m (Fig. 2c).

Why did the recruited bees search at twice the distance we expected from the distance calibration curve of Fig. 1? To explore this, we measured a new distance calibration curve for the northwestern direction. In this case, the waggle duration increased much more slowly with distance, compared with the south-directed



**Figure 2** Distribution of counts of searching bees recruited by tunnel bees. Searching bees, black bars; bees caught, white bars. **a**, Control stations at three different distances from the hive in the southern direction. The tunnel pointed due south. **b**, Control stations at three different distances from the hive in the northwestern direction. The tunnel pointed due northwest. **c**, As in **b**, but with an additional station at 220 m.

calibration curve (Fig. 1; details in Table 1). From this calibration curve we see that a waggle duration of 270 ms corresponds to an outdoor flight distance of 157 m. This is in good agreement with the preferred control-site distance of 140 m (see above). Thus, in this series of experiments, the recruits also read the dances of tunnel bees like a human observer and responded accurately.

We conclude from our study that tunnel bees communicate the optic flow they perceived on the way to the feeder. Other hive mates

**Table 1** Data for the duration of waggle runs

Experiment	Feeder distance (m)	Waggle duration (ms) (mean ± s.d.)	Number of bees analysed	Number of dances analysed	Number of waggle runs analysed
Calibration south	35	186 ± 75.3	3	23	214
	52	256 ± 73.3	6	30	434
	120	475 ± 123.4	17	89	992
	175	624 ± 111.4	13	43	418
	254	811 ± 116.8	4	10	142
	448	1,045 ± 127.1	3	4	127
Calibration northwest	35	143 ± 63.8	7	15	203
	70	152 ± 52.4	4	6	92
	140	229 ± 44	3	10	185
	220	424 ± 121.2	3	10	166
	Tunnel south	11	358 ± 104.4	5	11
Tunnel northwest	9	270 ± 81.5	19	62	828

s.d. is the standard deviation of waggle run duration determined for different individuals.

can take this information and fly to locations that are reached with a similar optic flow. The fact that calibration curves are different for flights in the southern and northwestern directions implies that the distance calibration of a bee's 'odometer' is not absolute; rather, it depends on flight altitude and the nature of the landscape through which the bee flies. This is to be expected from a visually driven odometer<sup>2,3</sup>. The flight path to control stations in the southern direction led up a slowly ascending hill. The 120-m control site was 10 m higher than the hive, and the 450-m control site was 30 m higher still. The route ran along a small paved road with some trees and wild flowers up to 1 m high on the left side of the road. Observers frequently saw the recruits approach along the paved road at an altitude of 1–2 m. In contrast, the trail in the northwestern direction led downhill over a meadow. The 140-m control site was 10 m lower than the hive. From 140 m on, the route ran along a fairly level paved road with high trees and bushes on both sides. Heran<sup>4</sup> already showed that bees indicate an uphill feeder as farther away than a downhill feeder. He attributed this difference to different energy requirements on the way to the feeder ('the energy hypothesis') and not to differences in optic flow<sup>3</sup>.

The navigational information that a scout bee provides to a potential recruit in her waggle dance is fairly simple. The dance conveys only the direction of flight and the total amount of image motion that is expected to occur on the way. There does not seem to be any information on the nature of the environment in which the recruit must move (if there were, the recruits in our experiments would have ended up in the tunnel). In nature, therefore, the accuracy of distance information gained from dances depends critically on the directional information received at the same time, for it is the direction of flight that determines the environment through which a recruit flies. Clearly, then, there must be a high selection pressure to ensure that a dance signals the direction of the food source as precisely as possible. As long as the recruit flies in the same direction as the dancer, she will translate the image motion signalled by the dancer into the correct flight distance and find the goal.

Considering the large differences in dance behaviour that we have observed in the same hive in this study, future experiments ought to explore whether the reported racial differences in honeybee waggle dances<sup>1</sup> arose merely from differences in the environments in which the bees flew. □

## Methods

Bees (*Apis mellifera ligustica*) were kept in a two-frame observation hive. All dances of returning foragers were recorded on videotape. Essential features of the tunnel setup were described elsewhere<sup>2</sup>, but some dimensions were different. The tunnel was 6 or 8 m long, 8 cm wide and 18 cm high. The walls and floor of the tunnel were covered with a texture composed of random black and white 1 cm<sup>2</sup> pixels printed on paper. The top of the tunnel was covered with black insect screen mesh, and a feeder was placed at the far end. The feeder provided 2 M sugar solution in a glass vessel 2 cm high and 5 cm in diameter, placed inverted on a grooved plastic plate, 7 cm in diameter, on top of a yellow star 10 cm in diameter, painted on a blue background. No scent was used at the feeder. Foragers in the tunnel could see the sky through the mesh. Bees could enter and leave the tunnel only through the near end, as the far end was closed off. The tunnel and observation hive were outdoors, in hilly, open farmland at the Giesberg farm of the University of Wuerzburg.

The dances of foragers returning from the tunnel were videotaped and analysed frame-by-frame. Recordings were made with a digital camera and replayed at 25 frames per s. Waggle duration was determined by counting the number of frames per waggle run.

Identical settings were arranged at all control stations. The same type of feeder as used in the tunnel was filled with water and placed on a small wooden table (15 cm<sup>2</sup>, 1 m above ground) on top of a yellow star painted on a blue background. A bright yellow camping chair next to the feeder made each control site conspicuous from a distance.

Received 23 February; accepted 3 April 2001.

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## Acknowledgements

This research was supported by grants from the Whitehall Foundation to H.E.E., from the Deutsche Forschungsgemeinschaft to J.T. and partly by grants from the Human Frontiers in Science Program, the US Defense Advanced Research Projects Agency and the Office of Naval Research to M.V.S. We thank C. Baum, A. Meikus, A.-K. Scheuerman and C. Sylvester for their help during experiments and data evaluation.

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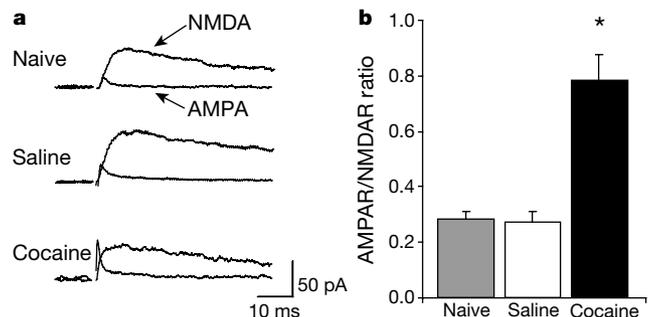
# Single cocaine exposure *in vivo* induces long-term potentiation in dopamine neurons

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How do drugs of abuse modify neural circuitry and thereby lead to addictive behaviour? As for many forms of experience-dependent plasticity, modifications in glutamatergic synaptic transmission have been suggested to be particularly important<sup>1–4</sup>. Evidence of such changes in response to *in vivo* administration of drugs of abuse is lacking, however. Here we show that a single *in vivo* exposure to cocaine induces long-term potentiation of AMPA ( $\alpha$ -amino-3-hydroxy-5-methyl-isoxazole propionic acid)-receptor-mediated currents at excitatory synapses onto dopamine cells in the ventral tegmental area. Potentiation is still observed 5 but not 10 days after cocaine exposure and is blocked when an NMDA (N-methyl-D-aspartate) receptor antagonist is administered with cocaine. Furthermore, long-term potentiation at these synapses is occluded and long-term depression is enhanced by *in vivo* cocaine exposure. These results show that a prominent form of synaptic plasticity can be elicited by a single *in vivo* exposure to cocaine and therefore may be involved in the early stages of the development of drug addiction.



**Figure 1** A single exposure to cocaine induced an increase in the AMPAR/NMDAR ratio of glutamatergic synaptic currents in VTA dopamine cells. **a**, Sample EPSCs in neurons from naive animals or animals pretreated with cocaine or saline. **b**, Peak AMPAR- and NMDAR-mediated EPSCs expressed as a ratio. Single cocaine injection ( $n = 6$ ) results in a significantly increased AMPAR/NMDAR ratio compared with saline-injected ( $n = 6$ ;  $P < 0.05$ ) or naive animals ( $n = 5$ ;  $P < 0.05$ ).