Fig. 2. Immunogold localization of the plasma membrane H^+-ATPase in statocytes of the root cap of Lepidium sativum L. a) Electron microscopic image of an LR White-embedded section incubated with both primary antibody (raised against the plasma membrane H^+-ATPase) and secondary antibody (goat anti-mouse IgG conjugated to 10-nm gold particles); cy cytoplasm, cw cell wall, v vacuole, × 7700. b) LR White-embedded section incubated only with secondary antibody. The section was processed identically to a) but incubation with primary antibody was replaced by PBS; am amyloplast, × 5700

tion shows that in vertically growing roots the current fluctuates between inward and outward direction at the root cap, and becomes a quite stable inward current at the meristem zone. This current pattern, with a current source at the root cap and a current sink at the meri- stem, reflects the sharp boundary in distribution of the plasma membrane H^+-ATPase reported here. The H^+-ATPase may be responsible for the outward current measured at the upper side of the gravistimulated root tip, too [1, 10]. It therefore seems most likely that the plasma membrane H^+-ATPase of the statocytes is involved in early steps of the graviresponse.

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How Honeybees Perceive the Information of the Dance Language

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Honeybees are able to inform their nestmates about the distance and direction of a profitable food source. Since the discovery of this amazing communication system by Karl von Frisch [1], the behavior of the „sender", i.e., the dancer, has been studied intensively. However, little attention has been paid to the behavior of the „receiver" – the follower bee – in this communication process. The honeybee is said to be the only creature other than man that communicates by a symbolic language. Bees of the species Apis mellifera have to decode the enciphered information about distance and direction to a food source in the darkness of the bee hive, hence, they cannot use any visual cues. The aim of the present study was to identify the sensory channels used by follower bees the perceive the dance. The informative part of the figure-eight path of the dance is the wag-tail run during which sound signals are produced [2]. Wagging movements of the dancer and airborne sound signals, both providing information about a location, have been proven to be essential for successful communication [2]. The dance sound is characterized by air-particle movement of high intensity in the acoustic near field of the dancer [3]. Bees are able to perceive sound, as it was shown

by conditioning experiments [4, 5]. Sensory organs suitable to detect this air-particle oscillation are either sensory hairs on the head, including eye bristles, or the Johnston organ, located in the pedicels of the antennae, which may detect vibrations of the antennal flagellum. On the other hand, the tail-wagging movements of the dancer may provide tactile signals, which could be perceived by mechanoreceptors on the tip of the antenna. Wagging also modulates the sound amplitude in the near field of a dancer.

Here, we report experiments which for the first time allow one to distinguish these possible channels of signal transmission in a natural situation by performing differential ablations of sense organs in individually marked follower bees. Groups of 40–60 forager bees were marked individually and trained to forage at an artificial feeder 200 m away from the hive. These bees were then captured in a wooden box and their feeder was removed. A second feeder was installed at a different site (500 m away, opposite direction) and a group of 4–10 foragers of the same hive was allowed to forage there. This newly established feeder provided the same food (2.0 M sucrose solution, unscented), but it was unknown to the bees which previously foraged at the first feeder.

After releasing the bees of feeder I, these unemployed forager bees were attracted by dancers advertising feeder II, because their own foraging site was shut down. They followed the dances, flew out, and searched for the indicated new feeding site.

For each experiment half of the group was manipulated. The other half remained unmanipulated as control group (CON). Three different manipulations were carried out: (1) Removal of all hairs on the head (CH); (2) amputation of one antenna (CA); (3) clipping the antennal tips, 2–4 segments, of both antennae (CT).

CT impairs the tactile interactions between the follower bee and the dancer, because most mechanoreceptors are located on the last segments of the antennal flagellum [6]. Sensory hairs on the head and the antennae are suitable candidates for near-field sound perception. Therefore, either removal of the hairs (CH) or removal of an antenna (CA) should prevent sound perception. It is not possible to remove both antennae

because the olfactory system is also located on the antennae and bees without antennae are no longer able to interact with their nestmates by antennalation. Experiments were conducted 1 day after manipulation. Only treated bees which did not show reduced foraging activity were used.

The experimental bees were motivated to find the new feeder and thus followed the dances. The recruitment rate for manipulated followers was compared to that for control bees. The results are shown in Fig. 1. Removing all hairs on
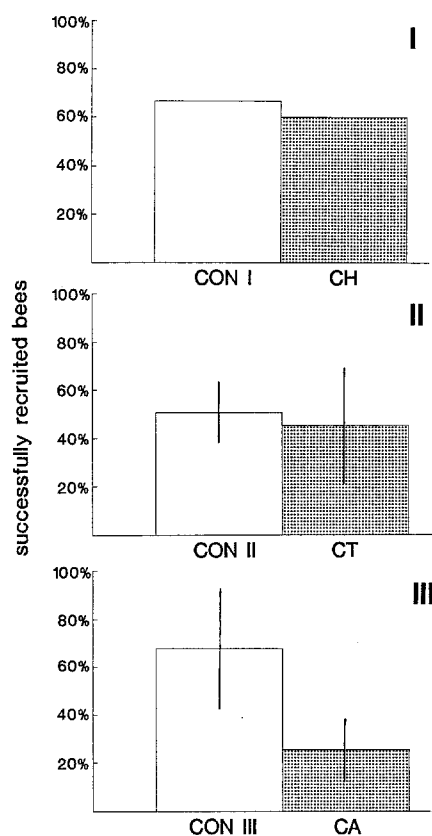

Fig. 1. The percentage of successfully recruited bees (mean ± SD) in three series of experiments testing the recruitment of follower bees which were manipulated in three different ways. Groups of individually marked follower bees (manipulated and control) were recruited to a feeding station 500 m away from the hive. I) Bees lacking all sensory hairs on the head (CH; $n = 20$) are recruited at the same rate as unmanipulated control bees (CON; $n = 24$); ($P = 0.5$). II) No difference is found between recruitment rates for bees lacking the distal 2–4 segments of both antennae (CT; $n = 113$) compared to the control group (CON; $n = 112$); (3 experiments, $P = 0.746$). III) Recruitment rate for bees lacking one antenna (CA; $n = 186$) is significantly lower than for control bees (CON; $n = 187$); (7 experiments, $P < 0.01$)

the head did not lead to any reduction in recruitment success ($\chi^2 = 0.21$; $P < 0.7$). Thus, sensory hairs on the head are apparently not involved in the detection of dance information. The same was true for bees lacking the tips of both antennae. They found the new place indicated by the dancer as well as the intact control bees (U-test: $Z = 0$, $P = 1$). However, bees with only one antenna were not able to understand the information given by the dancing bees. The number of recruited bees was significantly lower for amputated bees (CA) than for the control group (U-test: $Z = 2.366$, $P < 0.05$). No difference in the time from the beginning of dancing for feeder II to arrival of a marked bee at this feeder was found between CH, CT groups, and the respective control groups, but follower bees with only one antenna needed significantly more time to become successfully recruited than control bees (Table 1). The mean number of dancers in the first series of experiments (CH, CON I) was 5, in the second series (CT, CON II) 6.5, and in the third (CA, CON III) 10.6. This difference may have caused the differences between the absolute time spans of the particular experimental series.

The effect observed when one antenna was removed was not due to the inability to fly over a distance of 500 m: In control experiments such bees were manipulated at a 500-m distant feeder and tested for foraging activity. 96 % of the treated

Table 1. The time (mean ± SD) recruited bees need until they arrive at the new feeder. There is no difference between bees lacking all sensory hairs on the head (CH), bees lacking the tips of both antennae (CT), and the respective control group (CON I, CON II). Bees lacking one antenna (CA) need significantly longer than the control group (CON III) to understand the dance information; n indicates the sample size, P is the level of significance using the U-test

	Time [min]	n	P
CON I	115.5 ± 52.2	16	0.4
CH	131.5 ± 51.0	12	
CON II	143.8 ± 53.3	31	0.7
CT	148.5 ± 59.0	27	
CON III	80.5 ± 42.0	129	< 0.01
CA	104.6 ± 51.0	47	

bees immediately continued foraging at this feeder.

The effect was also not caused by a loss of motivation to search for new feeding sites: In order to investigate the stimulating effect of dances, control experiments were conducted during which the observation hive was turned in a horizontal position. As von Frisch [7] has shown, under such conditions dancers of *A. mellifera* continue dancing but cannot indicate directions in the darkness, because gravity as reference system is removed and the sun or the blue sky cannot be seen. Thus, the stimulating effect of dances could be tested independently of the site-specific information. In two experiments carried out, no difference between the recruitment rate in manipulated (CA) and control bees was found. A total of 8 out of 70 control bees and 3 out of 61 bees with one antenna arrived at the feeder ($\chi^2 = 1.796$, $P = 0.2$). Thus, the stimulating effect of the dances does not seem to be affected for bees with one antenna ablated, but under normal conditions in a vertical hive obviously the site-specific information given by the dance is not perceived by bees lacking one antenna.

We can conclude from these experiments that tactile interactions do not seem to be necessary for successful communication because bees lacking the antennal tips, where most of the mechanoreceptors are located, arrived at the feeder in the same number and time span as untreated bees. Sensory hairs on the head are also not used as a sensory channel for dance communication. However, our experiments show that both antennae are necessary for a follower bee to obtain the information from the waggle dance. One can assume that the distance information provided by sound duration can be perceived by manipulated as well as control bees. It has been speculated that the direction of the food source, which is indicated by the direction of the wagging run, can be calculated using both antennae from the sound signal emitted by the dancer during the wagging run [3]: A bee standing behind or next to a dancer places her antennae in the zone of intense particle movement. The near-field sound of a dancing bee shows a considerable change in intensity over short distances. Because of the widely spaced tips of the antennae, the follower bee may obtain two sufficiently different sound measurements from both antennae to calculate the direction of the wagging run. The results of the experiments presented here strongly support this view of the dance language as an auditory communication system. The antennae are used to perceive the near-field sound signals emitted by the dancers and a binaural mechanism seems to be used to decode the information regarding the direction of the food source.

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From the Toad to a Robot: Implementation of Neurobiological Principles of Object Discrimination in Neural Engineering

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In the domain of applied neurosciences two research lines begin to converge [1]: One, called neuroethology (a branch of neurobiology), investigates principles of brain functions that underlie human and animal behaviors [2]; the other, termed neural engineering (a branch of neuroin-formatics), takes advantage of neural functional principles and seeks to develop artificial neuronal networks suitable for the construction of so-called intelligent machines [3,4]. In an interdisciplinary task, under the general label „sorting objects", we have established an experimental platform in which a robot must grasp certain objects moving on a conveyor belt. The required image processing should be possible for a variable camera position relative to the moving belt. Hence, the perceptual task involves (a) detecting a moving object, (b) dimensioning it, subject to (c) invariance under the object's location and its direction of movement, and (d) classifying the object based on (b) and (c). At a first glance the task does not seem to be very difficult, if there were not the condition (c). To illustrate one of the problems: a bar oriented in the direction of the belt's movement must be recognized independent of which direction it traverses the camera's viewing field. This case must be distinguished from a bar oriented perpendicular to the direction it is transported. In machine vision, such detection problems can be managed