



Review

Invariant visual object recognition and shape processing in rats



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HIGHLIGHTS

- Rats are capable of invariant visual object recognition.
- Rats spontaneously perceive different views of a visual object as similar to each other, that is as instances of the same object.
- Rats are capable of a multifetural, shape-based visual processing strategy.
- Rats can learn complex, configural visual discriminations.
- Rats spontaneously process composite visual patterns according to perceptual grouping cues.

ARTICLE INFO

Article history:

Received 21 June 2014

Received in revised form

19 December 2014

Accepted 25 December 2014

Available online 2 January 2015

Keywords:

Invariant recognition

Rat

Rodent

Shape processing

Pattern vision

ABSTRACT

Invariant visual object recognition is the ability to recognize visual objects despite the vastly different images that each object can project onto the retina during natural vision, depending on its position and size within the visual field, its orientation relative to the viewer, etc. Achieving invariant recognition represents such a formidable computational challenge that is often assumed to be a unique hallmark of primate vision. Historically, this has limited the invasive investigation of its neuronal underpinnings to monkey studies, in spite of the narrow range of experimental approaches that these animal models allow. Meanwhile, rodents have been largely neglected as models of object vision, because of the widespread belief that they are incapable of advanced visual processing. However, the powerful array of experimental tools that have been developed to dissect neuronal circuits in rodents has made these species very attractive to vision scientists too, promoting a new tide of studies that have started to systematically explore visual functions in rats and mice. Rats, in particular, have been the subjects of several behavioral studies, aimed at assessing how advanced object recognition and shape processing is in this species. Here, I review these recent investigations, as well as earlier studies of rat pattern vision, to provide an historical overview and a critical summary of the status of the knowledge about rat object vision. The picture emerging from this survey is very encouraging with regard to the possibility of using rats as complementary models to monkeys in the study of higher-level vision.

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1. Introduction

The greatest challenge that any vision system (whether biological or artificial) has to face is the extraction of the behaviorally relevant content of visual scenes from the largely variable images collected, as an input, by the retina [1–3]. Within the domain of object recognition, this challenge manifests as the need of recognizing previously seen objects, despite the fact that any new encounter with these objects will often result in radically different retinal input images. The process of recognizing objects in spite of this substantial variation in their appearance is commonly known as *invariant recognition* or, more precisely, *transformation-tolerant recognition* [3–6]. Quite obviously, the problem of understanding how the brain achieves invariant recognition is tightly linked to the problem of understanding how the brain processes and represents the shape of visual objects. Although shape is not a well-defined concept, intuitively, shape features are those properties of the visual objects that more reliably allow distinguishing each object from any other one in the retinal input images. As such, global visual attributes that are not very diagnostic of object identity (because they are likely shared by many different objects), such as overall brightness, contrast, size, area, etc., are commonly considered as *lower-level* visual properties, rather than shape features (and a processing strategy relying on such features is commonly considered as a lower-level strategy). On the other hand, specific arrangements of local straight and curved boundaries, oriented edges and corners [7–10], as well as oriented and unoriented local contrast patterns [11–13] and image fragments [14,15] (i.e., attributes that more uniquely define visual objects) are typically viewed as proper, *higher-level* shape features (and a processing strategy relying on such features is commonly considered as a higher-level strategy). Bearing in mind that a rigorous (or agreed-upon) definition of shape feature complexity does not actually exist (e.g., see [16] for a discussion), one could tentatively define an *advanced* visual processing system as following – a system capable of extracting from the retinal input those higher-order (shape) features that are diagnostic of object identity across the many (unpredictable) image transformations each object undergoes during natural vision. Throughout the article, terms such as *lower-level properties*, *higher-level features* and *advanced processing strategy* will be used according to the definitions provided above.

These definitions make very explicit the challenge at the core of object vision – the requirement of maintaining a high degree of specificity for the features defining the identity of visual objects, while, at the same time, disregarding the huge variation in the

appearance of such diagnostic features [17]. Computationally, balancing this trade-off between specificity and invariance makes the development of machine vision systems extraordinary challenging [4,5,17,18]. On the other hand, humans are capable of detecting and classifying objects out of tens of thousands of possibilities [19] within a fraction of a second [20,21], which implies that their visual system implements an extremely efficient and reliable machinery to process object information. Studies in nonhuman primates have revealed that such a processing is carried out along a hierarchy of visual cortical areas known as the *ventral visual pathway* (or *stream*) [4,6,22–25]. This pathway starts in primary visual cortex and culminates in the anterior part of the inferotemporal cortex, which conveys the most explicit representations of visual objects – that is, the representations that allow the easiest read-out of object identity (and generalization to identity-preserving image transformations) using simple linear decoders [16,26–28]. Unfortunately, the neuronal mechanisms underlying the formation of increasingly explicit representations of visual objects along the ventral stream are still poorly understood. This is likely a consequence of the extraordinary complexity of the primate visual system [29–31] and of the limited range of experimental manipulations that primate studies allow at the molecular, synaptic, and circuitry levels. This disproportion between the complexity of the neuronal architecture under investigation and the limited array of experimental approaches that are available to carry out such an investigation has recently led several vision scientists to explore the potential of rodents as models of visual functions. With regard to object recognition, whether rodents can actually serve as useful models to understand its neuronal basis crucially depends on how advanced their visual recognition behavior is. In the following, I will critically review most of the literature concerned with rat pattern vision, shape processing and visual object recognition, arguing that there is enough behavioral evidence to suggest that this species does embody some of the core mechanisms underlying invariant object recognition. As such, the rat and, by homology, the mouse (given the similarity between the visual systems of these species [32–35]) may represent a powerful complementary model to the nonhuman primate in the invasive investigation of the neuronal substrates of object vision.

2. Visual or not visual?

Rats and mice are the more widespread laboratory animal species, accounting for over 80% of all research animals used in the European Union [36]. Vision, on the other hand, is arguably

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