

Fig. 1. Responses of a cell recorded from area 18 in right hemisphere 12 mm lateral to the midline, on the anterior tip of the lunule sulcus about 3 mm in front of the 17-18 boundary. Cell was in layer 6. It responded best to a slit  $1^\circ$  long and  $0.125^\circ$  wide, oriented  $20^\circ$  clockwise from the vertical. The receptive field was approximately  $1^\circ$  by  $0.75^\circ$  in size, and in the right eye was situated  $1.75^\circ$  below and  $1^\circ$  to the left of the fovea. In the left eye it was displaced, relative to this,  $0.5^\circ$  to the right and slightly downwards. I: Both eyes stimulated together in anatomically corresponding regions (A). In B-E, position of stimulus to left eye was horizontally displaced to the right on the screen in steps of  $15$  min of arc. Maximum responses were obtained with a displacement of  $30$  min. (Displacement was produced by shifting direction of gaze of left eye to the left, with a prism.) Duration of each sweep was  $4$  s. II: A, Left eye, stimulated alone; B, right eye, stimulated alone; C, both eyes, stimulus to left eye shifted  $30$  min to the right. Projection screen was  $1.5$  m away from the monkey. With eyes fixed on the screen, maximum response to a long object moved in front of the animal occurred when the object was  $0.5$  m in front of the screen. For eyes fixed at infinity this would be equivalent to a stimulus about  $3$  m from the animal.

system of columns containing areas of similar receptive field orientation as is found in area 17 (ref. 6). Sequences of cells with the same receptive field orientation are rather brief, suggesting that the orientation columns are very narrow compared with the depth columns.

We have also studied hundreds of cells in area 17, but have found no convincing examples of binocular depth cells. In this respect the monkey seems to differ from the cat<sup>1,2</sup>. Possible differences between binocular depth cells in cat area 17 and monkey area 18 are the failure of most depth cells in the monkey to respond to stimulation of

either eye alone, and the linking, in the monkey, of vertical disparity to receptive field orientation.

Area 18 in the monkey seems, therefore, to have at least two independent functions, that of linking the two visual half fields across the vertical midline (as in the cat<sup>5</sup>), and the elaboration of stereoscopic depth mechanisms. The parts of 18 near the vertical meridian representation have both functions, whereas more peripheral areas probably lack the first.

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## Stereoscopic Vision in the Macaque Monkey: a Behavioural Demonstration

STEREOPSIS is the sensation of relative visual depth that results from the neural integration of dissimilarities in the images seen by the two eyes. These dissimilarities arise because an object in front of or behind a surface of reference determined by the fixation of the two eyes produces images that fall on non-corresponding points in the two retinas. As a distinct attribute of human vision, stereopsis has been studied extensively for many years<sup>1</sup>. Julesz has recently developed random-dot stereoscopic patterns which minimize monocular and familiarity cues to depth perception<sup>2</sup>. Such patterns have enabled the psychophysical basis of human stereopsis to be defined more precisely<sup>3-7</sup>. These patterns also seemed to be well suited for the investigation of stereopsis in animals by behavioural methods. In this study, random-dot patterns were combined with standard operant conditioning procedures to determine whether or not macaque monkeys have stereoscopic vision.

The subjects, two young stump-tail monkeys (*Macaca arctoides*), were restrained in a standard primate chair modified for operant conditioning. A flat square response key was mounted in front of the animal below the line of vision. Two overhead projectors cast the visual stimuli onto an aluminium screen  $1.6$  m away. Sets of oppositely polarized circular polarizers, mounted on the projectors and on goggles worn by the monkey, made it possible to confine stimuli to separate eyes. Because the use of goggles made it necessary to restrain the monkey from touching its face, a liquid reward was delivered through a solenoid valve and a conveniently located water pipe. Automated programming and recording equipment operated the apparatus.

The monkeys were taught to perform visual discriminations on a simple operant schedule involving a random but predetermined sequence of two different stimuli. One of the two stimuli to be discriminated, the "positive" stimulus, was presented for  $20$  s, during which ten presses of the key was defined as a correct response and fewer presses an incorrect response. The other stimulus of the pair, the "negative" stimulus, was also presented for at least  $20$  s, during which five or more presses were defined

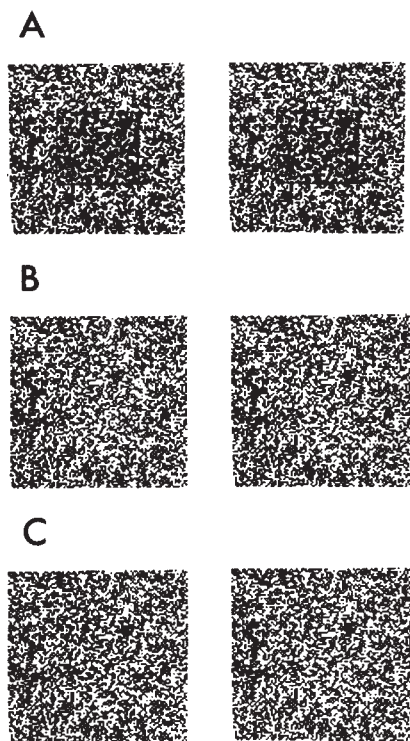


Fig. 1. Sets of random-dot patterns used in stereoscopic discriminations. *A*, Set of identical patterns with inner square 1.0 log unit darker than surround. *B*, Set of patterns giving rise binocularly to the appearance of an inner square lying behind the surround. *C*, Set of identical patterns, similar to those in *A* but without contrast, giving rise binocularly to no inner square.

as an incorrect response and fewer presses a correct response. The monkey was rewarded for correct responses by the positive stimulus. There were usually between forty and fifty discrete trials in a standard session, with approximately equal numbers of both positive and negative stimuli.

The visual stimuli were photographic copies of the stereoscopic patterns developed by Julesz, some examples of which are shown in Fig. 1. Each pattern consisted of a random-dot matrix containing two different areas, a surround and a small inner square. The entire pattern subtended a visual angle of  $11^\circ$ , and the inner square  $5^\circ$ . Because both areas were composed of random dots, the inner square could not be distinguished from the surround in a single pattern. The two patterns of a set were identical except that the inner squares in each were displaced horizontally in opposite directions relative to their surrounds. When a subject with normal stereoscopic vision views these patterns binocularly, each eye seeing only one pattern, the small inner square can be distinguished from the surround and appears to lie in front of the surround or behind it, depending on the direction of the horizontal displacement in the two patterns.

The monkeys were first taught to distinguish a set of identical random-dot patterns from a set of patterns similar in all respects except that the small inner squares were 1.0 log unit darker than the surrounds (see Figs. 1*A* and 1*C*). When the monkey had mastered this discrimination, the contrast was reduced stepwise until the inner square was barely distinguishable. The stereoscopic patterns were then presented to the monkeys. In the positive stimulus of the first discrimination, the inner squares were displaced horizontally toward the lateral edges of the separate matrices so that, when viewed binocularly, the small inner square would appear behind the plane of the surround. The animal was required to distinguish this from a set of random-dot patterns in which no inner square was distinguishable

during binocular vision. These stimuli are illustrated in Figs. 1*B* and 1*C*. During the first session of fifty trials in which this discrimination was presented, one animal performed with an accuracy of 90 per cent, the other with an accuracy of 70 per cent. Subsequently, the accuracies of the two animals rose to final levels of 98 per cent and 90 per cent during 200 trials, representing four or five separate sessions ( $P < 0.001$ ; see Table 1). This performance is at least as good as that of the average naive human observer tested on the same apparatus.

There still remained the slight possibility that the animals were somehow discriminating the fusion of two identical images from the fusion of two slightly dissimilar images, without really having any perception of relative depth in the one case. In a second series of tests, the positive stimulus was the same as before, but the inner squares of the negative stimulus were displaced horizontally toward the medial edges of the separate matrices so that the small inner square would appear in front of the surround. In this discrimination, the two stimuli can be distinguished only by appreciating the different relative depths of the inner square. During the first session of at least fifty trials, one animal performed with an accuracy of 86 per cent, the other with an accuracy of 73 per cent. Once again, their performance improved to final levels of 100 per cent and 95 per cent during 200 trials ( $P < 0.001$ ; see Table 1).

Table 1. BEHAVIOURAL RESULTS OF MONKEYS ON TWO STEREOSCOPIC DISCRIMINATIONS

	Accuracy (correct trials/total trials)			
	Discrimination 1		Discrimination 2	
	First session	Final level	First session	Final level
Monkey <i>A</i>	45/50 ( $P < 0.01$ )	196/200 ( $P < 0.001$ )	48/56 ( $P < 0.01$ )	200/200 ( $P < 0.001$ )
Monkey <i>B</i>	35/50 ( $P < 0.05$ )	179/200 ( $P < 0.001$ )	63/86 ( $P < 0.01$ )	189/200 ( $P < 0.001$ )

Discrimination 1 involves distinguishing a far inner square from no inner square. Discrimination 2 involves distinguishing a far inner square from a near inner square.

The adequacy of random-dot stereoscopic discriminations as a criterion for the presence of stereopsis is subject to one minor criticism. The different horizontal displacements of the inner squares in the two patterns create small differences along the boundaries between the inner square and the surround of each, which could conceivably provide monocular cues for an animal with deficient or absent stereopsis. The rapidity with which the two animals transferred from the contrast discrimination to the stereoscopic discrimination made it unlikely, however, that any such monocular cues were operative; several control sessions were performed. When both discriminations were repeated using a different set of random-dot matrices, there was no effect on the performance of either animal. When tested on the two discriminations with occlusion of either eye, animal *B* performed at a chance level. An artificial convergent strabismus was produced in animal *A* by sectioning the right rectus lateralis, and the animal thereafter performed both discriminations at chance levels.

The ability of these two animals to distinguish objects at different apparent distances in the absence of monocular cues is very strong evidence that monkeys have stereoscopic vision. The presence of stereopsis in the monkey further emphasizes the similarity of vision in man and macaque monkeys, a similarity which has already been demonstrated for acuity and colour vision<sup>8-12</sup>. This similarity may be of interest to neurophysiologists who have recently begun to investigate the neural mechanisms of stereopsis<sup>13-15</sup>. Finally, there occur a number of ophthalmological disorders in humans which involve the loss of stereopsis, a classical example being congenital strabismus. These behavioural techniques now make it possible to study such disorders in experimental animals.

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## Bouncing-core Theory of Pulsars

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The catastrophic collapse of a star probably results in a "bouncing-core" configuration rather than a neutron star. Bouncing-cores explain many of the properties of pulsars in a more natural way than rotating neutron stars.

THE study of dense stars has been inspired for many years by the idea that stellar evolution terminates often in catastrophic collapse<sup>1</sup>. Most theoretical work has concentrated on two distinctly different kinds of dense star. On the one hand there are the stable equilibrium structures such as neutron stars<sup>2</sup>, and on the other the continually collapsing objects which fail to attain stable equilibrium; both kinds are clearly distinguished in the work of Oppenheimer and Volkoff<sup>3</sup> and Oppenheimer and Snyder<sup>4</sup>. The suggestion<sup>5</sup> that pulsars are rotating neutron stars, emitting searchlight beams of optical and radio waves, has renewed interest in the equilibrium kind of structure. Less rewarding to astronomy so far is the study of continual gravitational collapse. (To an external observer the boundary of a collapsing star approaches the Schwarzschild radius asymptotically and the observed luminosity decays monotonically.)

The equilibrium and continually collapsing stars are, however, two extremes of a spectrum of possible configurations. I shall argue that the intermediate configurations with "bouncing-cores" are the more probable result of catastrophic collapse and that they have the observed properties of pulsars.

### Catastrophic Collapse

The general view is that a massive star evolves to an unstable state and thereafter collapses catastrophically<sup>7</sup>. A large quantity of energy is released during collapse in the form of photons and neutrinos and the outer layers of the star are expelled violently to form ultimately an extended supernova remnant. The centre of the star consists of a core of increasing density surrounded by a massive envelope whose inner layers participate in the collapse and whose outer layers are expanding.

The formation of neutron stars is obscure, but it is thought that the collapsing core region attains in some way a dense stable configuration and the envelope is partly accreted and partly ejected. For a given mass, radius and equation of state a neutron star has a unique structure, and it is highly unlikely that a collapsing core region has a structure in any way similar. The pressure outside the core is not zero, and the small pressure gradients within the core are further reduced by the effect of general relativity. The time available for readjustment to a stable structure is of the same order as the time required to

propagate signals through the core at the speed of light. A static neutron star of more than approximately one solar mass is unstable, so the chance of a falling core of roughly the same mass ever becoming a neutron star seems rather small.

The remaining possibility is that in the vicinity of nuclear density matter is virtually uncrushable. But so far there is no reason for believing that matter is incompressible; however strong the short-range interactions or however large the pressure gradients at nuclear or supernuclear density, they are always overwhelmed by gravity when the mass exceeds roughly a solar mass. My own view (and probably also the view of many others) is that catastrophic collapse offers no assurance that stable configurations at nuclear density are attainable except perhaps in rare cases. The problem with the concept of rotating neutron stars with searchlight beams is that many, if not all, supernovae must produce neutron stars in order to explain the estimated number of pulsars.

The argument so far is that the falling core continues to collapse. It is surrounded by an envelope whose outer layers are sufficiently dispersed to uncover intermediate shells that are neither expanding nor collapsing rapidly. Structures of this kind, with a central region collapsing dramatically and outer regions moving relatively slowly, fall between the two extremes of stable equilibrium and the continual collapse at uniform density<sup>8</sup> or uniform scaling of coordinates<sup>9</sup>. The intermediate configurations are implicit in the work of May and White<sup>10</sup>.

The principal properties of pulsars can be explained if the falling core rebounds at finite or infinite density as assumed in the oscillating model<sup>11</sup> of the universe. The condition that the metric remains non-singular (with the exception of the infinite density bounce) is easily satisfied. An attractive possibility<sup>12</sup> is that the bounce occurs in the neighbourhood of the Planck density<sup>13</sup>

$$\rho^* = c^5/G^2\hbar \sim 10^{94} \text{ g cm}^{-3} \quad (1)$$

The intermediate configurations thus become pulsating structures, and the rise and fall of the core is the basic regulating mechanism. During the collapsing phase radiation from the envelope is relatively weak, but in the rising phase the core and its adjacent shells emit a blast of intense blueshifted radiation.

In the present theory it is proposed that catastrophic