competent developmental stage, but has no direct effect on RAG expression or antibody gene rearrangement.

Most studies designed to assess the significance of receptor editing are predicated on elimination of autoreactivity as a major impetus; nonetheless, one can easily envision other situations in which continued light chain rearrangement would be beneficial. If receptor editing is not directly induced by BCR signaling but instead leads to developmental arrest in the rearrangement-competent pre-BII stage, then any situation that results in arrest at this stage may enable continued antibody light chain rearrangement. Because antibody gene rearrangement is an error-prone, inefficient process that often generates antibody products that are out-of-frame or incapable of forming heavy chain–light chain pairs, a large number of candidate B cells fail to express a functional BCR. The inability to express a functional BCR would block B cell development at the pre-BII stage, potentially allowing these cells to generate another antibody light chain before undergoing "death by neglect."

Finally, if the goal of receptor editing is to promote the generation of nonautoreactive BCRs, how does a cell know when this has been successfully accomplished? One possibility is that light chain rearrangement continues in pre-BII cells until a signal provided by cell surface expression of a functional BCR that displays little or no reactivity to self antigens promotes maturation into bona fide immature B cells, with a consequent down-regulation of *RAG* (*14, 15*) and termination of further receptor editing. If a pre-BII cell is unsuccessful in generating such a BCR, it may very well continue to undergo receptor editing until it draws its last breath. The recent identification of a protective niche in the bone marrow where the BCR-induced apoptotic response of immature B cells is blocked (*13*) suggests that the local microenvironment in which an autoreactive immature B cell first encounters antigen may also play an important part in determining its fate. An immature B cell outside the protective niche would undergo rapid apoptosis, whereas one inside the niche would have time to generate a nonautoreactive BCR by receptor editing. It is yet to be determined whether immature B cells that have functionally interacted with self antigens are drawn to the protective niche, or whether only those cells that are lucky enough to be in close proximity to the protective niche can be rescued. In either case, it is tempting to speculate that signals produced by a functional, nonautoreactive BCR serve as the impetus for the rehabilitated cell to leave its nurturing microenvironment and to make its own way in the world.

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PERSPECTIVES: EVOLUTION

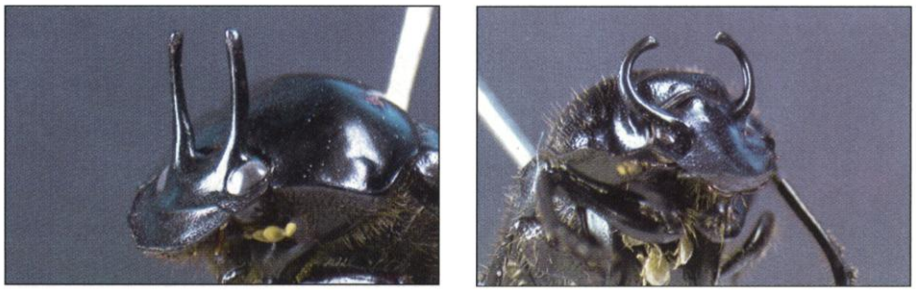
A Horn for an Eye

Paul H. Harvey and Charles J. Godfray

Despite his encyclopedic knowledge of natural history, Charles Darwin was puzzled by dung beetles. The males of many dung beetle species have elaborate horns, and Darwin's first thought was that these horns had evolved by sexual selection to make males more efficient in competing with other males for mates. But what confused Darwin was that the size and location of the horns varied—in some cases they were on the front of the head, in others on the thorax. Emlen's study of *Onthophagus* dung beetles (*1*) on page 1534 of this issue provides an elegant solution to Darwin's dilemma. Emlen discovered that possessing a pair of extravagant horns involves a cost—a reduction in the size of nearby organs, such as the wings, antennae, or eyes. The need for well-developed eyes versus well-developed antennae, or wings differs depending on the life history of the beetle species. Thus, the position of the horns is determined by the organ that a beetle species needs the least.

There are two types of sexual selection: The first is fighting (and other direct interactions) between males, and the second is the effect of female choice. Frequently, males fight for mating access to females and so have developed associated weaponry—the horns of beetles, the antlers of deer—to improve their chances. Alternatively, females may choose their mate according to an evolved preference—the peacock's iridescent tail is the classic case.

Darwin essentially held our modern view of how competition among males leads to the evolution of structures such as horns and antlers. However, he failed to solve the problem of how female choice could give rise to structures such as the peacock's tail, calling them ornaments and invoking innate aesthetic female preferences as the driving force. The horns of *Onthophagus* male beetles are extraordinarily variable in their size, shape, and location on the beetle's body (see the figure). Owing to these observations and the fact that Darwin could find no evidence that dung beetle horns were used in combat, he concluded that "they have been acquired as ornaments." This conclusion "is that which best agrees with the fact of their having been so immensely, yet not fixedly developed, as shewn by their extreme variability in the same species, and by their extreme diversity in closely allied



Horn of plenty. The Australian dung beetle *Onthophagus neostenocerus* (**left**) and the Central American dung beetle *Onthophagus crinitis panamensis* (**right**). The position of horns on the beetle's body influences the size of nearby organs such as the wings or eyes.

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species. This view will at first appear extremely improbable…" (*2*, p. 297). Darwin's view is, indeed, improbable, particularly given that naturalists have since observed that *Onthophagus* horns are used in combat between males.

Some dung beetles (Scarabaeoidea) lay their eggs on fresh dung and the larvae develop in situ ("dwellers"), but most bury small amounts of dung in tunnels that they must frequently defend from attack by other beetles. Defense is often essential as competition for dung is intense—some 16,000 dung beetles were observed to spirit away a 1.5-kg pile of elephant dung in under 2 hours (*3*). Many species, including the famous sacred scareb of ancient Egypt (*Scarabeus sacer*), roll balls of feces away from their source and bury them in a suitably protected location ("rollers"), but most dung beetles just dig a tunnel under or beside the dung ("tunnelers"). *Onthophagus* is the largest genus of tunnelers, with over 2000 species and a worldwide distribution. Members of this genus are morphologically very diverse—for example, some female Australian *Onthophagus* have prehensile claws that they use to grasp the perianal fur of wallabies until a pellet of dung is produced, which they grab as it is extruded (*4*). As Darwin noted, many *Onthophagus* species bear elaborate horns, but there is marked variation in their location. It is now known that these horns, wherever on the body they may be, are used to block the tunnel containing the female and the dung, preventing theft of either mate or food by other males.

But growing horns involves a cost, and it is this cost that lies at the heart of Emlen's work. If the horns are near the eyes, antennae, or wings (and they have to be near at least one of these three organs), then the organ that is closest is reduced in size. The evidence here is correlational: Within a species, the horns are located in the same position on the body, and variation in horn size among individuals negatively correlates with the size of the associated organ in males. An increase in horn size is not associated with a decrease in the size of nearby organs in female *Onthophagus* beetles, which have much smaller horns. Of course, cause and effect can only be inferred in such circumstances. However, investigation of an unusual *Onthophagus* species in which the female rather than the male has the large horns supports the negative correlation. Among females of the unusual species, horns are produced on both the thorax and at the center of the head, and as the horns increase in size, both wings and antennae become smaller in females but not in males of this species. This finding opens up new questions about the natural history of this particular species: Is it the females rather than the males that defend the burrow and, if so, why?

The next question is: Why do different species have horns in different locations on the body? Emlen suggests that the location of the horns depends on the organ that is least required by that particular beetle species. Nocturnal species need large eyes and, in support of Emlen's proposal, horns in these species tend to be positioned away from the eyes. Similarly, species that need to fly considerable distances to locate food are predicted to have horns that develop away from the wings, although whether this is the case in such species has not yet been determined.

The particular cost that the Emlen work uncovers provides a new focus to efforts to unravel the effects of sexual selection on the evolution not only of dung beetle horns, but also of the elaborate structures of other animals. As Emlen points out, the antlers of deer and the tail of the peacock are grown and shed throughout adult life, whereas nearby organs are laid down during embryonic development. The cost of developing antlers or a tail will not be incurred at the same time as the cost of forming nearby organs. Thus, an inverse correlation between antler or tail size and neighboring organ size would not be expected. There are other sexually selected organs, such as the canine teeth of male primates used for fighting and feeding, that grow continuously during childhood and adolescence. Perhaps here, too, costs could be identified that would help to explain the variation in size of canines and other organs both within and between primate species.

Whatever the result of further investigations of such costs, the Emlen study shows how natural history and evolution can come together to provide new solutions to old problems. In a previous study (*5*), Emlen experimentally manipulated horn development in dung beetles. This approach provides an opportunity to understand the reasons for variation in horn size and shape, and to investigate the effects of, for example, allometry (covariation in the size of organs) and compensatory growth.

Of course, we should not be surprised that Darwin occasionally got it wrong, for he was ever the pluralist. After all, it was in the preface to his book on sexual selection (*2*) that he reminds us that "in the 'Origin of Species' I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind." Such a statement sounds more akin to Lamark's theory of the inheritance of acquired characteristics than to Darwin's theory of evolution by natural selection.

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PERSPECTIVES: NEUROSCIENCE

Drums Keep Pounding a Rhythm in the Brain

Michael P. Stryker

The rhythmic activity of neurons in the brain has fascinated neuroscientists ever since electrical potentials were first recorded from the human scalp more than 70 years ago. The rhythms of electrical activity in sensory neurons that encode visual information are known to vary markedly with attention. How does neuronal encoding differ for a visual stimulus that is the center of attention compared with one that is ignored? To answer this question, Fries *et al.* (*1*) simultaneously recorded electrical activity from several clusters of neurons in the V4 region of the visual cortex of macaque monkeys that were shown behaviorally relevant and distracter objects (see the figure). On page 1560 of this issue, they report a rapid increase in the synchronization of electrical activity in the gamma frequency range (35 to 90 Hz) in V4 neurons activated by the attended stimulus (that is, the stimulus on which attention is focused) but not in V4 neurons activated by distracter objects (*1*).

The neurophysiology of attention remains a puzzle. A simple and attractive hypothesis is that an attended stimulus behaves as though it were bigger and brighter than all of the other competing stimuli. To encode this bigger and brighter stimulus, neurons would need to somehow increase their electrical response. Although some experiments have shown the

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