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Department of Biology, Williams College, Williamstown, MA 01267, USA.
E-mail: sswoap@williams.edu

Visual Cognition: Rats Compare Shapes Among the Crowd

Rats can discriminate simple shapes visually, even if they are moved around, made smaller, or partially covered up; the strategy they use may help shed light on human brain mechanisms for discriminating complex features, such as faces.

Alberto Cruz-Martín
and Andrew D. Huberman

Look at any two people, places or objects, and you can almost immediately tell if they appear the same or different from one another. Indeed, the remarkable speed with which we can discern things based on their appearance suggests that our brains evolved specific circuitries for realizing 'same *versus* different' by vision. Despite the significance of object discrimination for day-to-day survival, the neural circuits and mechanisms that enable us to distinguish even the most basic shapes still remain unclear. A new study reported in this issue of *Current Biology* from Vermaercke and Op de Beeck [1] provides exciting new insights into how the brain might distinguish visual shapes under both clear and uncertain conditions.

Rodents as Emerging Models for Studying Visual Perception

What tools are available to probe the mechanisms underlying shape discrimination? Vision has long been studied using psychophysics and neuronal activity recordings, mainly in monkeys, cats and humans. That approach continues to provide insights into the structures, cell types and receptive field properties in the visual pathway [2], and the neural correlates of certain aspects of visual perception, such as directional motion [3]. In recent years, however, new genetic tools have raised the opportunity not just to record from, but also to label and control the activity of highly defined sets of neurons [4,5]. Because these genetic tools are most easily applied to rodents, the field of visual neuroscience is now rapidly expanding to include rats and mice as staple models for probing the circuits underlying perception and decision-making [6].

There are obvious barriers to studying vision in rodents, not the least of which is that rodents view the world at much lower resolution than do primates [6,7]. Nonetheless, recent experiments have shown that rodent visual circuits bear many similarities to those of larger species [6,8–10]. Indeed, many neurons in the primary visual cortex of mice (V1) have receptive fields that are as highly tuned as those found in primate V1; mice just need to see larger stimuli in order to activate those neurons [10]. Are the boundaries on studying visual perception in rodents therefore simply a matter of scale? Or could it be that rodents are fundamentally limited in terms of their ability to carry out complex 'higher order' tasks? Moreover, given that the ultimate goal is to understand how humans make sense of the visual world, it is crucial to determine not just if rodents can perform complex visual discriminations, but the strategies they use.

A High-Throughput Paradigm for Probing Shape Recognition

In their paper in this issue, Vermaercke and Op de Beeck [1] report a paradigm for testing shape recognition in rodents. A water-deprived rat was placed into a chamber viewing two screens: one displaying a triangle, and the other displaying a square. In order to receive a water reward, the rat was required to touch a sensor near the screen displaying the square. Rats quickly learned this task, which is somewhat similar to tasks used in previous studies [11]. A key strength of this paradigm is that, because of their highly motivated state (the rats were thirsty) and the short time required to access reward (the chamber was small), the rats performed thousands of trials over a relatively short period of time. That provided a high-throughput, quantifiable platform for probing the strategies underlying shape discrimination.

'Bubbles' Reveal Where and How Rats Discern Shapes

Once they established that rats could perform the discrimination task, Vermaercke and Op de Beeck [1] explored which features of the visual stimuli the rats used to distinguish triangles from squares. Round masks called 'bubbles' were introduced to various portions of the visual stimuli such that, on any given trial, parts of both the square and triangle were occluded from view (Figure 1). After the experiment, the authors analyzed the

statistics of the images that led to errors (trials when the rat went to the screen displaying the triangle) *versus* the statistics of the images that led to reward (trials when the rat went to the screen displaying the square). By 'reverse correlating' the image statistics with trial performance in this way, the authors were able to determine which portions of the visual stimuli were most relevant for shape discrimination.

Vermaercke and Op de Beeck [1] found that rats relied more heavily on the information in the lower portion of the display. As the authors aptly note, this strategy deviates from the 'ideal observer' scenario [12] — a psychophysical metric based on the theoretically optimal strategy of evaluating every pixel in the visual scene. Thus, rats use only a portion of the visual information available to them in order to discriminate shapes.

Rats Distinguish Shapes Irrespective of Position
One could imagine that rats do not really compare visual shapes *per se*, but rather that they adopt a simple strategy based on local differences in screen brightness, such as "the square is displayed on the screen that is brighter at the bottom". Vermaercke and Op de Beeck [1] tested this idea by analyzing the set of trials when bubbles occluded the lower parts of the image. Interestingly, the authors found that, when the lower field was covered, the rats adapted their strategy to compare the upper visual field instead. Thus, rats are not cemented to a fixed spatial regime for discriminating shapes. They may indeed have a simple, reflexive strategy that relies on lower field analysis, but as Vermaercke and Op de Beeck [1] show, rats can adopt new visual search and shape comparison strategies if that is what is required to satisfy their thirst.

Scale-Invariant Shape Discrimination
Can rats learn the difference between a square and a triangle even if those shapes are made smaller or moved to different locations within the display? In a second set of experiments (called 'Phase II'), the rats were tested for their ability to recognize shapes that were reduced to half of their initial size, and randomly placed within each display. As Vermaercke and Op de Beeck [1] point out, this required the rats to shift from a simple strategy of comparing
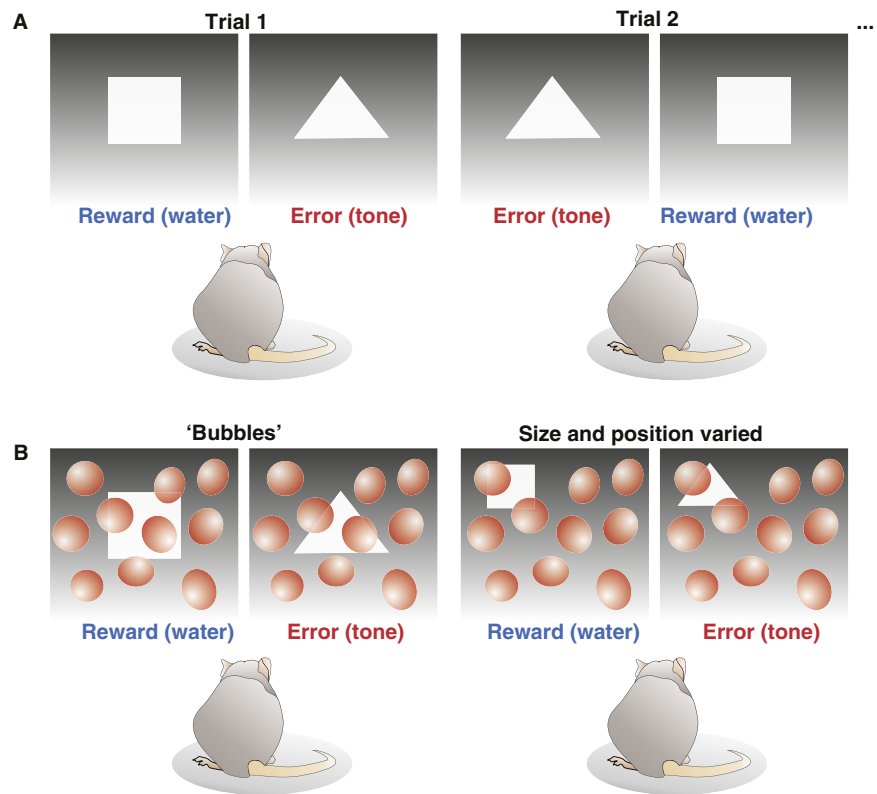
Figure 1. Shape recognition testing in rodents.

(A) Top panels display the basic stimuli and experimental design whereby a rat has to visually discern a triangle from a square in order to receive a water reward. The reward source is coupled to the location of the screen displaying the square, which varies randomly from trial to trial. (B) Lower panels illustrate the 'bubbles' paradigm in which the test shapes are partially occluded and in some cases are also moved and/or made smaller. In the actual experiment, achromatic Gaussian blobs, rather than red balloons, were used as 'bubbles'. See [1] for details.

matched locations in the two screens to a 'higher-order' strategy involving local comparisons of pixel content. In other words, the rats had to decide whether a given dark or light portion of the screen belonged to the shape or not. The rats' performance initially dropped under these conditions but, with time, they learned to identify the triangle and the square nested among the bubbles, and discriminate them from one another. This is particularly intriguing because position and size invariance are visual challenges that humans confront every day as they search for physical objects in space.

Rats *versus* Humans
Another unique strength of the Vermaercke and Op de Beeck [1] study is that the authors directly compared rat *versus* human psychophysical performance. After adjusting the task to account for differences in spatial resolution, and so forth, human subjects

were asked to distinguish squares and triangles masked behind bubbles. Some interesting differences quickly became apparent. First, humans never showed a bias towards particular portions of the display. Second, humans scanned and compared most of the visible area of the square and the triangle, indicating they act closer to the ideal observer model. Third, whereas none of the rats ever achieved >80% correct trials, humans achieved near perfect performance. The authors point out, however, that in a water-escape paradigm [13] rats too can exhibit near perfect discriminations, indicating that motivational state must be taken into account when comparing the performance thresholds of rodents and humans.

Implications for Understanding Visual Circuits
The new findings described by Vermaercke and Op de Beeck [1] extend on those from previous

studies [11,13–16] by exploring complex aspects of shape discrimination, its context dependence, and the underlying strategies that rats follow. Their work also provides an important step forward toward the goal of linking specific cell types and circuits with higher order visual perceptions. One can now imagine combining the psychophysics paradigm described here with a head-fixed or mobile imaging protocol [16–18], to directly monitor and control [4,5] the activity of the brain circuits hypothesized to mediate shape recognition. These are truly exciting times for studying visual perception in rodents. As Vermaerke and Op de Beeck [1] rigorously show, rodents not only see, they can also perform discrimination tasks that parallel the visual challenges humans face every day. The general neural circuit mechanisms of shape perception are therefore within reach.

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Department of Neurosciences, Neurobiology Section in the Division of Biology and the Department of Ophthalmology at the University of California, San Diego, CA 92093, USA.
E-mail: ahuberman@ucsd.edu

Human Microbiome: A Genetic Bazaar for Microbes?

A recent study suggests that lateral gene transfer has been particularly intense among human-associated microbes. What can this tell us about our relationship with our internal microbial world?

Morgan G.I. Langille,
Conor J. Meehan, and Robert G. Beiko

The transfer of genetic material between organisms, independent of a reproductive cycle, is referred to as lateral gene transfer or LGT. While no class of genes is unaffected by the phenomenon, LGT appears more frequently to involve genes that directly affect the adaptation of prokaryotes to their environment. For example, investigation of gene origins in *Legionella pneumophila* found that several genes of eukaryotic origin were involved in increased virulence in this pathogen [1]. This is a strong indicator that long-distance lateral gene transfer events can have a significant impact on the virulence of a bacterium, including species important to human health. If LGT is a major avenue of microbial adaptation, then microbes may be able to adapt very quickly to new anthropogenic habitats in unpredictable ways. In a recent paper, Smillie and colleagues [2] comprehensively analysed over 2000 prokaryotic genomes to examine the role of LGT in a range of habitats, including the human body; their most striking finding was that pairs of human-associated species have an implied rate of LGT that is 25 times higher than pairs living together in other environments.

A successful LGT event proceeds in three critical steps: transfer of genetic material from a donor to a recipient organism; integration of the transferred DNA into the recipient genome; and fixation of some or all of the transferred material due to selection or drift [3]. LGT between closely related organisms is most likely to be successful when there is a compatibility of exchange mechanisms (such as plasmids or transducing phage) and gene expression mechanisms, and the ready integration of acquired material via homologous recombination. However, genes have been shared between organisms from different phyla and domains of life, indicating that phylogenetic or taxonomic distance is not an absolute barrier to transfer [4–6]. An important question, difficult to answer by bioinformatics alone, is whether a putatively transferred gene is actually used by the recipient lineage, or is undergoing a process of mutational decay that will ultimately result in loss from the genome [7]. It is possible that many inferred LGT events are of no benefit to the organism, and merely reflect a "churn" of DNA into and out of the genome [8].

Robust identification of LGT events is challenging, and many phylogenetic and non-phylogenetic approaches have been developed [9,10]. Smillie *et al.* [2] utilised a public database of 2,235 completed bacterial and archaeal genomes, along with their associated