Temporal dynamics in appetitive matching experiments with honeybees

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Optimal decision theory has been used in the past to evaluate the choice behavior of foraging bees. This attempt was only partially successful, not only because too little is known about the actual energy expenditure during the foraging flights, but also because learning and memory processes were not considered. We have studied the choice behavior of single test bees collecting sucrose solution (33 %) from 4 computer controlled electronic flower dummies with the emphasis to understand how the two processes, energy collection and information collection, interact through memory processes to control decision making during foraging bouts. In a typical experimental condition the flowers differ in the rate with which they provide sucrose solution, e.g. N^0 1: .0625 µl/min, N^0 2: .125 µl/min N^0 4: .25 µl/min, N^0 8: .5 µl/min (the numbers 1, 2, 4 and 8 stand for the proportions of the rates of sucrose flow). Since the bee can imbibe up to 1 µl/sec the bee flies from flower to flower for about 20 – 30 min until it has filled its crop and returns to the hive. The computer reads in real-time the landing on each flower, the handling time, the sucking time, the amount of sucrose solution taken up (precision .02 µl), the post-sucking handling time and the flight time between landings (Greggers U, 1989. In: Erber J, Menzel R, Pflüger HJ, Todt D (eds) Neural mechanisms of behavior, Thieme Verlag, New York, 219).

The bee tends to match its choice behavior to the reward rate of the flowers which leads to a higher frequency of choice of 8 over 4 over 2 and 1. Overall the low reward flowers (N^0 1 and 2) are chosen more frequently than one would expect for perfect matching, and the high reward flower (N^0 8) less than expected. This leads to a lower amount of reward per visit for N^0 1 and 2, and a higher amount per visit for N^0 8. An analysis of the realtime protocols reveals that matching is better for return flights (R, the bee returns to the same flower) than for all alternating flights (A, the bee changes to one of three other flowers). A-flights from low reward flowers (N^0 1 and 2) are matching better than flights from high reward flowers (N^0 4 and 8). Choices performed at shorter intervals (< 4 sec, depending on average flow rate in the whole patch) are predominated by R-flights, those at longer intervals by A-flights. Most importantly, the different time dependencies of R- and A- flights reveal that different kinds of memories are used to control the choice behavior of bees foraging in a patch. A model is presented which explains the results on the basis of two mechanisms: (1) The informational capacity for updating the memory is proportional to the difference between the expected and the experienced amount of reward (difference rule, Rescorla and Wagner 1972. In: Black AH, Prokasy WF (eds) Classical conditioning, Appleton, New York, 64). (2) The retrieval of the expected amount of reward activates two forms of memory, a short-lasting working memory, which dominates the choices at short intervals (< 4 sec) and depends strongly on the amount of actual reward (amounts exceeding the average of the whole patch), and a long-term reference memory, which controls the choice behavior at longer time intervals. The difference rule applies to both memories. The model predicts certain deviations from perfect matching, e.g. a higher choice of flower N^0 4 and 1, and a lower choice of flower N^0 8 and 2 than one would expect from the matching rule. These deviations are actually found in the results if one evaluates choices predominated by the long-term reference memory. The deviations from the matching rule and other peculiarities appear as a consequence of a limited memory and an optimization process which takes into account net energy profit and informational gain.