Future studies, however, will make progress by running across study sites and geographic regions to test functional hypotheses of baboon social evolution. As a case in point, one of the most prominent behavioural differences between baboon allotaxa lies in the occurrence of coalitionary behaviour among unrelated, reproductively competing males: this is a problem of real substance, because this kind of cooperation is rare in nature. These differences are resistant to the effects of local ecology, and are likely to have a genetic basis reflecting selection of the physiological responses that allow males to modulate their interactions with each other (for example, increased inhibition and tolerance, and reduced aggression). As the EU-funded taskforce INCORE recognises, the fact of these population differences in behaviour, in conjunction with our expanding knowledge of the baboon genome and its complicated phylogenetic history, presents us with a unique opportunity to investigate the genetic underpinnings of complex social behaviour.

Where can I find out more about baboons?

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Primer

Rodents

Emily H. Kay[1] and Hopi E. Hoekstra[2]

To a first approximation, all mammals are rodents. Over 40% of mammal species are in the order Rodentia. While rodents are often thought of as just mice and rats, the more than 2000 species in this order encompass a staggering diversity of form and behavior (Figure 1). There are pocket gophers, beavers, jerboas, guinea pigs, springhares, chinchillas, and porcupines. Rodents are found on all continents except Antarctica, and in all habitats (from arid deserts to arctic tundra), except the ocean. They hop, jump, scurry, and glide their way through these habitats, and forage on seeds, grasses, bark, insects, fish and sometimes scorpions. Their ecological success has been largely attributed to their wide-ranging diet, small size and propensity to breed.

The term ‘rodent’ — derived from the Latin verb *rodere* meaning ‘to gnaw’ — is most appropriate for this group, as the unifying characteristic of all rodents is a pair of open rooted, chisel-shaped incisors (Figure 2). These ever-growing teeth have a hard external enamel layer and a soft internal dentine layer; because dentine wears faster than enamel, the incisors are continually sharpened. Rodents have also lost their canine teeth, so that a prominent gap, or diastema, separates their incisors from their cheek teeth (molars). This configuration gives them the ability to gnaw virtually anything, from grass and seeds to chitinous insects. In some species, teeth are routinely used for digging: some fossorial rodents like pocket gophers and mole-rats construct their underground tunnels largely by chewing through hard-packed soil.

Most living rodents are relatively small, having a compact body with short legs. Their range in size, however, is much larger than that of any other mammalian order. The largest rodent, the South American capybara, approaches 50 kg — approximately 7,000 times larger than the tiny pygmy mouse, which weighs in at a mere seven grams (Figure 3). But no modern rodent is as massive as some that once roamed the earth. In 1987, an Argentine fossil collector excavated a 53 cm skull in Uruguay. This two-to-four-million year-old fossil was promptly forgotten, sequestered in the bowels of Uruguay’s Natural History and Anthropology Museum attic. In 2007, it was re-discovered and immediately recognized as the largest known rodent in the history of life. *Josephoartigasia monesi*, as it was called, resembled a guinea-pig of hippopotamusian proportions, growing up to 2.5 m long and weighing over 1000 kg. In a prehistoric game of cat and mouse, the population of *J. monesi* might have been kept in check by sabertooth tigers.

Rodents are also prolific breeders. While litter size for most rodents ranges from one to eight offspring, naked mole rats can produce as many as 28 in a single litter. The fecundity of many rodents is further enhanced by a physiological quirk: postpartum or lactational estrus (ovulation immediately following birth), which enables females to be continuously pregnant. Although gestation periods are usually short (16 days in hamsters, for example), when longer, pups are often born precocial. In guinea pigs, which have a 68 day gestation, nearly half of newly born pups can survive without nursing. This assembly-line breeding, combined with the early sexual maturity of most rodents (two weeks in voles and lemmings), can lead to population explosions. (While the mass migration of lemmings during periods of overcrowding often results in natural deaths, it is not group suicide as Scandinavian legend has it.) In theory, a single pair of mice can produce nearly 500 descendants in just 21 weeks.

Because rodents can occupy just about any habitat, eat nearly anything, and reproduce rapidly, they have successfully invaded almost every continent and filled almost every niche. And their evolutionary history, well documented as it is, is remarkable.

Rodent history

Dentition is the key taxonomic character used to identify fossil rodents. Some of the earliest fossils

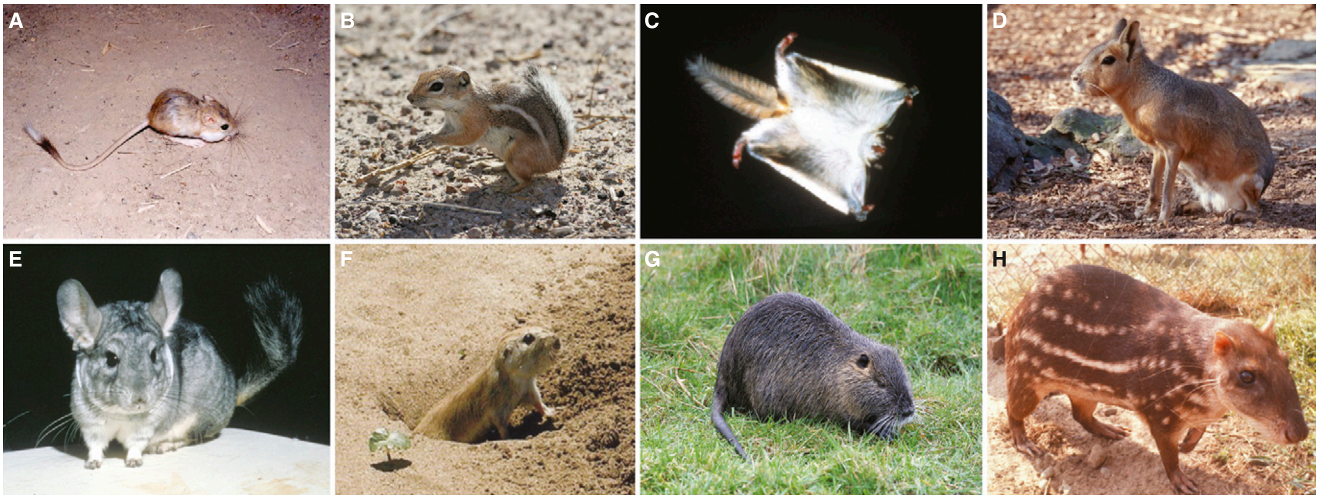

Figure 1. Diversity of rodents.

(A) Desert kangaroo rat (*Dipodomys deserti*). (B) Nelson's antelope squirrel (*Ammospermophilus nelsoni*). (C) Flying squirrel (*Glaucomy volans*). (D) Mara (*Dolictus patagonum*). (E) Chinchilla (*Chinchilla lanigera*). (F) Southern tuco tuco (*Ctenomys australis*). (G) Coypu (*Myocastor coypus*). (H) Lowland paca (*Cuniculus paca*). Photographs provided by G. Jensen (A), J. Gross (B,G), N.M. Wells (C), J. White (D), R. Altig (E), M. Mora (F), and F.A. Cervantes (H). (C), (E) and (H) courtesy of the Mammal Image Library of the American Society of Mammalogists.

collected in Wyoming and Europe suggested that rodents evolved in Laurasia late in the Paleocene, 55–60 million years ago. Molecular clock analyses, however, consistently show that rodents originated prior to the Cretaceous–Tertiary mass extinction (about 65 million years ago), dating back as far as 74 million years ago. Rodent diversification is documented throughout the Eocene (55–34 million years ago), and by 20 million years ago, many of today's recognizable rodent families had emerged. The most species-rich family, Muridae, began its spectacular radiation in North America during the last 5 million years. With the joining of North and South America via the Panamanian land bridge, murids could move south (though a few species, like porcupines, moved north). Some murid rodents also colonized new land over water — Australia twice (10–15 million years ago and again 2 million years ago) and Madagascar once (25–20 million years ago).

Based on the morphology of their lower jaw, living rodents are divided into two suborders: the Sciurognathi (squirrel and mouse-like forms) and the Hystriocognathi (cavy-like forms). A study of mitochondrial DNA in the early 1990s proposed that hystriocognaths should be a separate order; but despite the brief skirmish over the placement of guinea pigs in the mammalian phylogeny, newer molecular evidence has convinced mammalogists that guinea pigs are well nested within the rodent clade, and that rodents are indeed monophyletic. While Rodentia contains 29 families, five families comprise 89% of species: Muridae (mice and rats), Sciuridae (squirrels), Echimyidae (spiny rats), Heteromyidae (pocket mice and kangaroo rats), and Dipodidae (jerboas and jumping mice) (Figure 4).

New rodent species are still being discovered — for example, a Cuban hutia in 2004, a Costan Rican spiny pocket mouse in 2006 — and in recent years scientists discovered a squirrel-like rodent so unusual that it was placed in its own family — the first new mammalian family since 1974. *Laonastes aenigmamus* (meaning 'enigmatic rock dweller') was discovered in a Laotian meat market. But closer inspection in 2005 revealed striking similarities in tooth enamel, lower-jaw structure, and other cranial features between *L. aenigmamus* and fossils from an extinct clade, the Diatomyidae, a family whose last members were thought to have vanished 11 million years ago. This species is thus a 'living rodent fossil', the sole survivor of a family long thought to be extinct.

What's in a rodent name?

The ancient Romans did not differentiate between rats and mice, except based on size, referring to the former as *Mus maximus* and the latter *Mus minimus.* In fact, mice (genus *Mus*) and rats (genus *Rattus*) are close evolutionary relatives in the family Muridae. 'Mice' and 'rats', however, are not monophyletic groups. Although most murids include 'mouse' or 'rat' in their common names, other species in the same family, like gerbils, do not. To further add to the confusion, species from other families — kangaroo mice and kangaroo rats, for example, have names suggesting that they are closely related to murid mice and rats, when in fact they belong to a different family — Heteromyidae.

Common names of other rodents are also misleading. Guinea pigs are not pigs, prairie dogs are not dogs

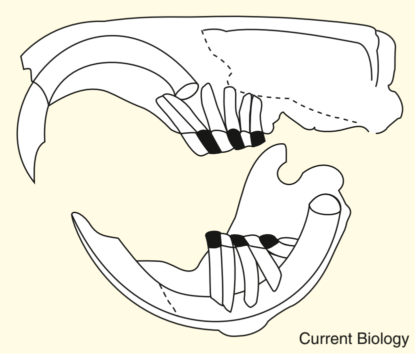

Figure 2. Typical rodent skull.

The unifying characteristics of all rodents are their continuously-growing incisors, reduced molars, and diastema.

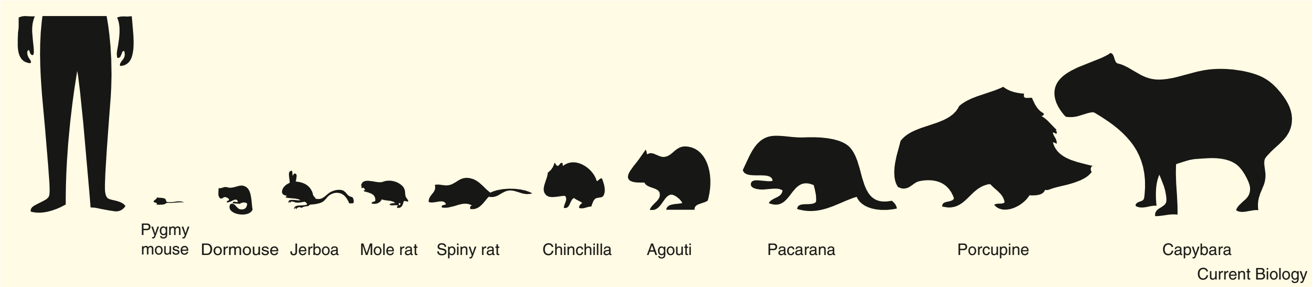

Figure 3. A representation of rodent shapes and sizes.
(Adapted with permission from MacDonald 2001/Brown Reference Group.)

and mole-rats are not moles. Mountain beavers (family Apolodontidae), considered the most primitive of rodents, are not true beavers, nor are they found in mountains. Mountain beavers are most closely related to squirrels (Sciuridae), even more so than are scaly-tailed squirrels (Anomaluridae). Similarly, the species we call 'porcupines' are not monophyletic, and neither are mole-rats, pacas, hutias or dormice. Further, the South American chinchilla rat does not belong to the family Chinchillidae, which instead are viscachas and 'true' chinchillas, and kangaroo rats of the genus *Dipodomys* do not belong to the family Dipodidae, which are jerboas.

Although Rodentia is composed of many forms, there are some species that are often erroneously thought to be rodents. These include species like pikas and rabbits that belong to the order Lagomorpha, and shrews, moles and hedgehogs that belong to the order Insectivora. Although hyraxes (Greek for 'shrewmouse') look superficially rodent-like, they belong in the Hyracoidea and may be more closely related to elephants. Likewise, elephant shrews are not rodents: they belong in the Macroscelidea.

Diversity: more than just mice

Because rodents live almost everywhere, they have adapted to a range of habitats. Often different ancestors have invaded similar habitats, leading to the evolution of many convergent traits (this has almost certainly contributed to the misleading convergence in common names). One of the most robust patterns among rodents is that the color of their dorsal coat often matches the substrate on which they live, camouflaging them from visually hunting predators. Rodents have repeatedly evolved dark coats on dark substrates and light-color coats in sandy environments. But more complex convergences also occur.

Aquatic rodents, such as marsh rats or fish-eating rats, have webbed feet and hairy tufts on their tails that act as rudders. Tree-dwelling species like flying squirrels and scaly-tailed squirrels have independently evolved exaggerated membranes that extend from the forelimb to the hind foot as well as and flattened tails that help them to glide up to 100 m. Fossorial species like gophers, tuco-tucos and mole rats have reduced eyes, ears, tails and fur as well as large claws for burrowing. Hardened hairs have evolved in spiny mice and, in an extreme case, porcupines. Desert specialists like pocket mice have a complex of physiological traits, including kidneys that can concentrate urine, to conserve water. In fact, some species never need to drink water; they can extract moisture from seeds. Desert-dwellers have also evolved kangaroo-like bipedal locomotion that is accompanied by a convergent group of morphological traits including reduced digits in kangaroo rats and jerboas, which literally hop on their toes (Figure 5). Although generally herbivorous or omnivorous, some rodents have more specialized diets. Salt marsh mice can drink salt water when fresh water is scarce, and field voles can digest poisonous bark by neutralizing the toxins with special enzymes. There are even carnivorous rodents: water rats feed on frogs and fish, and grasshopper mice eat insects and scorpions.

In addition to being physically well-suited to their environments, rodents have also evolved many behavioral adaptations. Some rodents are diurnal, whereas most are nocturnal; some experience summer torpor, whereas others hibernate in the winter, and many are active year-round. Perhaps the most fascinating behaviors involve interactions between males and females. Rodents range from being entirely solitary (porcupines and pocket gophers) to highly social, with some species living in large aggregations. Prairie dogs, for example, live in large groups that are divided into smaller neighborhoods, in which individuals help construct each other's homes, baby-sit young and guard the colony. The different social and mating systems result from many divergent reproductive strategies, ranging from monogamy to full-blown promiscuity. Some rodents practice obligate monogamy. In marmots, senior breeding females will sometimes beat younger, pregnant females until they abort — alpine habitats are so harsh that a marmot family can provide warmth for only one hibernating litter. At the other extreme, some rodents are highly promiscuous, and strongly skewed sex ratios can create fierce competitions for mates. Cape ground squirrels have as many as 11 males for every female, resulting in intense sperm competition. It is not surprising, then, that males have extremely large testes, among the largest for their body weight of any mammal. The Rodentia also boasts the only eusocial mammal: the naked mole rat.

Of rats and men

If you look up 'rat' in a thesaurus, you will see the following synonyms: tattler, tattletale, traitor, turncoat — and those are only words that start with ‘t’. Then there are the perjorative terms like rat race (an endless self-defeating pursuit), ratty (dilapidated), mousy (timid), rathole (to withhold goods). When we think of rodents, we first think of disease-carrying pests. This reputation may be deserved. Rodents — mostly mice and rats — cost humans billions of dollars each year. Rodents contaminate stored grains, gnaw on crop plants, and destroy electrical wires. They are also responsible for spreading disease. Through bacteria carried by rodent-borne fleas, the Black Death, one of the most deadly pandemics in human history, killed about 75 million people worldwide — between 30% and 60% of Europeans — in the fourteenth century. Even today, rodents pose a threat to human health: most rodent-borne diseases (for example, hantavirus, plague, rat-bite fever, Lassa fever, Lyme disease and salmonellosis) are transmitted to humans through either direct contact with infected animals (bites or wounds) or indirect contact with food, water, or dust contaminated by rodent urine or feces.

Although rodents are a prime carrier of disease, they are also ironically our premier models in biomedical research; laboratory mice and rats have been used to study almost every human disease. These laboratory strains were developed from wild ancestors for scientific research in the early 1900s. Because of their small size, ease of maintenance and profligate breeding (some mouse strains have been selected to produce more than 20 offspring per litter), over 450 laboratory mouse strains and 200 major rat strains are now used in biomedical research. Hamsters, deermice and guinea pigs also are maintained in the laboratory for disease research.

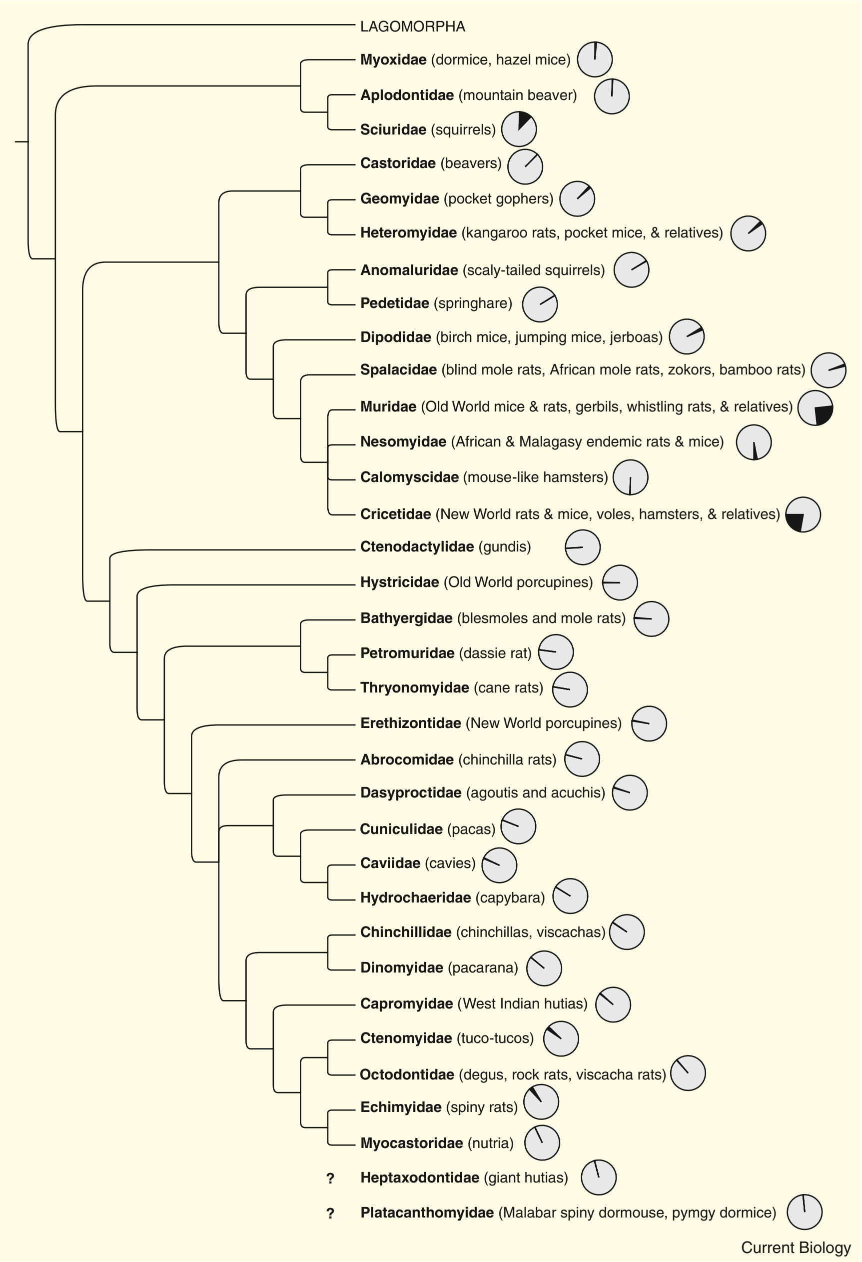

Figure 4. Typological relationships among rodent families.

Pie charts show the proportion of species belonging to each family relative to the total number of rodent species. The positions of the Heptaxodontidae and Platacanthomyidae families are uncertain. (Adapted with permission from Beck *et al.* 2006.)

Rodents help us in other ways too. Historically, they have been a source of meat and fur. In ancient Rome, dormice were considered a delicacy, either as a savory appetizer or, dipped in honey and poppy seeds, as a dessert. Humans have consumed over 80 species of rodents: cane rats and springhares provide sustenance for Africans, rice rats are hunted and trapped for meat in Asia, and roasted, stuffed, or fried guinea pigs are a popular fare in South America. Some rodents are even farmed — capybaras are raised for meat (each produces more than 17 kilograms of meat) as well as hides, and domestic chinchillas are farmed for their soft luxuriant fur.

Into the wild

While laboratory populations will always be important, the diversity of behavior and morphology among wild rodents has already yielded important biological and evolutionary insights. For example, comparisons among voles have pointed researchers to the vasopressin-1a receptor, which when over-expressed produces more ‘monogamous’ behavior. Hibernating squirrels have given insights into thermoregulation, fat

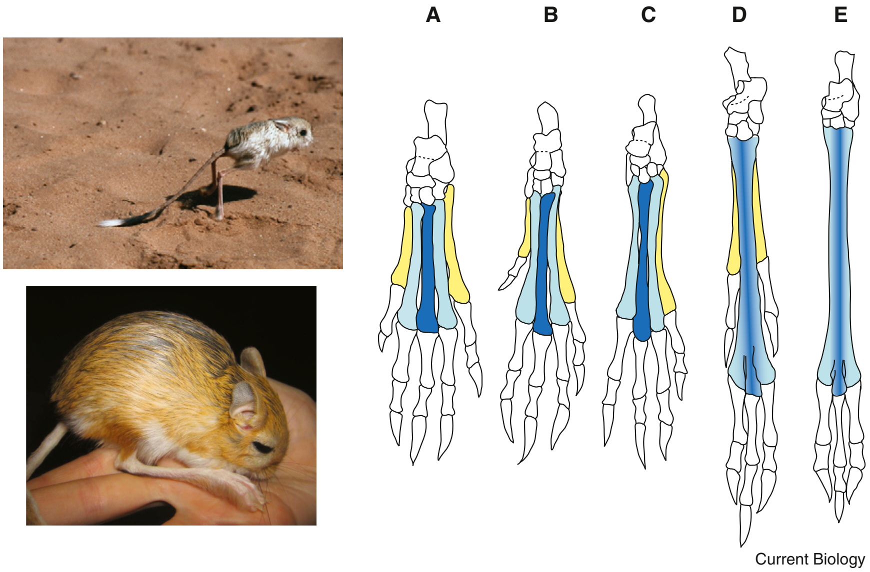

Figure 5. Digit reduction in desert-dwelling rodents.

(A) Gerbil (*Meriones sp.*). (B) Ord's kangroo rat (*Dipodomys ordii*). (C) Merriam's kangaroo rat (*Dipodomys merriami*). (D) Jerboa (*Allactaga sp.*). (E) Greater Egyptian jerboa (*Jaculus orientalis*). Digits I and V are shown in yellow; digits II, III, and IV are shown in blue. *Allactaga* and *Jaculus orientalis* have lost digits I and V, and digits II, III, and IV have fused together. (Adapted with permission from Berman 1985 / Blackwell publishing.) Photograph of a Desert kangaroo rat provided by E. Bartov (top); photograph of a Northern three-toed jerboa provided by K. Cooper (bottom).

storage and circadian rhythms. Memory and learning have been studied in squirrels that cache their food, sometimes not returning until the next year. Singing mice provide a new model for studying speech and learning. Studies of wild rodents will undoubtedly give us a window into the genetics underlying phenotypic variation, further promoted by genome sequencing projects that extend beyond the usual model species (see *www.genome.gov*).

All of this diversity can be traced back to the first fossil rodents (Ischyromyoidae) from the late Paleocene of Asia. These primitive rodents, although donning a beaver-like skull, had the teeth and feet of a squirrel, and skeletal features suggestive of an arboreal lifestyle. And from so squirrely a beginning evolved endless rodential forms most beautiful — species as distinct as ungulate-like capybaras, raccoon-like viscachas, rabbit-like springhares, and otter-like muskrats. Rodents are an evolutionary success story — they were here long before us and these opportunistic survivors will certainly be here long after we are gone.

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Perceptual processing is facilitated by ascribing meaning to novel stimuli

Gary Lupyan and Michael J. Spivey

Can the *interpretation* of a visual stimulus (normally conceived as a late visual process) influence the *recognition* of that same stimulus (normally conceived as an early visual process)? Access of meaning from vision can be extremely rapid [1–3]. If the visual processing of meaningful stimuli is supported by top-down feedback from conceptual representations [4,5], then meaningful stimuli may be processed more efficiently than meaningless stimuli. A difficulty with testing this prediction is that meaningfulness is often confounded with familiarity. It is well established that familiar stimuli are easier to process than unfamiliar stimuli [6]. In visual search tasks, finding a target among unfamiliar non-targets (such as Иs) is much more effortful than searching among familiar non-targets (such as Ns) [7]. However, poor performance on unfamiliar stimuli may be due, not only to inexperience with them, but also to a failure to represent them as members of meaningful categories. If so, then ascribing meaning to otherwise unfamiliar stimuli should facilitate perceptual processing. We report here data from experiments using a visual search task which show that, when perceptually novel stimuli are treated as members of a known category, they are processed more efficiently. These results are simulated by a model implementing top-down feedback from category representations to visual features.

Participants ($N = 62$, ages 18–22) searched for the perceptually novel symbols ⊔⊓ and ⊓⊔. These symbols are 90° rotations of the numerals 5 and 2 rendered in a 'digital' font. This simple rotation reduces search efficiency by a factor of two [8], while preserving the low-level visual properties of the familiar upright numerals. To investigate whether differences in processing efficiency hinge on differences in