Worm holes and avian space – time

Kathryn Jeffery and John O'Keefe

Can animals remember where and when events happened? A study of birds that hoard and then retrieve their food shows that they can, and may ultimately provide clues about how human memories are formed.

How do animal memories resemble human memories? This is an important question, because commonalities of memory in species whose evolution diverged aeons ago may point to the fundamental mechanisms of information storage in the brain. Birds, for example, are a class of vertebrates whose last shared ancestor with humans lived about 250 million years ago. Now, on page 272 of this issue, Clayton and Dickinson[1] show that one species of bird can, like humans, remember not only what happened, and where, but also *when* it happened. Unravelling the neural substrate of this memory for time in birds will therefore not only illuminate studies of animal behaviour, but also help to solve a problem in the field of human memory — where and how is memory for events (episodic memory) formed and stored?

The 'what' and 'where' of memory in birds has already been explored in an elegant series of ecologically motivated experiments. These studies capitalized on the ability of some species of bird to hoard food in many locations, in separate caches, to see them through the winter. Food-storing birds such as parids (titmice and chickadees) and corvids (jays, nutcrackers and magpies) readily do this in the laboratory, so the birds can be watched under controlled conditions to find out what information they use to retrieve their food caches.

A typical experiment involves allowing the birds to hoard food — either freely, or within experimentally designated sites in an enclosure — and then manipulating the caches before the birds go back to find them, to work out how the birds know where the food is hidden. Such research has revealed that the birds do not use sensory characteristics of the caches, such as their appearance or smell, but remember instead their spatial locations[2]. This requires a phenomenal memory capacity, and some birds can remember the whereabouts of more than a thousand caches. The neural substrate of this spatial memory is a region of the dorsomedial bird brain that shares embryological and anatomical features with the mammalian hippocampus — a structure that has long been implicated in spatial memory in mammals[3].

As well as remembering where they have stored food, birds can remember what they have stored. For example, black-capped chickadees recover their favourite food first and their least favourite food last[4]. Scrub jays that are fed to satiety on one type of food will retrieve an alternative type first[5]. Clayton and Dickinson[1] have now used the 'what' and 'where' abilities of these birds in an ingenious attempt to find out whether they can also remember when they stored the food.

Using the fact that birds retrieve their favourite food first, Clayton and Dickinson introduced time into the equation by allowing scrub jays (*Aphelocoma coerulescens*) to cache wax worms (Fig. 1). These are a favourite of the birds when fresh, but, in time, they perish and become unpalatable. So, wax worms are the birds' preferred food if retrieved soon after caching, but least preferred if they are retrieved some time after. If the birds can remember when they cached the worms, then they should retrieve them first if they were stored recently and last if they were stored some time ago.

This is exactly what happened. Birds given a choice between retrieving worms or retrieving peanuts chose the worms only if they had been recently cached (four hours earlier), and the peanuts if the worms had been cached a long time ago (five days earlier). Only birds that had previously learned that the worms degraded over time avoided the old caches, showing that this behaviour is not hard-wired. Moreover, Clayton and Dickinson also ruled out the possibility that the birds were using smell to identify the rotten worms.

In a second experiment, the value of old worm caches was degraded in a different way — by being pilfered (removed) by the researchers after five days, but not after four hours. Again, the birds showed a strong tendency to prefer the less tasty but more reliable peanut caches if the worms had been stored a long time ago. Thus, the birds could clearly remember not only what they had stored in which cache, but also whether or not it was stored recently.

How is the 'what', 'where' and 'when' of the food caches stored in the birds' brains? One possibility is that, at the time of caching, the birds form an internal map of the cache locations. Each location is 'labelled' with the contents and approximate time of storage, as well as other information (such as likelihood of the cache being pilfered). This would allow a bird to use the most efficient retrieval strategy to maximize its chances of survival during the winter (for example, by visiting the perishable caches early on, or by varying the types of food retrieved to obtain a range of nutrients). The labels attached to each cache location might be allocated to different regions of the brain, depending on the type of information — the contents of the cache in one region, the time of storage in a separate area that is specialized for temporal representation, and so on.

The experimental model used by Clayton and Dickinson provides a powerful tool for investigating these phenomena further. For example, can the birds remember the order in which different caches were formed, or merely whether each was made recently or some time ago? How fine-grained is the representation (for example, can the birds discriminate five days ago from three days ago)? What brain regions are used to store these different types of information? ▶

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Figure 1 **Memorable meal — scrub jay (*Aphelocoma coerulescens*) hiding food in the laboratory.**

100 YEARS AGO

Our present knowledge of the theory of errors receives an interesting addition at the hands of M. Charles Lagrange in the form of a contribution to the *Bulletin de l'Académie royale de Belgique* (vol. xxxv. part 6). Without going into details of a purely mathematical nature, certain of M. Lagrange's conclusions appear to be sufficiently important to be worth noticing. In taking the arithmetic mean of a number of observations as the most probable value of the observed quantity, common sense suggests that any observations differing very widely from the rest should be left out of count as being purely accidental, and thus likely to vitiate the result. But as it is impossible to draw the line from theoretical considerations between values retained and values omitted, any such omission would necessarily be unjustifiable. This discrepancy between theory and common sense is, to a large extent, reconciled by M. Lagrange's "theory of recurring means." According to this theory, the *weight* to be assigned to any observation is inversely proportional to the square of the error of the observed value relative to the most probable value. … The weighted mean is then taken as a second approximation to the most probable value. This mean determines a fresh series of weights to be assigned to the observations by which a new weighted mean … is found, and so on … These successive means are called by M. Lagrange "recurring means," and by their use the effects of sporadic errors are, to all practical purposes, eliminated, since the weight assigned to the corresponding observations soon becomes relatively small.

From *Nature* 15 September 1898.

50 YEARS AGO

In the possession of the Science Museum, London, there are six beautifully engraved buttons, classified as diffraction gratings, which are still regarded as masterpieces. They were the work of Sir John Barton, deputy comptroller of the Royal Mint in the early part of the nineteenth century, about whom little is known personally, but who must have been an ingenious inventor and capable engineer, for in 1806 he invented a differential screw measuring instrument capable of measuring 10^{-5} inch.

From *Nature* 18 September 1948.

These findings are significant because of the growing interest in the mechanisms that underlie the formation of episodic memory. Episodic memory is memory for events[6], each of which occurs in a unique setting of space and time. As such, it can be distinguished from semantic memory, which is memory for facts, or 'knowledge'. Episodic memory is disproportionately affected in some types of amnesia, such as that seen in Alzheimer's dementia, and it is thought to depend on the hippocampus[7], an important structure for spatial memory in both birds and mammals. To store an episodic memory, some method is needed for temporally ordering the sequence of happenings that make up an event. Perhaps episodes can be temporally ordered in the episodic memory of non-humans, as well as humans. In this light, the finding that animals as different from us as birds possess a mechanism for representing spatiotemporal events is enormously important, and could be a big step towards understanding how space, time and events are represented and remembered in the vertebrate brain. □

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Mathematics

Magic squares cornered

Martin Gardner

Dame Kathleen Ollerenshaw, one of England's national treasures, has solved a long-standing, extremely difficult problem involving the construction and enumeration of a certain type of magic square. The solution comes in a book* written with David Brée.

First, some background on magic squares, and their hierarchy of perfection. For many centuries, mathematicians — especially those concerned with combinatorics — have been challenged by magic squares. These are arrangements of n^2 distinct integers in an $n \times n$ array such that each row, column and main diagonal has the same sum. The sum is called the magic constant, and n is called the square's order. Traditional magic squares are made with consecutive integers starting with 0 or 1. If it starts with 0 it can be changed to a square starting with 1 simply by adding 1 to each cell.

No order-2 square is possible. The order-3 square (Fig. 1) barely exists. Why? Because there are just eight different triplets of distinct digits from 1 to 9 that add up to 15, the square's constant. Each triplet appears as one of the square's eight straight lines of three numbers. The pattern is unique — except for rotations and mirror reflections, which are only trivially different.

This little gem of combinatorial number theory was called the *lo shu* in ancient China, meaning 'Lo River writing'. Legend has it that in the 23rd century BC, a mythical King Yu saw the pattern on the back of a sacred turtle in the River Lo. (Modern historians, however, find no evidence that the pattern was known before the fourth or fifth century BC.) The Chinese identify it with their familiar yin-yang circle. The even digits, here shown shaded, are linked to the dark yin; the Greek cross of odd digits is linked to the light yang. For centuries the *lo shu* has been used as a charm on jewellery and other objects. Today, large passenger ships often feature the *lo shu* on their main deck as a pattern for the game of shuffleboard.

At order 4, the number of magic squares jumps to 880. Among them is a special subset of 48 squares called pandiagonal, which have three amazing properties. This is illustrated by the example in Fig. 2, whose constant is 30.

First, each broken diagonal also adds up to 30. The sequences 0, 3, 15, 12 and 7, 13, 8, 2 are examples. This can be expressed in another way: imagine an endless array of this square placed side-by-side in all directions to make a wallpaper pattern. Then every 4×4 square drawn on the pattern will also be a pandiagonal magic square — in other words, every straight line of four numbers will add up to 30. Second, every 2×2 square on the wallpaper also adds up to 30. Third, along every diagonal, any two cells separated by one cell add up to 15.

In general, a magic square is called pandiagonal if all its broken diagonals add up to the magic constant. Such squares can be constructed of any odd order above three and of any order that is a multiple of four. If a pandiagonal square also has similar properties to the order-4 pandiagonals, it is called 'most perfect': for example, the most-perfect order-8 square in Fig. 3 has a magic constant of 252, and its 2×2 sub-squares add up to 126, and any two numbers that are $n/2 = 4$

**Most-Perfect Pandiagonal Magic Squares: Their Construction and Enumeration.* Due for publication on 1 October by The Institute of Mathematics and its Applications, Catherine Richards House, 16 Nelson Street, Southend-on-Sea, Essex SS1 1EF, UK.