

Spatial association memory

Gayle Brown, James Thompson, and Christianne Wilhelmsen investigated another aspect of spatial memory, the ability of hummingbirds to learn to “connect” useful information available in different spatial locations using geometric relationships between them. Basically, they asked whether hummingbirds could use signal lights that reliably indicated whether feeders would provide food at any moment, if the lights and the feeders were situated apart from each other. How far apart could they be, and what other factors would determine how useful the lights would be?

The experimental design was to place 6 or 8 feeders in a horizontal row on a wall and a horizontal row of red LED lights varying distances either above them or diagonally up and to one side. The experiment was completely controlled by a computer. Just before each trial, the computer turned on one of the lights to indicate which feeder would provide food on that trial if the bird probed it (each feeder was fitted with a tiny photocell that detected probing). As soon as the bird left its perch, the light went out. If the bird probed any feeder but the “good” one that trial, the computer recorded the visit but the feeder provided no food. But a probe at the good feeder would result in a tiny squirt of nectar being deposited immediately (within the first lick). On the next trial 2 or 3 minutes later, a different, randomly-selected combination of feeder and light were “good”, over and over again like this for most of a day.

Hummingbirds learned so quickly to use the lights that we didn’t have to train them at all, even to the time-based experimental protocol. We just put them in the room, turned on the computer, and within a few minutes they were churning out data. Because we knew hummingbirds investigate brightly coloured objects and find ways to probe them, it was no surprise that they learned to use the lights when they were near the feeders. But they learned even if the lights were separated from the feeders by several body lengths, and even if the row of lights was displaced diagonally upward from the row of feeders to make a parallelogram. Performance did deteriorate with distance, and it was more difficult with more complex geometries, but the remarkable thing was that it was so much higher than without the lights regardless of where we put the lights.

Deterioration of performance with distance and geometric complexity allowed the experimenters to probe the phenomenon more deeply by exploring ways to make difficult arrangements easier for the birds. For example, performance improved again if the experiment included things like strips of coloured tape to act as “guides” from the lights to the feeders (like the honey guides bees follow in flowers). Those guides helped even if they were not straight but wavy, and even if they were discontinuous, like dotted or dashed lines.

All of those experiments into spatial association memory reinforced the idea from the spatial memory work that a big part of what hummingbirds learn about their environments is their geometric structure. They remember that structure in relation to the distribution of profitability, and use that knowledge strategically in foraging to increase the rates at which they are able to gain fat for migration and even to survive in a wild, competitive world that will have them for lunch if they don’t keep their wits about them.

Gayle’s hummingbirds learned spatial association memory tasks so well and so quickly that was able to show that they were better and faster than rats, mice, pigeons, and even

primates in similar experiments. The only possibilities we could think of to account for this striking difference were that either hummingbirds really are better than other species at this kind of task, or that something about the hummingbird experimental design could explain their much higher performance. Somehow, we doubted that hummingbirds were better than monkeys.

No one has addressed this aspect of the problem, but several aspects of our experimental design deserve mention here. Foremost in our thinking about this issue is that for many reasons we designed the laboratory foraging experiments to be as similar as possible to natural foraging situations, and in as many ways as possible. Our argument about this was simple; even simple-minded: if we wanted our birds to show us the best they could do, performing in our experiments should “feel” to them like performing in nature, where they evolved to perform just such tasks.

- The feeders were numerous and provided only small amounts of food at a time, if anything at all, then renewed themselves, predictably, on a realistic time scale.
- As in nature, the feeders were stationary and visually conspicuous. Hummingbirds have evolved to forage using this information, and their flowers have evolved just those characteristics. We say that the hummingbird-flower system has coevolved in a mutually beneficial, positively synergistic way that revolves around those flower qualities. Unlike rats and mice, hummingbirds forage in the daytime and use mainly visual cues, and we designed accordingly. It would be much more difficult to design naturalistic situations for rodents, who are primarily nocturnal and navigate largely by olfaction.
- As in nature, the hummingbirds had to expend significant amounts of energy to harvest energy, because of their high cost of flight. Their actions bore consequences that they could sense in the same ways they would sense them in nature: volume of food ingested per foraging bout, body weight trajectory during the day, etc. To give some idea of the magnitude of this difference, our hummingbirds had to fly about 25 body lengths just to and from the array of feeders, and fly as far as 5 body lengths to move from feeder to feeder while foraging. In contrast, the monkeys in some of the spatial association memory experiments could play the entire game by moving nothing more than an arm. When considered in relation to the entire energy budget of the individuals, these cost differences are enormous.
- We imposed so-called “closed economies” in most hummingbird experiments, so the birds actually made their living by foraging in them. Only if they performed well could they gain fat at a normal rate during the day and maintain their body weight from day to day. If they did poorly in the experiments, they also did poorly physiologically. This motivated them to attend to the tasks and do as well as possible. This was in stark contrast in the standard open economies of most psychological experiments, where it did not cost animals much to perform poorly. Whereas most experiments are like a game for the subjects, ours were more like the real world.
- The timing of trials in experiments also closely mimicked natural hummingbird foraging cycles. Consequently, we could expect the details of digestion, metabolism, fat production, and hunger over the experimental foraging cycle to

unfold in a relatively normal way. Thus, any cognitive processes that were coupled to those physiological variables should also function relatively normally. In designing this aspect, we did not consider it necessary to know much if anything about any of those details to make the timing as natural as we could.

At least as profound as the realization that learning and memory are as deeply engineered into hummingbird biology as feathers, flight, and foraging from flowers was that our work was helping to change notions about how other kinds of animals make their own way in the world. As our work was completed and appeared in the literature, others referred to it in designing and interpreting their own work, and each of us in the research group felt a part of a world-wide effort to understand the economy of nature.