remembered that each event occurred in a distinct room.

Crystal and Smith [3] argue that keeping separate in memory multiple episodes that share similar components is a central feature of bound memory representations. If the rats instead had just remembered each of the unbound aspects of each event, then performance would have suffered because the two events shared some of these aspects. Rats would have struggled to find the preferred chocolates in the correct locations when revisiting the mazes. But the authors found that rats were likely to go to maze arms that held chocolate, taking into account which room they were in, and how they had found chocolate in that room previously. This suggests that they remembered each experience (in each room) as an event with multiple, bound features.

Whether these results indicate that the rats' bound memories meet everyone's definition of episodic memory (for example [1,2,16,17]) should not be the main issue. Perhaps they do not, but that makes these results no less important. Questions about whether animals do or do not show 'mental time travel' [16–18] sometimes can distract us from the equally important (and perhaps more immediately pressing) goal of establishing just how accurate and flexible the memories of animals can be when those memories are needed to generate intelligent behaviors (or, for those studying prospective cognition, just what kinds of anticipatory behaviors we can find in nonhuman animals). Certainly, consideration of whether these kinds of experiences have the qualities that are critical for human mental time travel will highlight aspects of the nature of animal consciousness, and can offer insights into the evolution of human cognitive abilities and consciousness. But there is at least equal importance in comparative cognitive science in documenting where and why success and failure occur in memory tasks, and how bound the components are for personal memories of the past, along with how episodic memories may serve an adaptive function in future oriented behaviors such as prospective memory and planning [19,20]. Crystal and Smith [3] have provided compelling new data in this debate, showing that the binding of features is likely a widespread aspect of animal memory and one that is potentially of high translational value in terms of understanding some of the fundamental aspects of human memory.

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Sensory Biology: Echolocation from Click to Call, Mouth to Wing

Echolocators use echoes of sounds they produce, clicks or calls, to detect objects. Usually, these signals originate from the head. New work reveals that three species of bats use their wings to generate echolocation signals.

M. Brock Fenton[1] and John M. Ratcliffe[2]

Donald R. Griffin [1] coined the term 'echolocation' to describe the use of echoes of self-generated acoustic signals for orientation, as seen in bats and some blind people. However, not all bats echolocate. The list of echolocating animals also includes toothed whales, some shrews and tenrecs, as well as oilbirds and some swiftlets [2]. Most bats produce their echolocation signals in their voice boxes (larynges) [3] but at least two species of Old World fruit bats, (Pteropodidae) *Rousettus aegyptiacus* (Figure 1) and *Rousettus leschenaulti*), use tongue clicks as echolocation signals [2]. Some blind people also use tongue clicks as echolocation signals [4]. But the arsenal of bats for producing echolocation signals is even broader than we had realized. In this issue of *Current Biology*, Arjan Boonman, Sara Bumrungsri and Yossi Yovel [5] show that some bats

produce echolocation clicks with their wings.

The authors experimented with lesser dawn bats and two other species of Old World fruit bats: greater long-tongued fruit bats (*Macroglossus sobrinus*) and lesser short-nosed fruit bats (*Cynopterus brachyotis*). These bats had not previously been identified as echolocators. Boonman and co-workers tested the bats by flying them in total darkness and in an anechoic chamber. In these settings the bats successfully used echolocation to identify an appropriate landing site. But none of the bats could use echolocation to negotiate obstacle courses or localize targets. Compared to greater long-tongued fruit bats, both lesser dawn bats and lesser short-nosed fruit bats clicked more readily and adjusted their click rates according to the situation in which they flew. In these species, increased rates of wing flapping corresponded to higher rates of clicking. The bats' clicks were composed of a range of frequencies, including some audible to humans. The bats produced fewer clicks when flying in light. These bats used echolocation to detect targets (landing sites) in the dark. While they used the surface characteristics of landing sites, they could not precisely locate them. This study [5] shows that the bats generated the clicks with their wings not in their mouths or vocal tracts. However, in spite of several efforts, the researchers could not demonstrate the exact mechanism the bats used to produce clicks. Importantly, while wing beat and call rate were positively related, the researchers convincingly demonstrate that clapping the wings together did not produce the clicks, as had originally been proposed by Gould [6].

Compared to other echolocating animals, the three species Boonman and colleagues [5] studied exhibited a rudimentary capacity for echolocation. This reality does not appear to reflect echolocation with clicks, as opposed to structured sounds. In 1980, Buchler and Mitz [7] showed that echolocation performance was not limited by signal design. Both clicks and tonal sounds could be equally effective echolocation signals. Most echolocating bats and toothed whales increase their rates of call production as they search for, detect, and close with a target [8].

Recent research on the performance and information processing by human echolocators [4] adds another perspective on the importance of the work by Boonman and colleagues [5]. Humans use click-like sounds in echolocation and information processing is not restricted to the auditory cortex. In humans, some processing of echolocation information occurs in the lateral occipital area of the brain, which in sighted persons is activated by moving visual stimuli [9]. Furthermore, humans can use echolocation to identify shapes and materials as well as the size of an object [10,11]. Echolocation at this level of performance does not require a brain evolved to echolocate. Echolocation can be accomplished with a brain that is plastic in its use of different sources of information available in the environment.

The work of Griffin and his colleagues, notably Robert Galambos and George Pierce, made clear that some echolocating bats use sounds beyond the range of human hearing (ultrasonic, or >20 kHz, by definition) [12]. But as Boonman *et al.* [5] and others have demonstrated, echolocation signals do not have to be ultrasonic [2,13]. More than this, the new findings make clear that, at least for rudimentary spatial orientation, echolocators are not bound to produce their signals using structures found in the head and/or neck, as in all other echolocators described to date.

The findings of Boonman *et al.* [5] also set the stage for developing a better understanding of the evolution of echolocation. Echolocation has evolved independently in at least six evolutionary lineages [2] — two orders of birds, and in at least four orders of mammals. Echolocation evolves when animals must operate in low levels of light, or when lighting conditions are uncertain. Boonman *et al.* [5] suggest that these and other pteropodids may be 'living fossils' and offer insight into the mechanisms used by the earliest echolocating bats. Synchronization of sound production with wingbeat would have meant that flying echolocators could collect information at rates appropriate to their flight speed. Speakman and Racey [14] demonstrated this for some laryngeally echolocating flying bats. Using sounds associated with the wingbeat cycle directly ensures appropriate timing.

Figure 1. Echolocating Egyptian rousette bat (*Rousettus aegyptiacus*). Photo by M.B. Fenton.

In bats, the occurrence of echolocation involving different signals produced in different ways may inform us about plausible steps, missteps, or both along the way in the evolution of echolocation in bats and other groups. Echolocation is not characteristic of bats, or is at least unknown in the vast majority of the roughly 200 species belonging to the family Pteropodidae. We do not know if echolocation using laryngeally produced sounds was basal to the lineage leading to bats or if it evolved independently in two or more lineages of bats [15,16]. Boonman *et al.* [5] remind us that signal type, signal source and phylogenetic position do not constrain the evolution of echolocation. Griffin [12] and others [17,18] have provided robust protocols for proving whether or not flying, swimming, and walking/running animals echolocate. Such protocols allowed Shusterman *et al.* [19] to refute the proposal that pinnipeds echolocate. Boonman *et al.* [5] kindly provide a refresher course on this topic and demonstrate that echolocation signals need not be emitted from an echolocator's head, even when echoes will be received there.

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Life History: Mother-Specific Proteins that Promote Aging

A yeast mother cell progressively ages with each cell division and yet produces daughter cells that are largely rejuvenated, suggesting that mothers accumulate aging factors. Two current studies address this issue by identifying mother-specific long-lived proteins and, in the case of Pma1, evidence that asymmetric distribution drives mother cell aging.

Chuankai Zhou[1,2], Rong Li[1,2], and Brian K. Kennedy[3,*]

The study of yeast replicative aging, defined as the number of cell divisions that one mother cell can undergo, has proven to be a major vein of aging research [1]. Genetic studies have led to numerous aging genes that modulate lifespan, many of which have orthologs conserved in other eukaryotic species [2]. Less well understood is how an aging mother cell, at least until very late in its lifespan, can bud to produce a rejuvenated daughter cell [3]. Most current models suggest that aging factors, such as extrachromosomal rDNA circles (ERCs) and oxidatively damaged proteins, accumulate specifically in mother cells [4,5]. Two recent reports from the Gottschling lab offer insights into mother–daughter asymmetry and its relationship to aging. One study identifies long-lived asymmetrically retained proteins (LARPs) that stay in the mother cell and may underlie aspects of aging [6]. The second focuses on one protein, Pma1, which is retained in the plasma membrane of mother cells and promotes aging by transporting protons out of the cytoplasm and raising cellular pH [7].

Proteins in each organism tested display a wide range of stability. At one extreme, some proteins last for the entire life of the host organism; examples include the crystalline protein of the eye lens and collagen. While recent studies expand this pool of long-lived proteins to those localized inside the cell, such as histones and nuclear pore complexes in post-mitotic cells, dividing cells were generally thought to continuously turnover their proteome and to be largely spared of long-lived proteins likely to accumulate damage [8]. This concept was challenged when it was shown that a number of long-lived multidrug resistance (MDR) proteins are not replenished in the mother cell during cell division because the majority of newly synthesized proteins during each cell cycle are asymmetrically targeted to the daughter cell [9]. As the mother cell ages, limited replenishment of these MDR proteins is insufficient to maintain their levels in the mother cell, while the function of the existing proteins decline. This is likely a