Neurons with Complex Visual Properties in the Superior Colliculus of the Macaque Monkey*

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Summary. Single neurons were recorded from the superficial layers of the superior colliculus of immobilized monkeys (Macaca mulatta and Macaca irus). Two main functional types of neurons were found. The neurons of the first type (Type I neurons) responded well to simple stationary and moving stimuli such as spots, bars or slits of light. The latency of their response was 41 ± 6 ms. They were not directionally selective and responded to a large range of velocities.

The neurons of the second type (Type II neurons) responded very poorly to simple visual stimuli and their activation required real objects or certain two-dimensional patterns. The mean latency of response of these units was 66 ± 26 ms. Habituation was always present. Type II neurons were located in the lower part of the superficial layers.

The characteristics of Type II neurons suggest that in the primate superior colliculus there is a mechanism that allows the recognition of the complexity and the novelty of a stimulus and guides orienting responses to those stimuli that are worth analyzing in detail.

Key words: Superior colliculus – Monkey – Receptive field characteristics

In the superficial layers of the superior colliculus (SC) of the new world monkeys (Cebus apella and Cebus albifrons) there are neurons that respond particularly well, and sometimes exclusively, to com-plex visual stimuli such as three-dimensional objects (Updike, 1973). The presence of such neurons has not been reported in the old world monkeys (Schiller and Koerner, 1971; Goldberg and Wurtz, 1972) although units difficult to trigger have been occasion-ally observed (Schiller and Koerner, 1971; Cynader and Berman, 1972). The aim of the present work was to study whether units with complex characteristics do exist in the old world monkeys (Macaca mulatta, Macaca irus) and, if this is the case, to provide more data on their properties.

Methods

The experiments were performed on 2 Rhesus monkeys (Macaca mulatta) and 7 Java monkeys (Macaca irus). The preparation of the animals before the actual experiment was basically the same as used for cats (Rizzolatti et al., 1974). On the day of the experiment, the animal was anesthetized with ketamine, intubated under laryngoscope control, curarized, and artificially respirated. The animals were kept warm and EEG, EKG and expired CO_2 were monitored. The pupils were dilated with atropine and the corneas were protected by neutral contact lenses. Corrective lenses were used whenever necessary. Retinal landmarks (fovea, optic disc) were projected on a white hemisphere dome (1 m in radius, luminance 20 cd/m^2) located at 1 m from the eyes of the animal using a reversible ophtalmoscope. Since the superior colliculus is a visual center known to be associated with attentional mechanisms (Sprague and Meikle, 1965; Wurtz and Goldberg, 1972; Rizzolatti et al., 1973, 1974; Rizzolatti and Camarda, 1977) other general anesthetics after the initial injection of ketamine were not employed. The criteria outlined by Doty (1975) were used to ensure that the animals were not in discomfort (see also Mountcastle et al., 1957, 1969; Poggio and Mountcastle, 1963). The experiments lasted not more than 10 h after which the administration of curare was terminated and the animal allowed to recover. The recovery was usually quick and in about 1 h the animal was back in its cage. On the morning following the experiment the animal's behavior was indistinguishable from that of the unoperated animals.

The recording and stimulation methods were essentially the same as described in previous papers (Rizzolatti et al., 1973, 1974; Camarda and Rizzolatti, 1976). Single neuron activity was

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recorded by tungsten microelectrodes and, after conventional AC amplification, monitored on an oscilloscope, recorded on a magnetic tape, and sent to a Schmitt trigger, whose signals were fed into a computer for the construction of response histograms. Two classes of visual stimuli were used: (a) white and dark spots and slits front-projected onto the screen (Hubel and Wiesel 1965), (b) three-dimensional objects (simple geometric solids and common objects found in the laboratory) or configurational stimuli (pieces of black paper on a white surface in different configuration ranging from a single square to a scattered pattern of small irregular shapes). We will refer to the first class of stimuli as "conventional" stimuli, to the second class as "complex" stimuli. All units were studied using stationary and automatically moving conventional stimuli and hand-moved complex stimuli. Many units have been tested also with stationary complex stimuli. To compare the neuron responses to conventional and complex stimuli, the optimal stationary conventional stimulus (usually a restricted square of light, 200 cd/m^2) was projected onto the screen dimly illuminated (1 cd/m^2), with or without the complex stimulus. The opening of a shutter placed in front of one of the eyes (the other eye was occluded), permitted the vision of the stimuli, and triggered the computer operations for the construction of the response histograms.

During the experiments the stereotaxic positions of the electrode tracks were noted and subsequently located histologically by means of Nissl and Weil stains. Reference points, usually at the end of the penetration, were indicated by small electrolytic lesions (10 µA, 5 ms). Since no differences have been found between the neuron properties of the two species of macaques, the data have been pooled together for description.

Results

We recorded the activity of 120 neurons from the superficial layers (stratum griseum superficiale and opticum) of the monkey superior colliculus (SC). The neurons were tested using conventional and complex stimuli (see Methods). According to their response to these two classes of stimuli we subdivided them into two functional groups: neurons optimally responding to conventional stimuli (Type I neurons) and neurons preferring complex stimuli (Type II neurons).

Type I Neurons

Type I neurons (n = 68) responded briskly to both stationary and automatically moving conventional

visual stimuli, provided that the stimulus was smaller than the unit receptive field. They were neither orientation specific nor directionally selective and responded to a large range of velocities (Schiller and Koerner, 1971; Goldberg and Wurtz, 1972a). The stimulation of these units with complex visual stimuli left response intensity virtually unchanged. (By evaluating very small changes in the response it could be observed that in 75% of the units there was a decrease of the response, and in the remaining units an increase). The latencies ("on" response) of Type I neurons are shown in Table 1. The peak of the response occurred approximately 20–30 ms after its beginning regardless of the presence or absence of a complex stimulus in the unit receptive field.

The average receptive field size of Type 1 units was 16 (deg)^2 with a range from 0.3 to 47 (deg)^2. Most units of our sample had parafoveal receptive fields, in 85% of the cases the near border of the discharge area was within 20° of the fovea.

Type II Neurons

Type II neurons (n = 52) were driven very poorly by stationary and smoothly moving conventional visual stimuli (Fig. 1). Some of them responded better when a conventional visual stimulus was moved in jerks inside their discharge area. However, for all units the presentation of a complex stimulus, especially of a real object, produced a strong and sustained discharge (Fig. 2).

Type II units did not require a unique object or a two-dimensional stimulus configuration to be triggered and many complex stimuli were able to elicit a vigorous response. Simple geometric solids, such as cubes and cylinders produced only weak responses, while objects with a rich texture or a complex pattern of contours were usually very effective (Fig. 3). Among two-dimensional stimuli equalized for black and white area the least effective was a single square and the most effective was a speckled pattern.

The histograms in Fig. 3 have been arranged in the order of the luminance of the stimulus. One can

	Simple light stimulus	Complex stimulus	**Table 1.** Mean response latencies and standard deviations
Type I neurons	41 ± 6 ms 30 neurons tested 30 neurons responding	43 ± 8 ms 24 neurons tested 24 neurons responding	
Type II neurons	54 ± 16 ms 22 neurons tested 17 neurons responding	66 ± 26 ms 20 neurons tested 20 neurons responding	

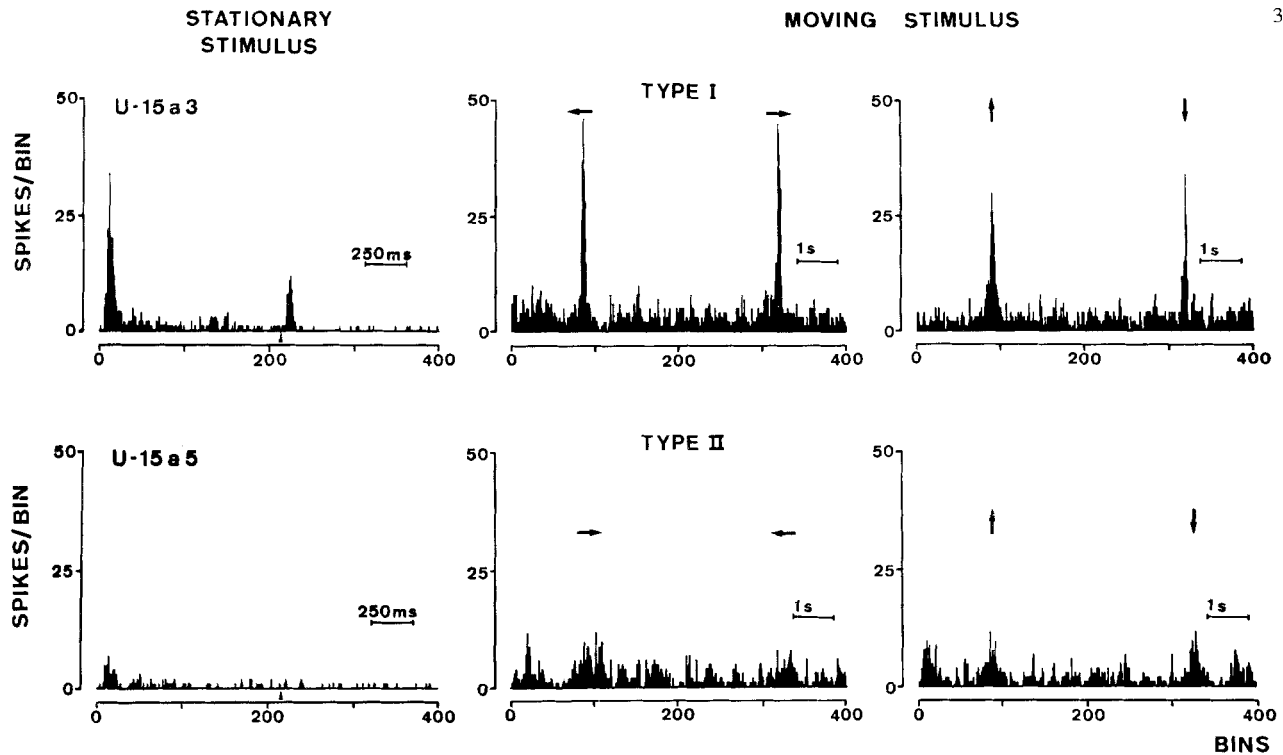STATIONARY
STIMULUS

MOVING STIMULUS

Fig. 1. Typical responses of a Type I neuron (upper histograms) and a Type II neuron (lower histograms) to conventional visual stimuli. The two neurons were recorded in the same penetration, 275 and 675 μ, respectively, below the SC surface. For U-15 a 3 the stimulus was a square of light (1.9° × 0.9°) presented either stationary or moving at a speed of 20°/s. For U-15 a 5 the stimulus was a bar of light (2.9° × 4°; 20°/s). Stationary stimuli histograms: bin width 5 ms; the triangle under the abscissa indicates the closing of the shutter; the opening of the shutter was synchronized with the beginning of the histogram. Moving stimuli histograms: bin width 20 ms; arrows indicate direction of movement. All histograms in this and later figures are the sum of 10 responses
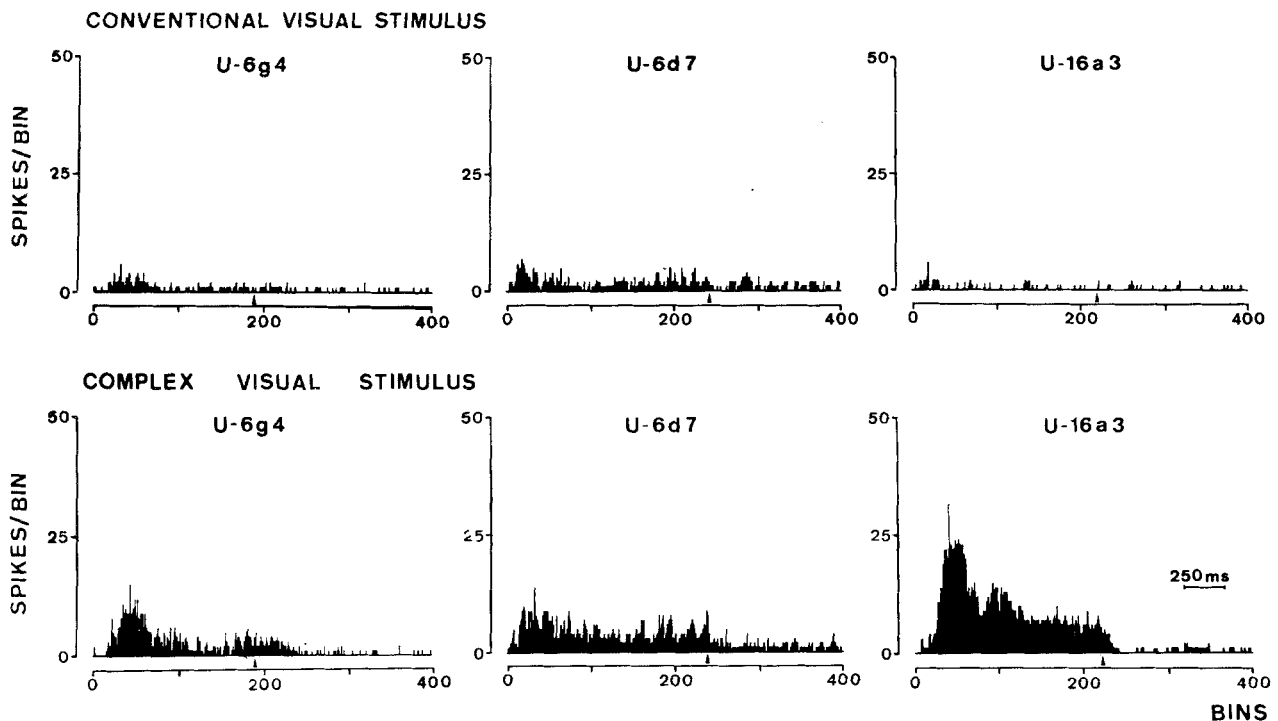

Fig. 2. Responses of Type II neurons to conventional and complex stationary visual stimuli. The size of the conventional stimuli for the three units was 4.8° × 4.8°, 3° × 3°, and 1.5° × 1.2°, respectively. The complex stimuli were a small pink plastic bottle, a small brown bottle with a red label, and a yellow plastic cap. The objects were illuminated by the conventional stimuli. Bin width 5 ms. Presentation rate 1 every 30 s
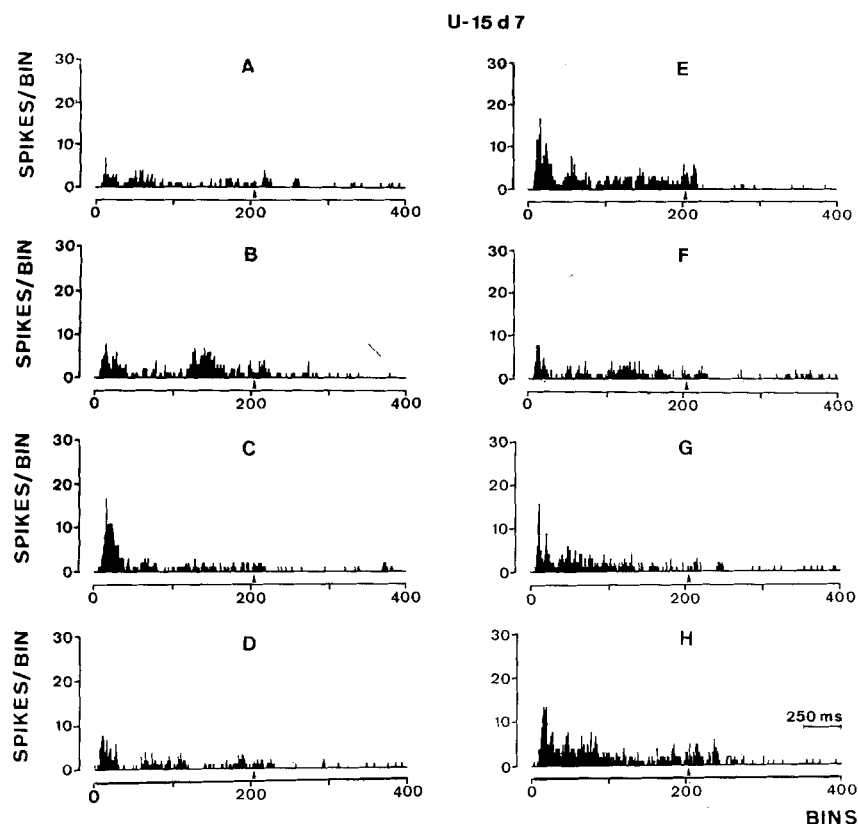
U-15 d 7

Fig. 3A–H. Responses of a Type II neuron to different visual stimuli. The histograms are arranged in order of total luminance of the stimuli. A light stimulus alone; B yellow cube; C two-dimensional irregular black and white pattern; D pale blue cube; E crumpled paper; F clear plastic bottle with a blue label; G and H brown glass bottles with different labels. All objects were illuminated by the stimulus indicated in A. Bin width 5ms. Presentation rate 1 every 30 s

see that there is no obvious relationship between the stimulus luminance and the response strength. Of seven units tested with three or more complex stimuli, there was no correlation between size of the response and luminance in five cases, in one case the bright stimuli were more effective, in one the dark stimuli produced the better responses.

In five units formal tests have been made in order to determine whether the meaningfulness of the stimulus could be an important parameter. A comparison of the response histograms produced by stimuli consisting of pieces of food (fruits, bread, etc.) with those produced by objects without any obvious meaning for the animal gave no indication that motivational factors were relevant variables. Informal tests on a large number of units gave the same results.

A striking property of Type II units was a strong tendency for their response to decrease with repetitive presentation of the same stimulus. Examples are shown in Fig. 4 (upper part). This figure also shows that a new stimulus could restore the strength of the response, indicating that the diminished effectiveness of a stimulus repetitively presented was not due to fatigue. A habituated unit could recover its response not only when a new stimulus was presented, but also by changing the orientation of the stimulus. Habitua-

tion was absent when the same stimulus was presented repetitively outside the unit receptive field (Fig. 4B).

For 22 neurons we compared the histograms of the responses to conventional and complex stationary stimuli. Each unit was studied with various objects. Table 1 shows the number of units responding to conventional and complex stimuli and the latencies of their responses. The apparent increase in the mean response latency with complex stimuli is due to the fact that a few units (n = 5) which did not respond at all to conventional stimuli, had a long response latency. The other units had latencies of the same magnitude with both conventional and complex stimuli.

The average receptive field of Type II neurons was 42 (deg)^2, the range of receptive field areas being from 1 to 174 (deg)^2. Most of the units of our sample had parafoveal receptive field; 83% of them had their receptive field center within 20° of the fovea; all had their near borders within 20° of the fovea.

In all penetrations Type II neurons were encountered only after many Type I neurons. Histological controls showed that Type II neurons were located in the lowest part of the stratum griseum superficiale and in the stratum opticum. The proportion of Type I and Type II units in our sample is biased in favor of
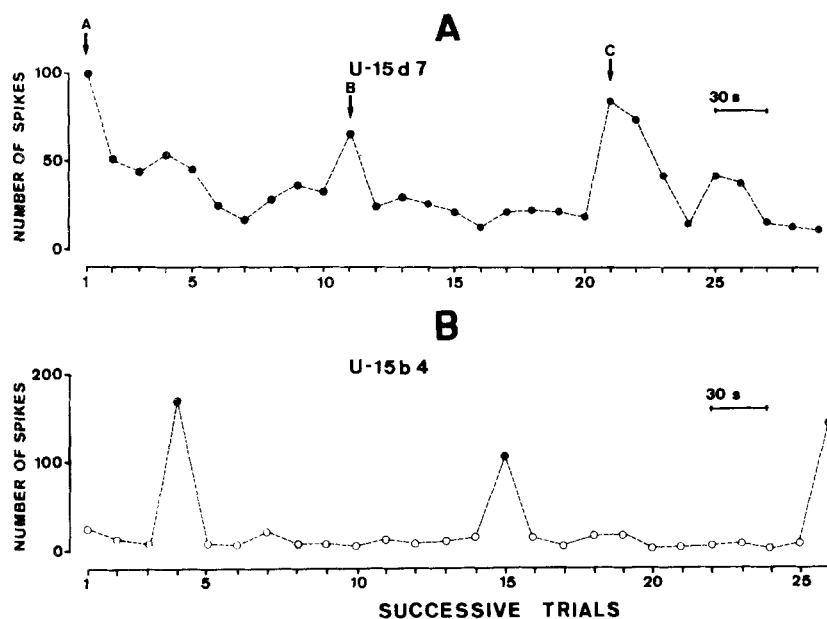
Fig. 4A–B. Habituation properties of Type II neurons. A shows the responses of a neuron to repetitive presentation of complex stimuli. The arrows indicate the first presentation of a stimulus. *A* brown bottle with green label; *B* two-dimensional irregular black and white pattern; *B* again the stimulus described in *A*. B shows the effect on the neuron response of the repetitive presentation of the same stimulus (crumpled brown paper) outside the neuron receptive field. Filled circles are trials on which the stimulus was presented within the receptive field; empty circles are trials on which it was presented in various positions around the receptive field

the latter class since, in several penetrations, we skipped the units superficially located.

Discussion

We have shown that in the superficial layers of the superior colliculus of the macaque monkey there are two main functional classes of neurons. The neurons of the first class responded well to conventional visual stimuli and would correspond to the units studied in detail by Goldberg and Wurtz (1972) and Schiller and Koerner (1971); the neurons of the second class, never previously described in the macaque, preferred complex stimuli and were similar in many respects to those found by Updyke (1973) in the Cebus monkey. Furthermore, our data on latency, receptive field size, and location of Type II units rule out the possibility that these units are eye movement cells and indicate that they are true visual neurons. Thus, since neurons with "conventional" properties are present also in the Cebus (Updike, 1973) we can conclude that the SC organization in old world and new world monkeys is basically the same.

Type II neurons required stimuli that are difficult to unify in a single class. The term complexity, as we have used it, means simply that stimuli different from those usually employed in vision studies were necessary to trigger these neurons. On the other hand since stimuli rich in details, lacking homogeneity and with many contours were constantly the most effective, we believe that the term complexity is not unappropriate.

A final point which deserves comment is how Type II neurons could fit into a general model of the role of the SC in vision. It is usually accepted that one of the functions of the SC is to bring visual stimuli into foveal vision (Apter, 1945; Hess et al., 1946; Schiller and Koerner, 1971). In principle, the function of recognizing which stimuli are worth analyzing may be attributed to nervous circuits involving exclusively the cerebral cortex, assigning to the SC the ancillary role of transmitting the cortical instructions to the brain stem or spinal cord motor centers (reviews and criticism of this idea may be found in Sprague et al., 1973). However, it is plausible and more economical that in addition to signaling the position of the stimulus and effecting foveation the SC possesses a mechanism for the identification of those stimuli that require a more detailed and more precise analysis by the visual cortex. We propose that Type II neurons fulfill this role, determining, on the basis of the complexity and novelty of the stimulus, the desirability of further analysis.

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