

recurrent hybridization events may be recognized as a single well-defined morphospecies [1,16]. This finding challenges commonly held beliefs that new species evolve from a single common ancestor — that they are monophyletic. Nevertheless, allopolyploid ‘species’ with polyphyletic origins often exhibit coherent phenotypes and occupy distinct ecological niches [7].

A remarkable example of recurrent hybrid origins of an allotetraploid ‘species’ was recently reported for the gray treefrog, *H. versicolor* [6]. Earlier studies revealed that this tetraploid species is related to the diploid gray treefrog, *H. chrysoscelis*, and may be a hybrid that had multiple origins, but other putative parental forms could not be identified with the available genetic markers [17]. The new phylogeographic study [6], examining one mitochondrial and three nuclear gene sequences, revealed that *H. versicolor* has a complex reticulate makeup consisting of DNA sequences from *H. chrysoscelis* (species C) and two hypothetical ancestors, extinct species A and B (Figure 1). Regional populations of *H. versicolor* possess unique alleles that reveal traces of ‘missing’ progenitors that once occupied the northeastern and northwestern part of the tetraploid’s present range. Recurrent hybridization events involving progenitors A, B and C are believed to have generated an array of allotetraploid biotypes — *AACC*, *BBCC* and *AABB* — that might be expected to behave as separate biological species, as is often the case in allopolyploid plants [1,16]. But apparently in the treefrogs, these biotypes merged into a single interbreeding sexual species.

Why should divergent allotetraploid biotypes merge reproductively, given the prominent mating calls that typify treefrog species? The merger may be a direct consequence of tetraploidy. *Hyla versicolor* has a slow-pulse mating call and the diploid, *H. chrysoscelis*, has a fast-pulse trill [18]. If all the putative allotetraploid biotypes — *AACC*, *BBCC* and *AABB* — shared the slow-pulse recognition system, they could have

recognized one another as mates and merged to form the interbreeding complex recognized as *H. versicolor*. Each component of this complex scenario — polyploidy, recurrent hybrid origins, and merger of parallel evolutionary lineages — has been seen before in sexual or asexual taxa, but to my knowledge this is the first report of these elements converging during the origin of a single species.

Traditional species concepts do not readily embrace reticulate entities like this frog, but evolution is not necessarily straightforward or parsimonious. Discerning the bifurcating and reticulating paths that accompany recent evolutionary events is not easy. This study of allotetraploid treefrog evolution is a testament to the value of examining multiple genetic markers for reconstructing evolutionary histories. Furthermore, it shows us another way in which polyploidy and hybridization might converge as creative forces in evolution. Perhaps scenarios like this can provide additional insight into steps that might have occurred during the major genomic transitions that occurred during evolution of the vertebrate genome.

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Memory: Obstacle Avoidance without Visual Cues

Avoiding obstacles is essential when we move about the world, yet little is known about how we do this when visual cues are not present to guide us. Recent evidence from behavioural studies in cats suggests that working memory may be crucial.

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Although we usually depend on visual input to avoid obstacles in our path, there are some situations where visual information is either

not available, or is unreliable. For example, when moving through a familiar environment in the dark, we rely heavily on memory for the location of objects in the room to guide us. Similarly, when driving, objects in the mirror are closer than

they appear, yet, through experience, we learn to adjust our responses appropriately to avoid them. In non-humans, a striking example of this occurs in quadrupeds such as horses, dogs, or cats, who cannot generally use visual information to guide the placement of their hind legs with respect to potential obstacles.

McVea and Pearson [1] have recently investigated this issue by examining the leg movements of cats as they moved over obstacles in a naturalistic setting. Once their front legs, but not their hind legs, had passed over the obstacle, a plate of food placed in front of the cats encouraged them to pause and eat. There was sufficient food to allow them to eat for several minutes, during which time the obstacle was covertly removed. By measuring the step height of the hind legs as they passed over where the obstacle had been, the authors found that the cat's memory of its position and height had been retained during the delay, and was accurate for durations of up to 10 minutes. Furthermore, there were no signs of a decline in accuracy, even for the longer durations, confirming that this type of memory is very stable. In fact, an upper time limit could not be determined, as the naturalistic setting allowed the cats to move on when they desired, rather than in response to a specific experimental cue.

A straightforward explanation for this effect is that the cats remember only that the next step should simply be high in order to avoid the obstacle. McVea and Pearson [1] discounted this possibility by demonstrating that, when obstacle height was changed, the step height changed accordingly. And, on some trials, the animals corrected their leg movement mid-step, clearly avoiding where the obstacle had been, indicating a precise representation of its size and position relative to the body.

The neural basis of the type of memory responsible for mediating such behaviour is not known, although recent studies in patients with discrete brain lesions may provide some clues. For example, Schindler and colleagues [2] have

shown that patients with damage to the superior part of the parietal lobe fail to take obstacles into account during a reaching task. The patients do, however, take account of the objects when asked to point to locations midway between them. This confirms that their behaviour on the reaching task is not simply a failure to perceive the obstacles, but rather, a failure to use visual information appropriately to avoid them. In contrast, a related study by McIntosh and colleagues [3] found that patients with damage to the inferior part of the parietal lobe show the reverse pattern. That is, they fail to bisect the distance between two objects, but nevertheless, they are able successfully to avoid them when they are presented as obstacles in a reaching task.

These findings demonstrate that conscious perception of obstacles is not necessary for avoiding them, and suggest that the neural systems responsible for perception and avoidance are likely to be different. In the study by McVea and Pearson [1], the cats were not consciously attending to the obstacle during the delay because their focus was on their food, however, they still automatically adjusted their next step to avoid where the obstacle had been. The studies by McIntosh and colleagues [3] and Schindler and colleagues [2] suggest that the superior parietal lobe may be involved in this automatic process.

McVea and Pearson [1] remark on the fact that the cat's memory for the obstacle lasts much longer than memory described in other locomotion tasks. Because the cat has both seen and stepped over the obstacle, the authors speculate that these two lines of information may converge to produce particularly persistent memory traces. A second possibility, not discussed by the authors, is that memory for the obstacle is mediated by the system that is responsible for maintaining a constant margin of safety around the body (sometimes termed 'personal space'). Clearly, a representation of one's body parts and their relationship to various obstacles is necessary to make the sort of adjustments that avoid

collisions. To be effective, such a system must maintain these representations over time and be resistant to interference. Recently, neurons located in the parietal lobe have also been implicated in this system [4]. The receptive fields of these neurons are usually limited to space near the body, and appear to encode location and movement of nearby objects with respect to the body's surface.

What remains unclear is how the memory that mediates object avoidance relates to other memory systems in the brain. Clearly, its characteristics suggest the involvement of working memory, which has been described as a cognitive system that is active and only relevant for a short period of time, and is used to guide behaviour in the absence of external cues or prompts [5,6]. Traditionally, areas of both the frontal and parietal lobes have been implicated in working memory. But recently, several authors have argued that the sensory areas responsible for early processing of visual, auditory, and tactile information may also contribute to working memory through the short-term storage of that information [7]. Similarly, motor regions may use and store relevant information when memory is needed to guide movement. Certainly, cells in the motor cortex are active after a cat's forelimbs and before its hind limbs have passed over an obstacle during normal, uninterrupted walking [8], perhaps suggesting a role for these neurons in memory. However, it is not known whether this neuronal activity persists when the animals stop for the long intervals described by McVea and Pearson [1].

To accommodate such findings, existing models of working memory, which focus predominantly on frontal and parietal cortices, will need to integrate possible contributions from sensory and motor areas, and memory-guided stepping may provide a useful paradigm in this respect.

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Meiosis: Checking Chromosomes Pair up Properly

Faithful recombination and chromosome segregation in meiosis require regulated steps of homolog recognition and association which are monitored by meiotic checkpoints. A recent study in the nematode *Caenorhabditis elegans* has identified a checkpoint mechanism that monitors chromosome pairing during meiosis.

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Finding a match is not only a fundamental problem in our lives but also a universal challenge during meiosis, the specialized cell division that generates haploid gametes from diploid parental cells. At the onset of meiosis, homologous parental chromosomes are faced with the challenge of finding each other and, ultimately, aligning along their entire length. This process goes hand in hand with meiotic recombination, which ensures the exchange of genetic information and establishment of a stable chromatin link between homologous chromosomes, termed a chiasma, which is needed for the accurate disjunction of homologous chromosomes.

As we all know, finding one's match is a knotty undertaking; things can go awfully wrong and the sequence of events has to be actively aborted, or if things look a little more favourable they may need to be interrupted to allow for adjustments to take place. During meiotic prophase, the processes prone to go wrong are the pairing of homologous chromosomes and meiotic recombination. To deal with these failures, meiotic cells have evolved checkpoint mechanisms which — dependent on the circumstances and/or the

species affected — either trigger meiotic cell cycle arrest in order to allow for a problem to be rectified, or cull faulty cells by triggering their apoptotic demise. A recent study by Bhalla and Dernburg [1], on the nematode *Caenorhabditis elegans*, has defined a meiotic chromosome-pairing checkpoint that, if activated, induces germ cell apoptosis. This work is likely to be important as a large portion of human male sterility is associated with defects in homolog pairing (reviewed in [2]).

In meiotic prophase, the initial recognition and pairing of homologous chromosomes (known as synapsis-independent pairing), and the initiation of meiotic recombination (which requires Spo-11 catalyzed DNA double strand breaks) have already occurred before the stage known as pachytene. Within pachytene, the intimate association between homologs into a proteinaceous scaffold — the synaptonemal complex — is completed in a process defined as chromosome synapsis, and double strand breaks are resolved either as gene conversion or as crossover recombination events (Figure 1, top panel).

Importantly, the initial synapsis-independent pairing is needed for meiotic double strand breaks to be generated ([3] and references

therein), an excessive number of which may have the potential to trigger the DNA damage checkpoint [1]. Synapsis of homologous chromosomes then allows the repair of double strand breaks (Figure 1, top panel) [4,5]. In most organisms differentiating between meiotic pairing and recombination checkpoints is a murky task, as recombination and pairing initiation go hand in hand and cannot be unequivocally mutationally separated [6–8].

This dilemma is nicely resolved by the recent study of Bhalla and Dernburg [1] who, taking advantage of the special property of *C. elegans* that meiotic chromosome pairing can occur unperturbed in the absence of meiotic recombination [9], have unequivocally identified a chromosome pairing checkpoint, demonstrated its *in vivo* importance and implicated two specific gene products in the process [1]. Their study builds on previous work which defined a meiotic DNA damage and recombination checkpoint that uses conserved proteins, such as Hus-1 and the *C. elegans* p53 orthologue Cep-1, to trigger apoptosis [10–13].

Armed with these tools, Bhalla and Dernburg [1] began by addressing whether apoptosis of pachytene cells is enhanced in various mutants where meiotic chromosome pairing and synapsis of all *C. elegans* chromosomes, or just the sex chromosomes, are affected [1]. Worms carrying two sex chromosomes, the X chromosomes, develop as hermaphrodites, whereas those with just one X chromosome develop as males.