

# Lateralization of Olfaction in the Honeybee *Apis mellifera*

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## Summary

Lateralization of function is a well-known phenomenon in humans. The two hemispheres of the human brain are functionally specialized such that certain cognitive skills, such as language or musical ability, conspecific recognition, and even emotional responses, are mediated by one hemisphere more than the other [1, 2]. Studies over the past 30 years suggest that lateralization occurs in other vertebrate species as well [3–11]. In general, lateralization is observed in different sensory modalities in humans as well as vertebrates, and there are interesting parallels (reviewed in [12]). However, little is known about functional asymmetry in invertebrates [13, 14] and there is only one investigation in insects [15]. Here we show, for the first time, that the honeybee *Apis mellifera* displays a clear laterality in responding to learned odors. By training honeybees on two different versions of the well-known proboscis extension reflex (PER) paradigm [16, 17], we demonstrate that bees respond to odors better when they are trained through their right antenna. To our knowledge, this is the first demonstration of asymmetrical learning performance in an insect.

## Results and Discussion

In invertebrates, there are relatively few examples of behavioral asymmetry. There is one report of laterality in the visual system of *Octopus vulgaris* at the individual level [13]. Another report shows asymmetrical injuries

in the legs of fighting spiders and laterality in the frequency of probing touches with the legs [14]. One study of insects describes preferred rotation behavior in foraging bumblebees [15], but this behavior could be repetitive rather than lateralized. Thus, it is pertinent to explore whether and to what extent lateralization exists in insects. In particular, do asymmetries extend to tasks that involve learning?

We searched for asymmetries in olfactory learning performance in the honeybee *Apis mellifera* by using the well-known proboscis extension reflex (PER) paradigm [16, 17]. Bees were conditioned to extend their proboscis in anticipation of a food reward when they received a scent stimulus.

We explored two versions of the PER paradigm. In version 1, bees were conditioned to extend their proboscis to a scented drop of sugar water but not to an unscented drop of salt water. In version 2, bees were conditioned to extend their proboscis to one scent but not to another. In this version, which is known as differential olfactory conditioning [18], the positive scent was associated with sugar water and the negative scent with salt water (see [Experimental Procedures](#)).

Each version of the paradigm was carried out on three groups of bees. One group had their left antenna covered with a silicone compound, those in the second group had their right antenna covered ([Figure 1A](#); details in the [Experimental Procedures](#)), and those in the third group constituted a control in which both antennae were left uncovered ([Figure 1B](#)). Each group comprised at least 70 two-week-old bees.

The results of tests following training on version 1 of the paradigm are shown in [Figure 2](#). Here the bees had to extend their proboscis only when they experienced a scent. [Figure 2A](#) compared the learning performance of the three groups of bees when the training scent was lemon. Logistic-regression analysis showed no significant difference in performance between the left-antenna-covered bees and the untreated control group ( $p > 0.36$ ). On the other hand, the right-antenna-covered bees performed significantly worse than the left-antenna-covered bees ( $p < 0.0006$ ) and also significantly worse than the control bees ( $p < 0.0057$ ).

Similar results were obtained when version 1 of the paradigm was repeated with a fresh set of bees and a new scent, vanilla, as the positive stimulus ([Figure 2B](#)). Here again, there was no significant difference in learning performance between the left-antenna-covered bees and the controls ( $p > 0.96$ ), whereas the right-antenna-covered bees again performed significantly worse than the left-antenna-covered bees ( $p < 0.0024$ ) and the controls ( $p < 0.00013$ ).

We also ran a control version of the above experiment in which both antennae were covered with silicone. These control bees ( $n = 40$ ) showed 0% learning performance (i.e., no proboscis extension), indicating that the silicone sleeve was effective in preventing the scents from stimulating the antennae.

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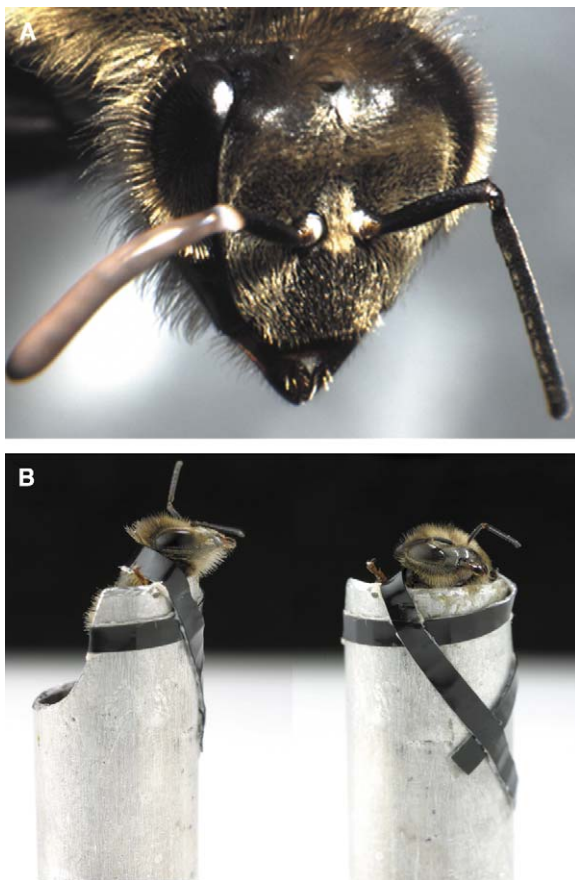


Figure 1. Experimental Setup

(A) Because there are no olfactory receptor cells at the base of the antennae, only the respective flagellum (upper part of the antenna) was covered with a silicone compound.

(B) Tethered bee (untreated control) used for the PER paradigm.

The above findings reveal that, in olfactory tasks, bees perform much better when they are trained with their right antenna than when they are trained with their left antenna. Furthermore, the performance of bees trained through the right antenna alone is just as good as that of bees trained with both antennae exposed. Because similar results were obtained with two different scents, these results were unlikely to be scent specific.

We extended the above findings by investigating the discrimination of two scents, using version 2 of the PER paradigm. Here, the bees were trained to extend their proboscis only to lemon, the rewarded scent, but not to vanilla, the punished scent. The results are shown in Figure 3. Logistic-regression analysis showed no significant difference in performance between the Left-antenna-covered bees and the untreated controls ( $p = 0.73$ ). On the other hand, the right-antenna-covered bees performed significantly worse than the left-antenna-covered bees ( $p < 0.0014$ ) and the control bees ( $p < 0.0038$ ).

Our results reveal, for the first time, that olfactory learning performance in honeybees is lateralized: Bees are significantly better at responding to odors when they are trained with their right antenna. In the majority of the test trials, right-antenna-covered bees performed significantly worse than those with the left antenna

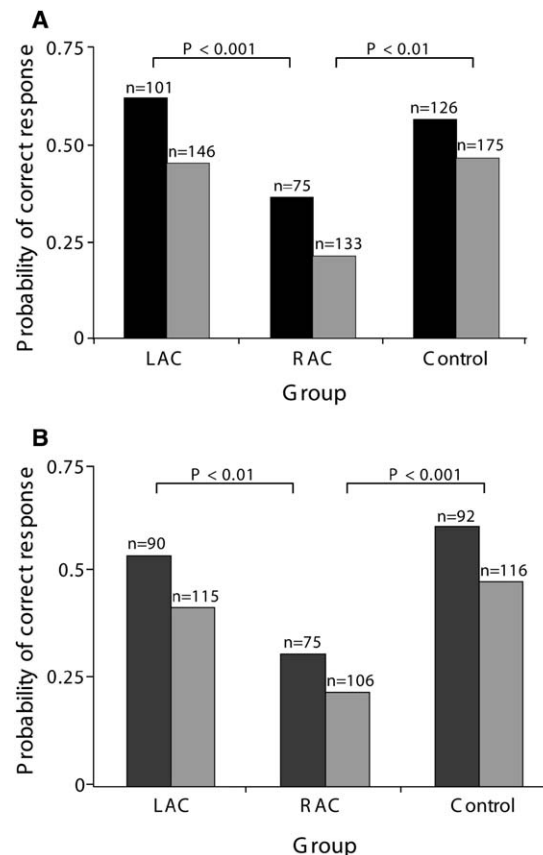


Figure 2. Version 1 of PER

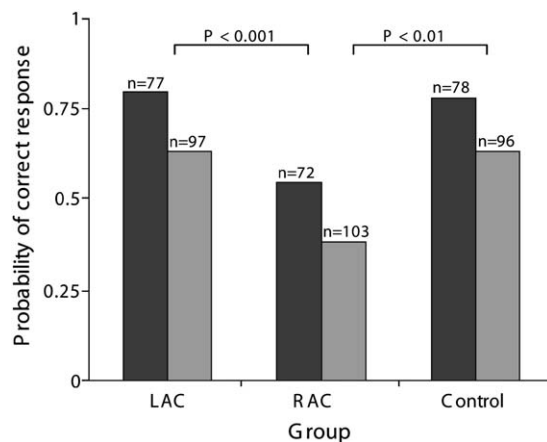
Performance of two-week-old honeybees in tests after training on version 1 of the PER paradigm. Bees were trained to learn one scent and to extend their proboscis to the scented stimulus only. LAC bees = left-antenna-covered bees, RAC bees = right-antenna-covered bees. Black bars show the probability of a correct response, if one discounts the D responses (no proboscis extension to either the positive or the negative stimulus, see Experimental Procedures). Gray bars show the probability of a correct response, taking the D responses into account.

(A) Performance during test after training with lemon scent. There was no significant difference between the LAC bees and the untreated control group. However, RAC bees performed significantly worse than the LAC bees and the untreated controls.

(B) Performance in tests after training with vanilla scent. Again, there was no significant difference between the LAC bees and the untreated controls, whereas the RAC bees performed significantly worse than the LAC bees and the control group. Significance levels shown in each case pertain to comparisons between black bars as well as comparisons between gray bars.

covered and control bees. Furthermore, honeybees trained with only the right antenna exposed performed just as well as the untreated controls. This implies that the right-antennal pathway is necessary and sufficient for learning odors.

An interesting incidental observation was that, of the three groups used, the right-antenna-covered bees showed the highest probability of producing response D, i.e., no response either to the rewarded stimulus or the punished stimulus (details in Experimental Procedures). In order to examine whether the type D response affected our conclusions, we conducted an additional analysis of the data including the D responses (light-gray bars in Figures 2 and 3; see the Experimental



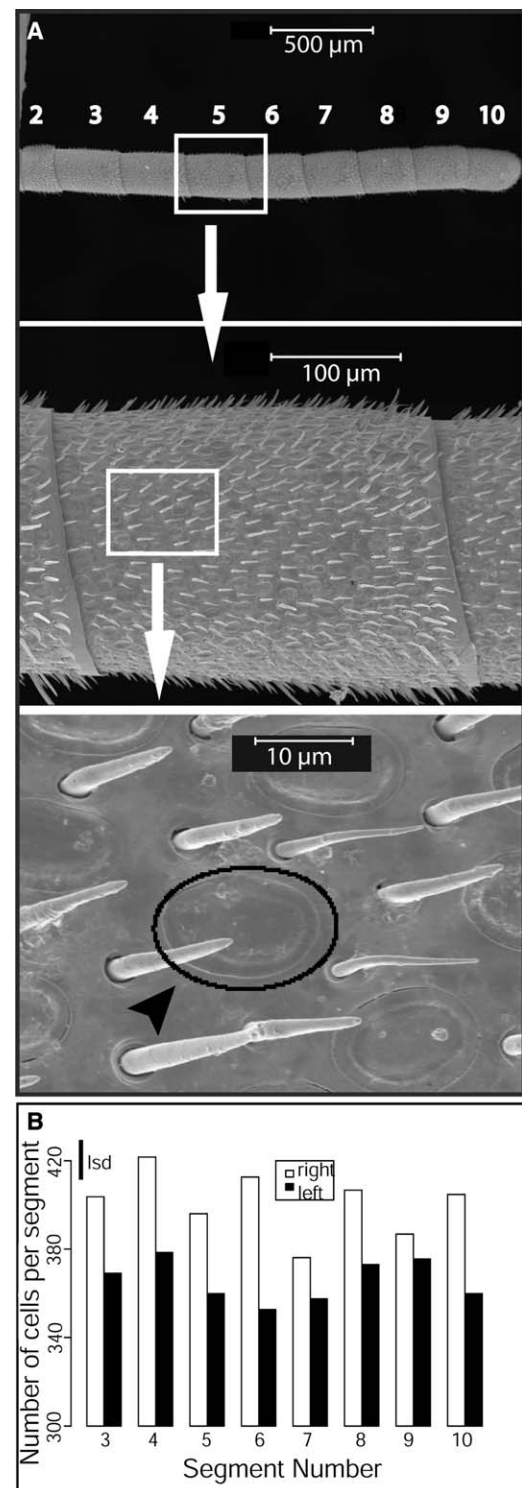
**Figure 3. Version 2 of PER**  
Performance of two-week-old honeybees in tests after training on version 2 of the PER paradigm. Bees were trained to learn two scents, lemon and vanilla, and to extend their proboscis only to the rewarded scent, lemon. There was no significant difference in performance between LAC bees and the untreated control group. However, RAC bees performed significantly worse than LAC bees and the controls. Notations are as in Figure 2.

Procedures for details). Logistic-regression analysis gave results similar to those obtained previously. Thus, the higher D response rate of the right-antenna-covered bees does not affect our conclusions in any way.

The overall learning performance in version 2 of the PER paradigm was on average about 20% higher than that in version 1. One reason for this could be that it is easier to learn to discriminate one scent from another than to distinguish between the presence and the absence of a scent. The differential olfactory conditioning paradigm is also more likely to teach the bees that the visual stimuli (such as the approach of the syringe) accompanying the scents are irrelevant to the discrimination task.

Why is learning performance significantly better when bees are trained with the right antenna? The basis for this could reside in differences between the left and right antennae, the left and right olfactory pathways, or the left and right halves of the central nervous system.

We have begun to explore this question by starting at the very periphery of the olfactory pathway and comparing the number of the olfactory receptor cells, *sensilla placodea*, in the two antennae. Earlier studies [19, 20] have counted such cells but have not looked for differences between the left and right antennae. We compared the numbers of olfactory cells in ten right antennae and ten left antennae from scanning electron micrographs. Seven of these left-right pairs originated from the same individuals. We compared the mean number of *sensilla placodea* per flagellum on the two sides. Our data, obtained with scanning electron microscopy (Figure 4A), revealed that the mean number of *sensilla placodea* is significantly higher in the right antenna (ANOVA,  $p < 0.001$ ). The mean number of olfactory receptors per segment was 401 in the right antenna, as opposed to 365.5 in the left antenna. Hence, on average, there were 35.5 more *sensilla placodea* per segment in the right antenna than in the left antenna (Figure 4B), with a standard error of 4.26. There was a significant



**Figure 4. *Sensilla placodea***  
(A) From above: Flagellum of the honeybee antenna, as imaged by a scanning electron microscope. The second panel shows a single segment. The third panel shows one olfactory sensillum in detail.  
(B) The bar plot compares the mean number of *sensilla placodea* per segment in the left and right antennae. White bars show right-antennal counts, and black bars show left-antennal counts. In all segments, the mean number of the olfactory cells is higher in the segments of the right antenna. This asymmetry is highly significant for all segments except segment 9. Isd = least significant difference.

interaction between side and segment; the difference in receptor counts between the left and right antennae was greater than average in segment 6 and lower than average in segment 9 (ANOVA,  $p < 0.04$ ). There was also a highly significant difference in sensilla counts between some of the individual segments within a given antenna; there were more cells than average in segment 4 and less than average in segment 7 (ANOVA,  $p < 0.002$ ). This was true for both antennae.

To ensure that there was no colony effect on the results, we analyzed antenna pairs of animals from three additional colonies. We analyzed at least two antenna pairs from each new colony. Again, there was a highly significant difference in receptor counts between left and right antennae in seven new pairs that we examined (ANOVA,  $p < 0.001$ ).

In order to explore whether the observed olfactory lateralization was solely due to differences in sensitivity between the left and right antennal pathways (and not due to any differences between the learning efficacies of these pathways), we analyzed data from LAC and RAC bees for the first training trial of each of the two PER versions described above (the responses of at least 100 individuals were analyzed in each case). At the first training trial, all bees were “naïve” with respect to the odor stimuli—no learning could have taken place as yet, so any lateralization of the response at this stage could only be ascribed to differences in sensitivity. For both PER versions, the probability of a correct response was much lower than in the trained bees (on average only 0.11), and in each case it was slightly greater when the right antenna was stimulated. However, the left-right differences at the first training trial were not statistically significant ( $p \geq 2.3$  in all cases, logistic regression).

These data lend support to the possibility that the observed lateralization derives partly from differences at the sensory level. However, although the observed lateralization is small and not statistically significant in the naïve bees, it is strong and highly significant in the same bees after they have been trained (see [Figures 2 and 3](#)). Thus, it is very likely that there are additional, inherent asymmetries in the learning processes per se at higher levels of the nervous system. Further work is required to disentangle the contributions of differential sensitivity and differential learning to the clearly lateralized responses that are finally exhibited by the trained bees.

Previous studies have shown that honeybees can be trained to produce side-specific responses [[21](#), [22](#)]. For example, they can learn to produce a positive response (proboscis extension) when one antenna is stimulated with a particular scent but to give a negative response (no proboscis extension) when the same scent stimulates the other antenna. Our study addresses a different question, related to lateralization of behavior. It shows that honeybees perform better at responding to odors, and at odor discrimination, when they are trained through the right antenna. A recent study in fruit flies [[23](#)] documented the existence of a single, asymmetrically positioned brain structure that appears to be important in the formation of long-term memory. That study does not demonstrate any functional asymmetry in behavior. Our study, on the other hand, reveals a left-right asymmetry in a *learned behavior*.

Although earlier studies in the honeybee have suggested that odors are coded symmetrically in the antennal lobes [[24](#)], it is important to examine the responses of the primary olfactory neuropil in greater detail. For example, it was recently reported that, in bees that were conditioned via side-specific training paradigms, the patterns of physiological response in the antennal lobes were symmetrical at a macroscopic level but showed local differences between the activations of corresponding glomeruli on the two sides [[25](#)]. Thus, it would be of interest to compare volume, cell numbers, and neuronal architecture in corresponding glomeruli on either side of the brain of naïve bees and bees that have undergone training procedures as in our study. It would be equally important to examine higher brain centers, such as the mushroom bodies, for anatomical and physiological asymmetries. The present results also raise the intriguing possibility of lateralization in the honeybee's other sensory modalities, such as vision.

Our findings parallel the recent observation that chicks learn odors better with their right nostril [[26](#), [27](#)]. This raises the question as to whether lateralization is determined by homologous genes in insects and vertebrates [[28](#)]. Alternatively, has there been an analogous evolutionary development of lateralized function in the two taxa? Either scenario would underscore the importance of lateralization for vertebrates as well as invertebrates.

It has recently been shown that, in the domestic chick, lateralized brain function enhances the ability to perform two simultaneous tasks, namely, seeking food and being vigilant for predators [[29](#)]. Another study has demonstrated that lateralized fish are better at using featural cues to reorient themselves than non-lateralized fish; i.e., lateralization confers advantages in spatial reorientation [[30](#)]. The evolutionary significance of lateralization in olfactory learning remains to be explored.

## Experimental Procedures

Freshly emerged bees were marked individually and returned to the beehive. After two weeks they were collected from the hive for experimentation.

### I. PER

For each experiment, individually marked two-week-old honeybees were collected from bee hives (in all three different colonies) and briefly immobilized on ice. Each animal was secured in a metal tube ([Figure 1B](#)), via thin strips of GAFFA tape so that the legs were immobilized but the head was free. This ensured that the silicone sleeve that was used to cover the antennae (see below) was not disturbed. Each restrained bee was then placed under a binocular microscope, and one of the two antennae was coated ([Figure 1A](#)) with a two-component silicone compound (Exaflex, GC America Inc.). The animals were fed with two to three drops of 1 M sugar solution and then allowed to recover overnight in an incubator at a constant temperature of 26°C. The next morning, the bees were trained. Animals that had managed to remove their cover or looked sluggish before the training were excluded from the experiment.

#### (1a) Paradigm Version 1

Two different stimuli were used in this version. One stimulus was a scent dissolved in a 1 M sugar solution (reward). The other stimulus was unscented saturated salt solution (punishment). The scents were in the form of commercially available flavoring agents for food (Queens essence). Ten microliters of the essence was dissolved in 3 ml of the sugar solution. The stimuli were presented as drops emerging from a size 23 syringe needle. A suction fan ([Figure 1B](#)) behind the bees ensured a constant flow of odor during stimulus presentation and quick removal of any lingering odor traces

before the next bee was trained. During each of the three learning trials, we first presented the positive stimulus for 5 s by holding the scented drop 1–2 cm in front of the bee. The antennae were then briefly touched with the stimulus drop, thus associating the scent with the sugar reward. If the bee extended her proboscis, she received a food reward in the form of the sugar solution. Next, the same procedure was performed with the negative stimulus, which was an unscented drop of salt water. Touching the antennae at the end of this 5 s period was intended to cause the unscented drop to be associated with the unpleasant-tasting salt solution. Bees extending their proboscis after touching the antennae received a punishment in the form of the salt solution. The three successive training trials were separated by 6 min.

#### (1b) Paradigm Version 2

Here, the bees were trained to discriminate between two different scents, lemon and vanilla. Lemon was combined with the positive reward (sugar solution), and vanilla was combined with the punishment (salt solution). The training procedure was identical to that described for version 1. In each version, after training, the honeybees were fed 2–3 drops of sugar solution and returned to the incubator for overnight storage.

#### (2) Testing

Tests were carried out on the morning after the training was performed. In each paradigm, the order in which the stimuli were presented during the test was reversed with respect to that used in the training. That is, during the tests, the negative stimulus was offered first. In all other respects, the tests for the two paradigms were performed in the same way. We presented each stimulus for 5 s by holding the drop at a distance of 1–2 cm in front of the bee, without touching the antennae at the end of the trial. Each bee was tested only once.

#### (3) Scoring of Responses

Performance was measured as the probability of a correct response (i.e., as the percentage of bees that produced a correct response).

There were four possible categories of response: response A, extension of proboscis to the rewarded stimulus only; response B, extension of proboscis to both stimuli; Response C, extension of proboscis to the punished stimulus only; and Response D, no extension of proboscis to either stimulus. Response A was regarded as being fully correct, and response C was regarded as being fully wrong (and occurred very rarely). Responses B and D were each regarded as being partially correct. The probability of a correct response was calculated as the ratio of the number of fully correct responses to the sum of all responses. In one analysis, bees that gave response D were not included in the sum because we could not be sure whether such bees were able to extend their proboscis at all. Here, the probability of a correct response was calculated as  $n_A/(n_A + n_B + n_C)$ , where  $n$  refers to the number of responses in the respective categories. A second analysis took the D responses into account, in order to examine whether their inclusion affected the results of the first analysis in any way. In this case, the probability of a correct response was calculated as  $n_A/(n_A + n_B + n_C + n_D)$ .

## II. Anatomy

### (1) Preparation of Antenna Samples for Scanning Electron Microscopy

We sacrificed two-week-old bees by placing them in a freezer (–18°C) for at least 4 hr. After the bees defrosted at room temperature for another 4 hr, the left and right antennae of a given animal were cut at the very base with a razor blade, and the basal segment of the antennae was glued to a cardboard platform (width = 2 mm, length = 5 mm). This way, the flagellum of the antenna could be scanned and viewed from different directions by rotation in the sample chamber of the scanning electron microscope (Cambridge 360). The platform with the antenna on it was fixed on a needle, and the latter was placed a sample box. The samples were air-dried at room temperature for a week and then coated with a thin layer of gold on all sides.

### (2) Scanning

The sample was fixed on a holder in the sample chamber, which was rotated from outside.

Because there are no olfactory receptors on the first two segments of the honeybee flagellum, only segments 3–10 were scanned. The segments were scanned horizontally one at a time.

Each segment was subjected to three horizontal scans that overlapped with each other to facilitate subsequent orientation, which we achieved by matching landmarks in subsequent scans. This procedure was used to scan each segment and count the receptors that it carried.

### (3) Counting

The three scans per segment were used in the order in which they were scanned. We counted the *sensilla placodea* in each of the three scans by using the lasso tool in Adobe Photoshop 5.5 to mark each sensilla, and prevent duplication of counts. The working path was saved after counting every 20 olfactory sensilla. Because the scans overlapped, they shared a few identifiable landmarks such as dust particles or conspicuous cells, and this facilitated orientation in the subsequent scan.

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