Addition and subtraction by honeybees

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Summary

Howard, Avargues-Weber, Garcia, Greentree, and Dyer (*Science Advances*, 5, 1–6, 2019) report experiments in which honeybees initially shown a number of shapes could subsequently choose a pattern that added or subtracted one from that number. Further, the operations of addition and subtraction were cued by the colors of the shapes.

Keywords Honeybees · Numerical cognition

Some years ago, it was shown that honeybees could “count” a sequence of landmarks (Dacke & Srinivasan, 2008). While flying down a tunnel, bees encountered successive landmarks and found food at the third landmark. After learning to visit the third landmark, tests were carried out in which the spacing of the landmarks was varied and in which novel landmarks were used. Honeybees still showed a preference for visiting the third landmark. Shortly after this finding, Gross et al. (2009) trained honeybees to match-to-sample using numerical patterns. After seeing a sample pattern containing two or three elements, bees learned to accurately choose a comparison pattern that contained the same number of elements as the sample. Bees continued to match accurately when tested with novel patterns and elements. Thus, honeybees could use number as a cue for correct choice when numbers of stimuli were encountered both sequentially and simultaneously. Performance was not perfect, however, as bees made numerous errors in both of these paradigms.

These earlier findings suggested a form of proto-counting in bees, similar to that found in a number of studies with vertebrates. Two recent articles now yield evidence for even more abstract numerical cognition in honeybees. Howard, Avargues-Weber, Garcia, Greentree, and Dyer (2018) reported experiments suggesting that bees comprehend the meaning of zero. To teach honeybees the concept of “less than,” bees were required to choose between patterns that presented different

numbers of elements (circles, squares, diamonds, or triangles) varying from two to five, with choice of the lower number pattern always rewarded with sucrose. After learning a significant preference for the lower number, bees were presented with a choice between a pattern containing one element and a pattern containing no elements (zero). Although one might expect bees to be confused and choose indifferently, they showed a significant preference for zero, and this preference for zero increased as the alternative number rose from one to six. Apparently, bees understood that the absence of stimuli was less than the presence of stimuli (a concept of zero). On all of these tests, bees made the correct choice significantly above chance.

Perhaps more surprising is the target article from the same laboratory. Howard et al. (2019) report that honeybees can add and subtract. A variant of the matching-to-sample procedure was used. Bees initially were given addition and subtraction training. In addition training, a bee viewed a sample pattern containing one, two, or four blue elements at the entrance to a Y-maze. After entering the Y-maze, a bee could choose between two patterns, one that contained one more element than the sample pattern (+1 addition) and one that contained a different number. Choice of the +1 pattern yielded a sucrose reward, but choice of the alternative yielded punishing quinine. In subtraction training, a bee viewed a sample pattern containing two, four, or five yellow elements. Within the Y-maze, it then chose between a rewarded pattern that contained one less element than the sample (−1 subtraction) or a punished pattern that contained a different number. Importantly, the color of the elements cued the bee to add one (blue) or to subtract one (yellow). Honeybees learned to choose +1 or −1 patterns to a level of 80% accuracy over 100

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trials. Notice that a sample pattern containing three elements was not used in training. Bees were now tested with the novel sample patterns of three blue elements or three yellow elements. On half the trials presenting three blue sample elements, bees chose between patterns containing four elements (correct) or five elements (incorrect). On the other half of the blue sample trials, bees chose between four (correct) and two (incorrect) elements. On half the trials presenting three yellow sample elements, bees chose between two (correct) and one (incorrect) elements. On the other half of the yellow sample trials, bees chose between two (correct) and four (incorrect) elements. On both of the addition tests and both of the subtraction tests, bees chose the correct pattern significantly above the chance value of 50% (scores varied between 63% and 72%).

Applying Morgan's Canon, one may seek to find a simpler (associative) account of these findings other than bees learning to add and subtract. Could bees have learned a conditional discrimination, such as choose the pattern with a larger number of elements after seeing blue and the pattern with a smaller number of elements after seeing yellow? If this were the case, bees should have chosen five elements instead of four elements after seeing the three-blue-elements sample and should have chosen one element instead of two elements after seeing the three-yellow-elements sample. In both cases, bees accurately chose the +1 or −1 alternative. Could bees have learned to go just to those patterns that were rewarded? No, because test trials were non-reinforced, with choice of either pattern yielding only a drop of water. This latter procedure also rules out the possibility that bees were using odor cues. This well-controlled study then leads us to the conclusion that honeybees indeed can learn to apply addition and subtraction rules.

The theoretical question then becomes how a relatively small-brained insect can perform the operations of addition and subtraction. Theories of nonverbal counting have

suggested that number might be represented by a magnitude, such as the number of pulses in an accumulator or the position of a pointer on an internal number line. A neuronal model suggests that numbers of objects activate different numbers neurons (Nieder, 2016). To explain bees' ability to add and subtract one element, these models would require some mechanism by which the colors blue or yellow add or subtract pulses in the accumulator, move the pointer forward or backward on a number line, or activate a lower order or higher order number neuron.

Interesting questions for future research are whether honeybees can perform addition and subtraction on numbers greater than one to four. Can they learn to add and subtract numbers greater than one? Finally, what neural structures in the bee brain allow it to count, to make greater than and less than judgments, to understand that zero is less than one, and to perform the operations of addition and subtraction?

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