

Perceptual Memory of Cognitively Defined Contours: A Rapid, Robust, and Long-Lasting Form of Memory

Many aspects of perceptual memory, such as the memory of cognitively defined contours, are difficult to measure objectively. To this end, we have developed stimuli made up of random polygon arrays, with an embedded figure made up of a subset of the polygons (see Figure 1). The contours of the embedded figure are initially hard to see, until the figure is cued in some manner, for example, by movement or closure. We tested both human and owl monkey subjects, and found that once subjects "learn to see" the embedded figure, it is readily seen again. This memory is robust and long-lasting. Additionally, this memory is not rotation invariant, that is, rotating the entire stimulus degrades both accuracy and reaction time. We hypothesize that this type of learning takes place in visual cortex, and that there are neurons that will respond differently to the same polygon array before and after cueing the cognitive contour. Our paradigm has the advantage that a monkey can easily learn a novel stimulus within the length of time that we can record from a neuron. We plan to record single and multi-unit activity in the owl monkey's visual cortex, before, during, and after learning these cognitively defined figures.

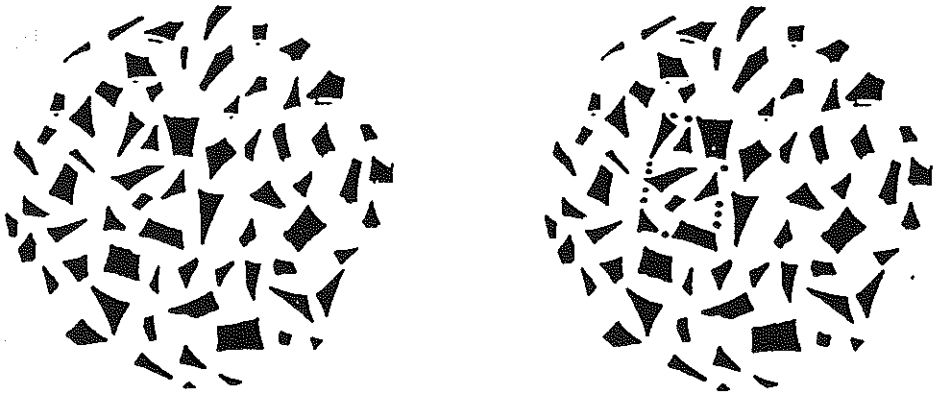


FIGURE 1 Sample stimulus pattern to test visual perceptual memory. A rectangular figure is embedded in the random polygon array. The figure is not obvious until it is cued (by closure in this example), shown on the right. The subject's task is to report the orientation of the embedded figure before and after cueing. The stimulus was generated by cutting up small slips of black paper and sprinkling them on a white background. The image was then captured as a computer bitmap, using a CCD camera and a frame grabber. We can generate an unlimited number of novel stimuli with this method.

INTRODUCTION

COGNITIVE CONTOURS

Viewed from an ecological perspective, the main task of the visual cortex is to extract behaviorally meaningful patterns from noisy and ambiguous images of the natural world. Because of the inherent ambiguity of natural images, multiple and conflicting interpretations may be possible. The task of the visual cortex is to select the most appropriate interpretation quickly and reliably. This task must often be performed on the basis of incomplete information. This function requires a kind of perceptual learning which, we hypothesize, occurs in the visual cortex.

A classic example is represented in Figure 2 taken from the Mooney series. Most subjects initially find it very difficult to see the greyhound embedded in the noisy background. Without cueing, most subjects eventually detect the dog's nose or trunk and the perceptual solution seems to spatially propagate to other parts of the dog's anatomy in the process of segregating the figure of the dog from the noisy background. The spatial propagation within feature space may involve an underlying propagation within a neocortical map.⁴ Once the dog has been discerned, it is quickly seen again if the figure is reexamined months or years later.

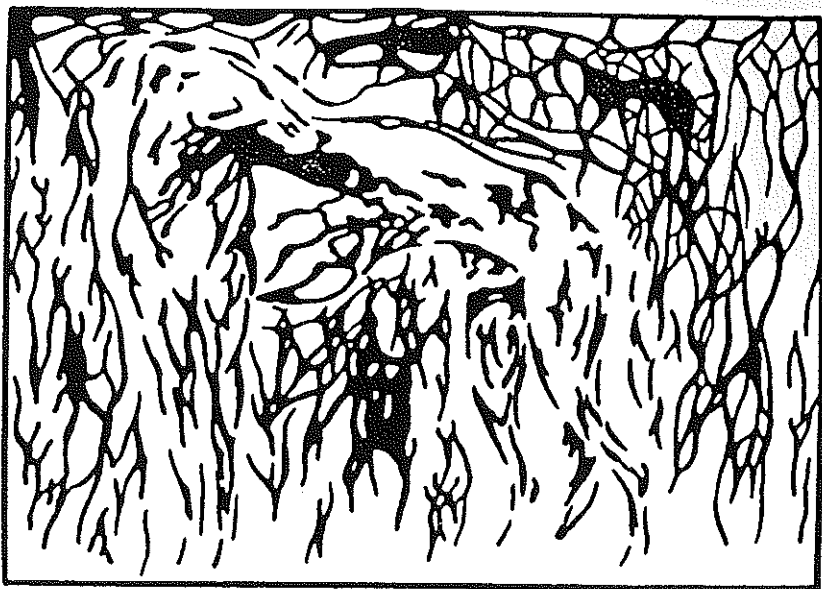


FIGURE 2 Greyhound embedded in a noisy environment. Copyright © C. M. Mooney¹⁵; reprinted by permission of the author.

These striking, but highly qualitative perceptual learning phenomena are difficult to study objectively. We have developed a method to study this putative learning function of visual cortex through the use of cognitively defined contours, which are the borders of patterns embedded in a noisy background. We create stimuli that are made up of randomly arranged polygons, with an embedded rectangle composed of a subset of the polygons.

The embedded figure is not obvious to the observer until it is cued in some manner, such as by closure (Figure 1) or motion. These patterns are difficult to see until revealed by special cues such as the brief movement of the embedded pattern with respect to the background of polygons. Our perceptual experience with these cognitive contours is that, once they have been revealed, they are very readily seen again and that this capacity persists for months or years for a particular stimulus pattern.

THE PERCEPTUAL MEMORY SYSTEM

The learning of cognitive contours is similar to a type of long-term learning described by Warrington and Weiskrantz²⁵ in amnesiac patients. These patients, who



FIGURE 3 Sample item from the incomplete-pictures task of Gollin.⁸ Reprinted from Milner, Corkin, and Teuber¹⁴ by permission.

had severe deficits in their capacity to remember recent events, showed a remarkable ability to identify visual patterns when they viewed fragmented residues of whole patterns. For example, in Figure 3, amnesiac patients who had previously viewed these images retained the ability to identify the airplane on the basis of the fragmented images in sets 1 and 2.

The amnesiac patient, HM, whose medial temporal lobe including hippocampus had been surgically removed bilaterally, showed retention of his capacity to identify fragmented images in these tests.¹⁴

This capacity has been termed "priming" and has been postulated to be performed by a "perceptual representation system" thought to reside in extrastriate visual cortex.²⁴ Retention due to priming is long lasting with no decay after 1 week^{11,16} and some retention after 3 months.²⁵

Recently, PET studies have revealed that priming with visual images produces reduced blood flow upon retesting in a region of right occipital extrastriate visual cortex in human subjects.²³ This result suggests that priming facilitates the neural mechanism for perceiving images. Consequently, less energy is expended and presumably the perceived image is represented with a higher signal-to-noise ratio in the neural populations involved. Access to priming memory is hyperspecific in that it depends, among other things, on the exact geometrical configuration of the priming stimulus.²⁴ Hyperspecificity of access suggests that priming memory may be stored within the visuotopically mapped cortical visual areas.

These experiments are an extension into the temporal domain of the exploration of the nonclassical responses of visual cortical neurons.

Although neglected until fairly recently, a large number of studies of visual neurons indicated that the true receptive fields for most neurons extended well beyond the classical receptive fields as mapped by conventional stimuli against a featureless background.^{2,3,6}

These results indicated that visual neurons often responded in very specific ways to stimuli presented outside their classical, defined receptive fields, which offered a potential mechanism for the local-global integration of visual information.

Recently these results have been extended to "illusory contours" that were implied by stimuli that were entirely beyond the classical receptive field for neurons in the second visual area.¹⁷ A similar "interpolation" of stimuli presented outside the classical receptive field has also been found in V1.⁷

The perceptual memory system is distinct from other forms such as declarative memory or habituation.²⁴ The neural mechanisms underlying the memory for cognitive contours are probably different from those for delayed-matching-to-sample^{5,13,10} and stimulus familiarity⁹ that have been studied in area V4 and inferior temporal cortex.

The functional properties of visual cortical neurons have been viewed as very highly specialized filters set to detect different aspects of visual stimuli such as the direction of motion, binocular disparity, orientation, or color. We suggest that in addition to these classical features of visual cortical neurons, there is the capacity to respond selectively to patterns on the basis of prior experience. In other words, we hypothesize that the visual cortex can "learn to see" ambiguous patterns embedded in a noisy background. The neural mechanisms of learning may be mediated by changes in functional connectivity. Ahissar and colleagues¹ measured functional connectivity *in vivo* by calculating spike cross-correlation between two or more neurons. They found that changes in functional connectivity are dependent on changes in firing correlation, but only for behaviorally relevant stimuli. Merzenich¹² has also observed changes during the learning of tactile discriminations in the synchrony of neural activity in somatosensory cortex. We plan to determine whether the spike cross-correlation between neurons changes during learning to see embedded figures.

We further suggest that these perceptual learning capacities may be localized in a manner analogous to the evident perceptual specializations present in the various areas. For example, perceptual learning related to differential motion might be preferentially related to area MT. To test this idea we will use different types of cues (differential motion, closure, shading and stereoscopic depth) to determine whether the nature of the cue might affect the site of storage within the visual cortical areas.

METHODS

WHY OWL MONKEYS?

Studies of the visual cortex have never been done in awake-behaving owl monkeys. The development of this preparation offers several major advantages for the study of the neural mechanisms of perception.

1. The organization of the cortical visual areas have been mapped in the owl monkey.^{20,21,22}
2. The visual cortex is relatively smooth. Areas DL and MT, and many other cortical visual areas are located on the exposed, smooth dorsolateral surface of the brain. This allows us to easily find and sample these extrastriate visual areas. Much of the comparable visual cortex lies deeply buried in the convoluted brain of macaque monkeys, and visual areas are more difficult to localize.

3. The accessibility of extrastriate visual cortex facilitates possible future experiments. Specific portions of the visual field map in particular areas could be temporarily deactivated by local injections of drugs blocking neural activity. Additionally, the owl monkey's smooth visual cortex is particularly well suited for optical recording.

We have developed new training procedures and built equipment specially adapted for owl monkey training and electrophysiology. Owl monkeys do not respond well to standard procedures used for training macaque monkeys. Owl monkeys, and all other new world monkeys, cannot sit comfortably in training chairs designed for macaque monkeys because they lack ischial callosities. We designed a special training apparatus consisting of a lexan alcove with two keys that attaches to the cage in which the monkey lives. This alcove is designed to accommodate the owl monkey's natural squatting posture. The monkey learns to enter the alcove and report discrimination of various images by pressing one of the two keys for a fruit juice reward.

PSYCHOPHYSICAL METHODS

In order to measure perceptual learning and memory, we tested the capacity of both monkeys and humans to detect these figures embedded in noise. The embedded figures were either horizontal or vertical in orientation. The subjects task was to report the orientation in a forced-choice paradigm, by pressing right key for horizontal and the left for vertical figures.

In a typical experiment, blocks of 10 to 30 novel stimuli were presented in pseudo-random order. For the initial block, each stimulus was presented without any cue for the embedded figure, and the subject was to respond to the novel stimulus. After the subject responded, we immediately activated the cue for the embedded rectangle. Owl monkeys were allowed to respond to the cued figure, while human subjects only viewed the cued stimulus. For the next block of presentations, the stimuli were cued only for incorrect responses. For the owl monkeys, a final block was added, during which the stimuli were presented without any cues, to prevent the monkey from simply waiting for the cues before making a judgment.

As a control condition, to ensure that the subjects are performing the figure detection and not simply memorizing the entire figure, we measured the effects of rotating elements in the surround with rotating elements forming the contour boundary in the embedded figure. If the subject is responding to the embedded figure and not simply memorizing the entire array, changing elements forming the boundary of the embedded figure should disrupt performance more than changing surround elements (see Figure 7).

INITIAL RESULTS

OWL MONKEYS AS BEHAVIORAL SUBJECTS

Owl monkeys have been used extensively as subjects for motor, auditory and somatosensory tasks.^{18,19} Not surprisingly, we found that owl monkeys are easily trained to perform visual discrimination tasks, and are very good psychophysical subjects—we have trained two owl monkeys to successfully perform this task. Both monkeys that we trained performed this task very well; one monkey learned over 100 different stimulus patterns. The monkeys work daily and performs up to 1500 trials, in two to three hours of steady work.

PSYCHOPHYSICS

We hope to record neural activity while the monkey is in the process of learning new stimuli. The time that it takes for the monkey or a human subject to learn a new stimulus varies from one cued presentation for easy figures, to many viewings of the stimulus for more difficult ones. Reaction time and its standard deviation both decrease as the stimuli are learned (see Figure 4). The monkey can learn novel stimulus patterns in a single training session, within the approximate time that we can record from a single neuron. Data from the first 50 trials of learning a new pattern is shown in Figure 5.

The memory is very long lasting. After several weeks without exposure to the same stimuli, there is no decrease in accuracy. There is an initial increase in reaction time followed by a return to previous performance levels (Figure 4). We tested subjects up to six months after the initial learning and found that the memory of learned figures was still intact.

We also found that performance is not rotation invariant for both owl monkey and human subjects. Rotating the entire polygon array, or displaying the array as a mirror image degrades both accuracy and reaction time. Typical human performance is shown in Figure 6.

Results after rotating elements in the embedded figure within Figure 7. Rotating elements in the embedded figure significantly disrupts learning. Rotating elements in the surround had no significant effects.

CONCLUSIONS

We have demonstrated that owl monkeys can be easily and successfully trained as psychophysical subjects. This will allow us to exploit the major advantages of

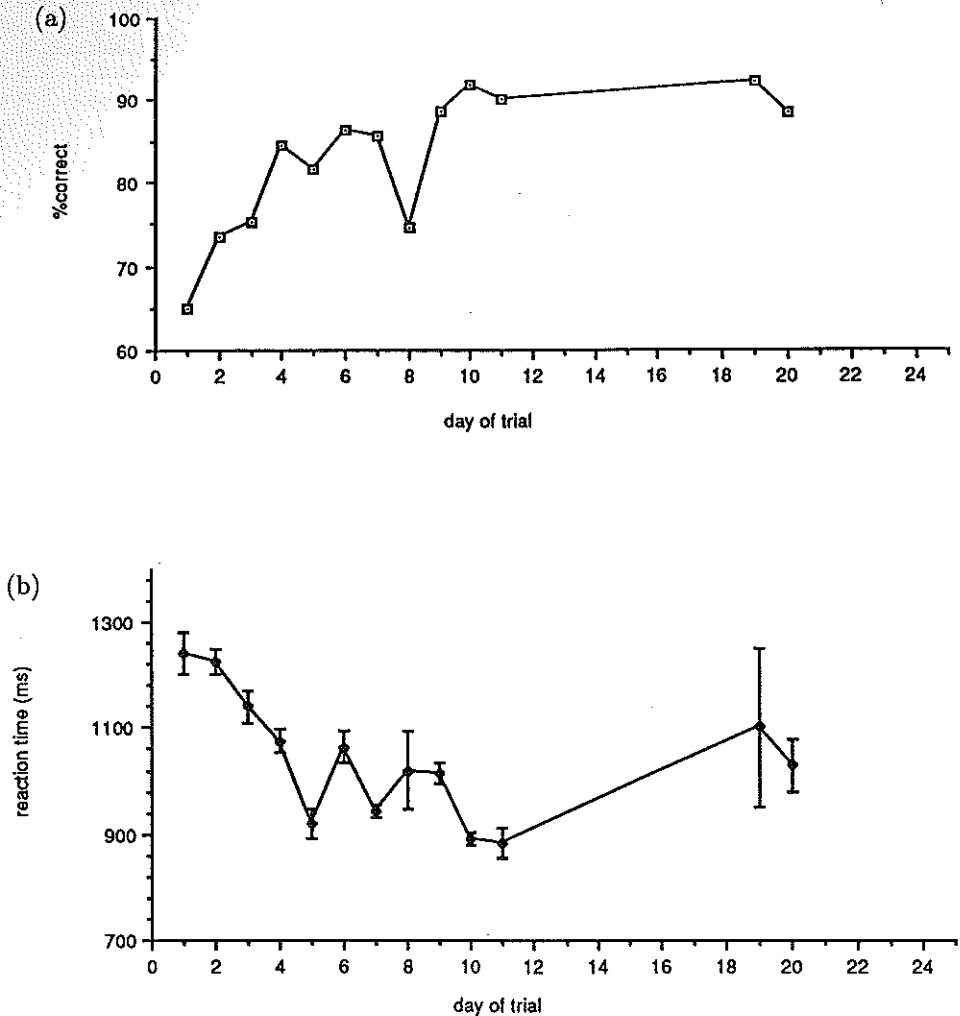


FIGURE 4 Typical owl monkey performance for ten new stimuli. Top: Performance goes from chance levels (54 percent, Day 1 .w/ cue) to 76 percent (Day 1 after cue), and stays at steady levels, even after a 13-day break (Day 5–Day 18). Bottom: Reaction time and standard deviation. Reaction time improves slightly from Day 1 to Day 5. Standard deviation of reaction time also decreases from Day 1 to Day 5. After a 13-day break, there is an initial increase in the standard deviation of the reaction time, followed by a return to previous performance levels.

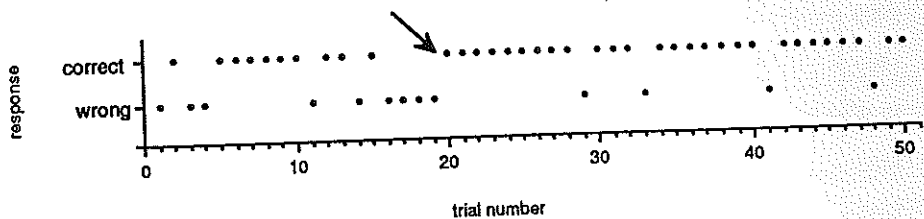


FIGURE 5 Monkey's performance for learning a new stimulus pattern on a trial by trial basis. Trial numbers 1-20 were cued and trial numbers 21-50 were presented without cues. This pattern was pseudorandomly interleaved with a group of 30 stimulus patterns. The elapsed time for the 50 trials was about 45 minutes (516 total trials within this time).

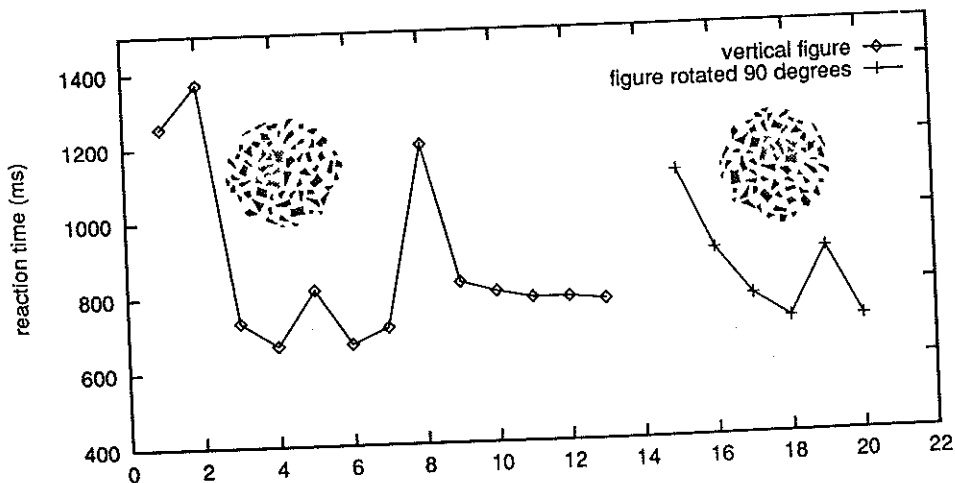


FIGURE 6 Typical human performance, measured by reaction time, when the entire stimulus is rotated by 90 degrees. Trials 1-13 show an improvement in reaction time, which stabilizes around 800 ms. Trials 15-20 show an initial increase in reaction time after the entire figure is rotated by 90 degrees.

the owl monkey preparation, the visuotopic maps of many visual areas on the smooth dorsolateral cortical surface. We have developed unique stimuli to test the phenomenon of perceptual memory, through the use of cognitive contours. The monkey can learn new stimuli within the time that we can record from single neurons. This learning is robust and long-lasting. Additionally, we can easily and quickly

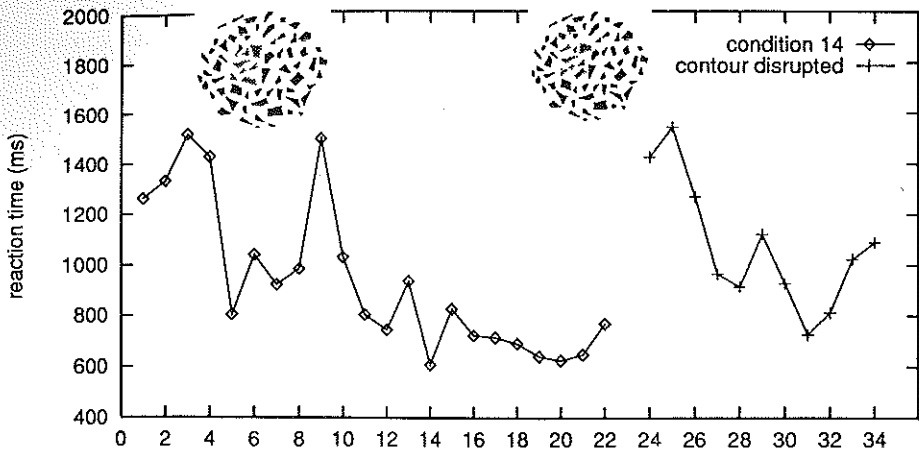


FIGURE 7 Control experiment where the contours of the embedded figure are disrupted. Polygons that make up the contours of the embedded figure are rotated by 90 degrees. These stimuli were interleaved with other learned stimuli. Trials 1–22 show typical reaction time improvement. Rotating the polygons in the embedded figure increases the subjects reaction time, reflected in trials 24–34.

generate an unlimited number of new stimuli and can tailor the contours of the embedded figure to the receptive field of each cell. We are now preparing to do single and multi-unit electrophysiology while the monkey is performing the perceptual memory discrimination task. We will also continue to study the phenomenon psychophysically using human subjects.

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