

Chapter 2

Is Visual Processing in Primates Strictly Hierarchical?

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Abstract Over the past four decades, the dominant view of visual processing in primates is that the complexity of feature analysis increases as information flows from primary visual cortex rostrally through regions of the temporal lobe, into area TE, where whole complex objects are represented. This view is consistent with observations that TE neurons are selective for complex objects such as hands and faces. We test a major prediction: bilateral removal of area TE will damage high-level visual object categorization, such as distinguishing cats from dogs. After removal of TE, this type of categorical classification is only mildly impaired in old-world monkeys. However, when the images are degraded by a small amount of visual noise, the monkeys are virtually unable to correctly classify morphs of cats versus dogs. This raises the possibility that area TE makes it possible to identify partially obscured objects, that is, it is critical for pattern completion.

Keywords Visual hierarchy · Visual categorization · Drift diffusion models

2.1 Introduction

For decades, it has been known that bilateral removal of inferior temporal cortex, specifically area TE, in rhesus monkeys is followed by a severe deficit in learning to discriminate between two simple black and white shapes [1]. It is also known that a subpopulation of neurons in area TE are sensitive to the categorical membership of stimuli, even when those stimuli are made perceptually ambiguous by mixing between categories (morphing) [2]. These two sets of data are considered consistent with the hierarchical model of visual image processing, where simple features are analyzed in the early visual system, and these features are combined as information

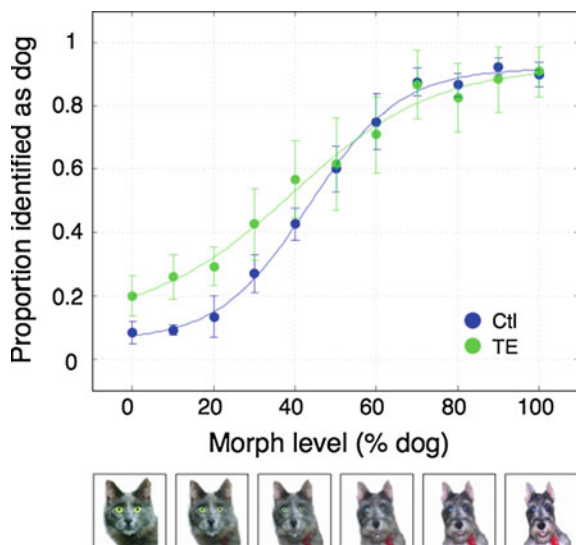
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flows from primary visual cortex to inferior temporal cortex, giving rise to the representations, and presumably perceptions, of complex images such as face and hands in area TE [3–5]. Based on these two observations, and the idea of hierarchical processing of visual stimuli in the primate visual system, it has been proposed that area TE would be critical for monkeys to categorize morphed stimuli according to the stimulus that comprises the largest proportion in the morph, although this had not been tested directly. Here, we report briefly on the outcome of experiments designed to probe the assumption directly.

2.2 Methods

In preparation for neuronal recording experiments, we carried out a behavioral experiment using a method for rapid training of monkeys to perform categorical discrimination based on visual generalization. Monkeys are taught to detect when a red visual target turns green by releasing a touch sensitive bar (see [6] for detailed method). A second visual stimulus, in this case an image morphed between cat and dog, is presented. When the stimulus contains a greater proportion of dog-like features, the monkey receives a drop of liquid reward by releasing when the green target appears. If the stimulus is more cat-like, no reward is available; the monkeys quickly learn that the best strategy is to release the bar as early as possible to get to the next trial, where a reward might be available. The performance of unoperated control monkeys was compared to monkeys with bilateral inferior temporal area TE removals.

Fig. 2.1 Performance of normal monkeys (*blue line*, $n = 3$, +se) and monkeys with bilateral area TE removal (*green line*, $n = 3$, +se) in categorizing morphs between (on the abscissa) cats (*left*, fully cat) and dogs (*right*, fully dog) in the first session that the morphs were presented. The proportion of trials identified as dog is on the ordinate (color figure online)



2.3 Results

Within one session, normal monkeys and those with bilateral area TE removals learn to categorize morphed images (Fig. 2.1).

In overall performance, the monkeys with the TE removals are slightly less accurate when compared to control monkeys. When the images undergo some transformation such as rotation, or decrease in signal such as adding even small amounts of visual noise to the stimuli, the monkeys with the TE removals show a considerably greater deterioration in performance than controls (Fig. 2.2).

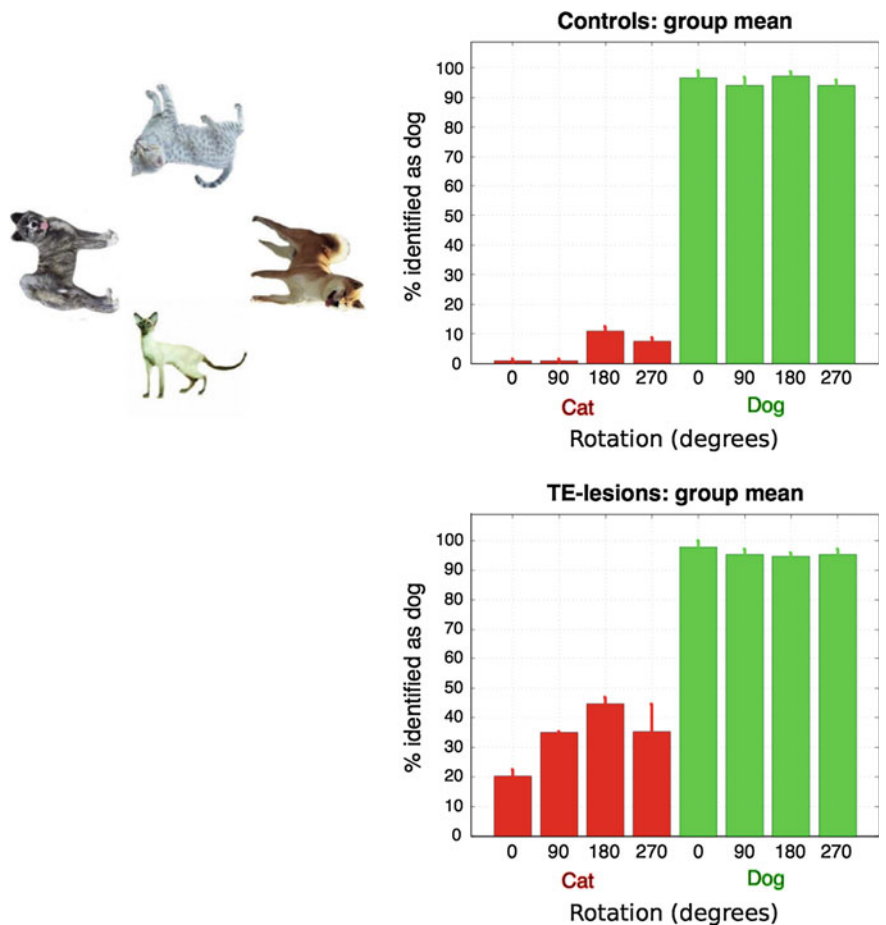


Fig. 2.2 Performance in distinguishing cats from dogs, as a function of rotation. For cats (*red bars*) the optimal response would be to release during the presentation of the red target, indicating that a cat appeared. The monkeys with TE removals have considerable difficulty in doing so, especially for exemplars that are rotated away from normal upright. Illustration to *left* shows examples at the degrees of rotation tested (color figure online)

When we measure the reaction time to abort unrewarded trials, both groups take considerably longer to respond as the stimulus mixture approaches a 50:50 proportion. This occurs in the face of less accuracy despite the longer time taken to decide. Data like these are often described with a drift diffusion model, where a particle takes a random walk in one dimension with a constant drift. The predicted decision time is the time to reach a boundary. In our task, for the morphs with greater mixing, the monkeys are deciding earlier than predicted by the drift diffusion model, a situation that has been seen and modeled before [7]. Our interpretation is that the monkeys are willing to sacrifice time to collect additional information up to a point, but then in a probabilistic manner they make a decision to end trials that are taking too long; they act as if there is an upper bound on how long to wait that is conditioned on the degree of morphing. Because both groups of monkeys increase their reaction times to the same degree, we suggest that the integration of visual information occurring before the monkeys make a choice is independent of area TE.

Based on the physiological results previously published, just as happened with lateral prefrontal cortex removals, we expected our monkeys with TE removals to be devastated in tests of categorization [2, 8] and they were not. These results raise an issue that is central for studying neural coding; how to infer the contribution of a brain region to a behavioral function based on neuronal selectivity alone in the absence of any manipulation to demonstrate causality.

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