

Responses of Striatal Neurons in the Behaving Monkey. 2. Visual Processing in the Caudal Neostriatum

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The activity of single neurons was recorded in the tail of the caudate nucleus and adjoining part of the ventral putamen, which receive projections from the inferior temporal visual cortex, in order to investigate the functions of these regions. Of 195 neurons analyzed in two macaque monkeys, 109 (56%) responded to visual stimuli, with latencies of 90–150 ms for the majority of the neurons. The neurons responded to a limited range of complex visual stimuli, and in some cases responded to simpler stimuli such as bars and edges. Typically (in 75% of cases) the neurons habituated rapidly, within 1–8 exposures, to each visual stimulus, but remained responsive to other visual stimuli with a different pattern. This habituation was orientation specific, in that the neurons responded to the same pattern shown in an orthogonal orientation. The habituation was also relatively short-term, in that at least partial dishabituation to one stimulus could be produced by a single intervening presentation of a different visual stimulus. These neurons were relatively unresponsive in a visual discrimination task, having habituated to the stimuli which had been presented in the task on many previous trials. It is suggested on the basis of these results and other studies that these neurons are involved in pattern-specific habituation to repeated visual stimuli, and in attention an orientation to a changed visual stimulus pattern. Changes in attention and orientation to stimuli as a result of damage to the striatum and its afferent and efferent pathways may arise in part because of damage to neurons with responses of this type.

INTRODUCTION

The caudate nucleus and putamen represent major structures through which information in the nervous system can access the motor system. Anatomically, these neostriatal structures project to the globus pallidus and substantia nigra which in turn project to the ventral anterior and ventral lateral thalamic nuclei and thence to the premotor cortex^{6,7}. Damage to the basal ganglia has been associated clinically and experimentally with disorders of movement^{1,8,14,36}. Furthermore, recordings of the activity of single neurons within these structures reveal that many of the neurons are influenced by movements or by information pertinent to the initiation of movements^{7,27,28,30–32}. The caudate nucleus and putamen receive inputs from the cerebral cortex, and there is some topography to this projection^{15,37,40}. Thus, direct visual inputs from the inferior temporal cortex arrive mainly, although not exclusively, in the

tail of the caudate nucleus and in the posteroventral portions of the putamen^{15,19,37,39,40}. Since these regions of the caudate nucleus and putamen are adjacent and have a common anatomical input they are referred to together as the caudal neostriatum.

Although the inferior temporal visual cortex and pre-striate cortex project directly into the caudal neostriatum, there have been few studies of the functions of these visual pathways and their importance in visually controlled behavior. Divac et al.¹⁰ reported that stereotaxic lesions placed in the tail of caudate nucleus in the region which receives input from the inferior temporal visual cortex produced a deficit in visual discrimination learning. The lesion did not produce impairment in an object reversal task, though in two out of four monkeys it did disturb delayed alternation performance. Buerger et al.² found that lesions of the ventral putamen in the monkey produced a deficit in the retention of a pre-operatively learnt visual discrimination problem but the lesion

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did not disturb retention of auditory discrimination or delayed alternation tasks. The deficit produced by both neostriatal lesions seems therefore to reflect predominantly a loss of visual functions rather than a general loss of cognitive functions. It is notable that the visual discrimination deficit produced by lesions to either the tail of the caudate nucleus or the ventral putamen is less severe than that produced by lesions of the inferotemporal cortex (e.g. ref. 5).

Since so little is known about the nature of visual processing within the caudal neostriatum and the fate of the visual input from inferior temporal cortex to this area, the study described here was made to investigate the responsiveness of the cells in the ventral putamen and tail of the caudate nucleus to visual stimuli¹⁷. To obtain direct evidence on the role of these structures in visual discrimination, cellular activity was recorded during the performance of a visual discrimination task.

METHODS

Recording techniques

Chronic single unit recording techniques that have been described previously^{18,24,26,29,31}, were used to record the activity of single neurons from the brains of two rhesus monkeys seated in a primate chair. The electrical activity of single cells was recorded with glass-insulated tungsten microelectrodes, amplified using standard techniques²⁶, and analyzed on-line using a PDP11 computer. X-rays were used to define the position of the electrode on each recording track and the position of cells was reconstructed from histologically verified micro-lesions made at the end of recordings and the X-rays²⁹. Horizontal electro-oculogram (EOG) recording was performed with silver/silver chloride surface electrodes. These were attached during experiments to the skin lateral to each eye with collodion glue (S.L.E., Croydon, U.K.). Electrode jelly (Neptic, Smith Pharmaceuticals, Welwyn Garden City, U.K.) was used to ensure good electrical contact. The monkey's behavioral reactions to the sight of the stimuli were monitored using a video camera with closed circuit T.V., by direct observation through a small hole in the side of the chair, and in some experiments by galvanic skin response (GSR) recordings made with surface electrodes attached to the feet.

Procedure

The monkeys were first trained on a discrimination task in which when one visual stimulus (S+) was shown, they could make a lick response to obtain fruit juice reward, and when the other visual (S—) was shown, they had to withhold the lick response in order to avoid obtaining aversive hypertonic saline. The discriminative stimuli were presented in a pseudo-random order from behind a fast rise time (less than 15 ms), large aperture shutter (Compur Electronic 5FM 6.4 cm aperture) which opened for 1.0 s after a 0.5 s signal tone (600 Hz)^{25,26,31}. After the task had been learned, the discriminative stimuli were shown on trials interspersed with other test visual stimuli, which included geometrical stimuli and junk objects. Lick responses to these test stimuli were normally neither reinforced nor punished but responses to the discriminative stimuli were always reinforced (S+ with fruit juice reward and S— with saline). In this situation, the inclusion of discriminative stimuli every 5–10 trials (varied as necessary), and the monkeys' natural interest in the various stimuli, ensured good attention to and fixation of the stimuli. Other studies have reported that monkeys display an interest in (as demonstrated by their eagerness to look at) visual stimuli despite lack of reinforcement for such behavior³. Further, in the present situation adequate fixation of the shutter before it opened was obtained by providing only a limited reward availability period on each trial, which required the monkey to fixate the shutter before it opened if he was to obtain several rewards in the period in which the positive discriminandum was shown²⁹. This adequate fixation, which was monitored, allowed reliable perivisual stimulus time histograms of the neuronal responses to be made and the neuronal responses to be measured accurately. This shutter controlled visual stimulus presentation was used to compare the responses of individual neurons to a number of types of stimuli including simple geometrical stimuli, and complex three-dimensional objects. All stimuli were presented against a uniform white background seen through the shutter. The shutter was placed in a dark screen which surrounded the monkey in order to limit visual stimulation to that seen through the shutter.

Stimuli

Geometrical stimuli. High contrast square wave

gratings, bars, slits and spots of various sizes were produced by placing black stencil material onto the surface of 1 mm thick transparent perspex sheets. These stimuli were placed behind the shutter either singly or stacked in combination to make more complex shapes.

Three-dimensional objects. Over 1000 three-dimensional objects were collected together from laboratory, home, etc. Objects were chosen to differ from one another in size, shape, color, surface pattern and texture, but for convenience of storage the objects were less than 20 cm long. Since these junk objects, which included, for example, crayons of different colors and boxes of different shapes, varied along different visual dimensions, testing neuronal responses to several of them could potentially reveal selectivity for particular visual characteristics. Objects were placed on the surface of a matt black board tilted towards the monkey, or were held by long forceps or by hand, between 2 cm and 1 m behind the shutter. The shutter was situated 25 cm from the monkey.

Subjects

The tail of the caudate nucleus, and the posterior and ventral portions of the putamen, were studied in both hemispheres of two male rhesus monkeys, *Macaca mulatta* (wt 4.5–6.0 kg).

RESULTS

Tail of the caudate nucleus

Types of cell recorded

Reconstruction of the position of recording tracks from X-rays made at the end of each track, and from microlesions placed at the termination of the experiment, revealed that 147 cells had been recorded in or within 0.5 mm of the tail of the caudate nucleus, between 1.0 mm and 8.0 mm anterior to the interaural plane (see Fig. 1). After testing with a variety of visual stimuli, 60 remained unresponsive, and were hence unclassified. Seventy-six cells, however, were found to have visual responses, and the responses of

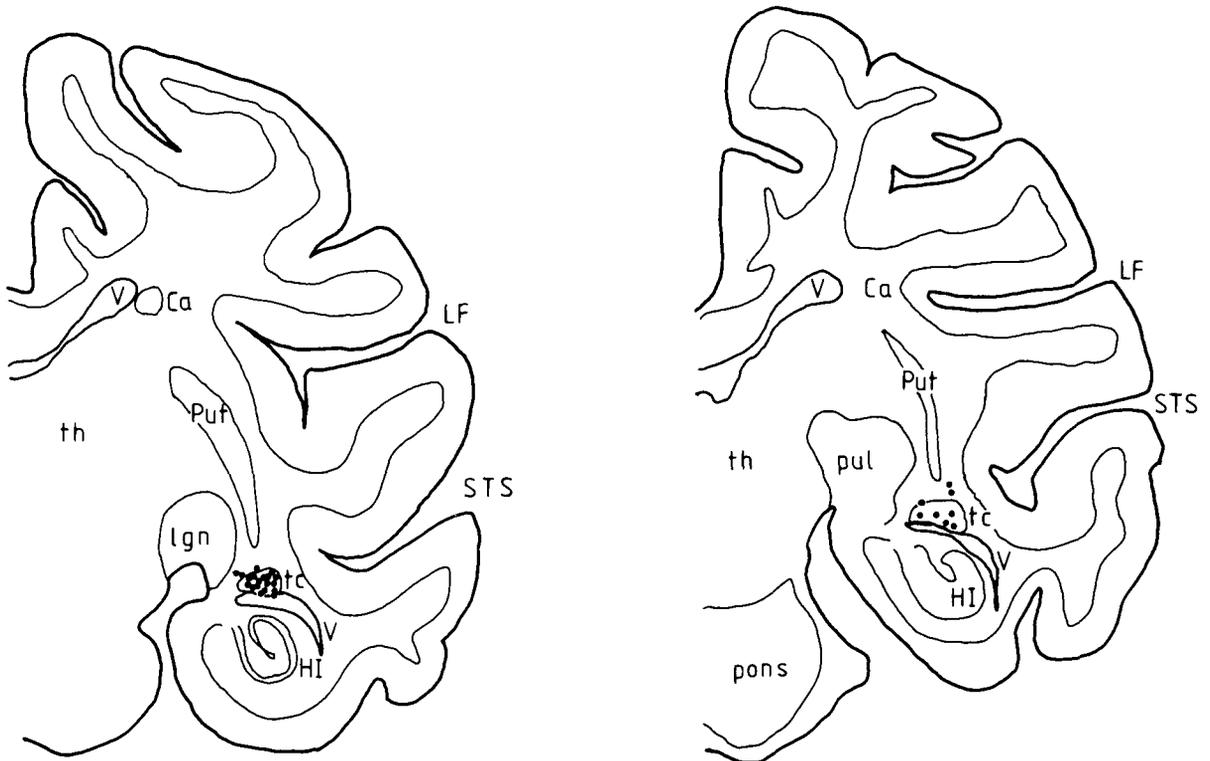


Fig. 1. Reconstructions of the positions of cells recorded in the tail of the caudate nucleus in one monkey. Outline drawing of structures evident in serial coronal sections (of the left hemisphere) from 3 to 9 mm anterior to the interaural plane. Abbreviations: Put, putamen; TC, tail of the caudate nucleus; Gl, globus pallidus; Cl, claustrum; Hip, hippocampus; LGN, lateral geniculate nucleus. The positions of cells with habituating visual responses are marked by dots.

these neurons are described below. The discharges of an additional small number of visually unresponsive cells were found to be related to auditory stimuli (3 cells) or to certain movements such as reaching (7 cells). No specific investigation was made of auditory responses, which have been described elsewhere⁴, or motor responses, and these cells will not be considered further here.

Effect of stimulus repetition on tail of caudate visual cells

It soon became clear that many of the cells in this area became rapidly less responsive to stimuli when they were repeatedly presented. Of 55 cells tested for the effects of stimulus repetition, 41 (75%) had visual responses which habituated, and these will be referred to as visual habituation cells. Habituation was measured in this study as a reduction in the neuronal response to a stimulus when that stimulus was shown repeatedly. For most of the cells described here this habituation was to the level of the spontaneous firing rate within 10 trials (see below). Nine cells responsive to particular types of visual stimuli showed no tendency to habituate. A further 5 cells responded inconsistently or erratically to stimuli showing neither a tendency to become more responsive nor less responsive when the same stimuli were repeatedly shown. These cells because of their response variability were not further analysed.

Non-habituating cells. These cells were heterogeneous in nature. Two cells showed very short latency (30 ms) sustained responses to diffuse light stimuli. One cell was found to respond at an early latency (60 ms), but only to stimuli in the periphery of one visual field. Two cells responded well to the movements of the experimenter made while reaching to the monkey's left to a food tray which itself was out of sight. These cells could simply have been sensitive to the direction of movement of a visual stimulus, or could be similar to cells in the head of the caudate nucleus which respond to cues signalling the imminent presentation of stimuli^{27,31}. Extensive studies were not made of the various types of non-habituating cells as they were not commonly found. They are described only to give an indication of the possible variety of visual inputs reaching the tail of the caudate nucleus.

Visual habituation cells. The 41 cells with habituating responses to visual stimuli comprised a relatively

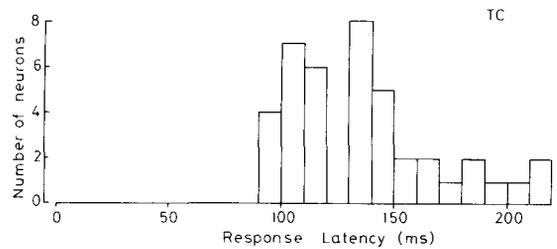


Fig. 2. Histogram of the response latencies of visual habituation cells recorded in the tail of the caudate nucleus. Ordinate: number of cells; abscissa: latency of earliest visual responses (ms). Forty-one cells sampled.

homogeneous population. The cells had very low spontaneous firing rates (with a mean and standard deviation for the population = 1.8 ± 1.8 Hz), with 60% having no spontaneous activity. The latencies of the earliest visual responses for different cells ranged from 90 to 220 ms, with the majority responding between 90 and 150 ms (see Fig. 2). The visual responses tended to be transient in nature and about 100–200 ms in duration (Figs. 3, 4 and 7).

Visual selectivity

When tested with a variety of junk objects, virtually all cells displayed a high degree of selectivity, responding to only a minority of the objects (less than 25%). The particular visual dimensions common to objects to which cells did respond were not usually clear. For 20 of 27 cells tested particular simple stimuli such as bars and gratings were found to produce some response, but in general cells in the tail of the caudate nucleus were less responsive to simple geometrical stimuli than to 3-D junk objects. The cells were not usually orientation sensitive in that if they did respond to particular stimuli they could respond irrespective of the orientation of presentation. This lack of orientation selectivity is illustrated in Fig. 3. It is shown in the first 4 trials that the cell responded to a bar stimulus irrespective of its orientation. The cell did not respond to diffuse light or to colored red/white or yellow/white edges (trials 5–7). Some neurons responded preferentially to stimuli of a particular color.

Habituation

The rapid habituation process is illustrated in Fig. 3. Though the cell responded well on trial 8 to a grating stimulus, it became very unresponsive when

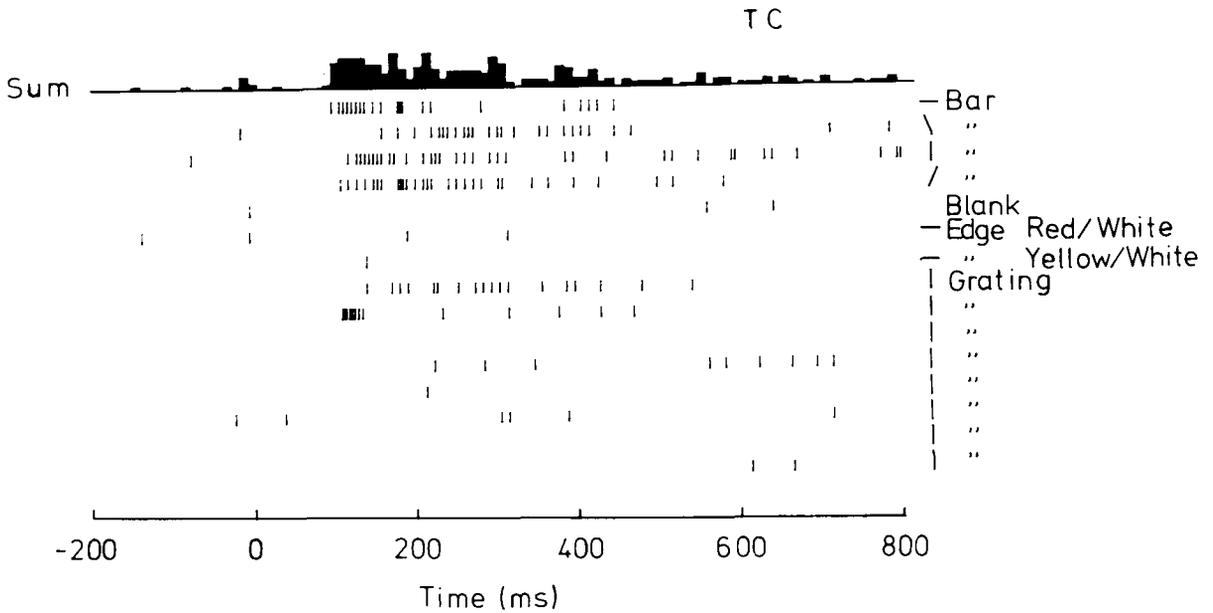


Fig. 3. Orientation tolerance and habituation in the visual responses of a neuron in the tail of the caudate nucleus. Action potentials are represented by short vertical dashes. Each horizontal row records the activity of the cell during a single trial with the visual stimulus presented at time 0 ms. For each trial, the type and orientation of the stimulus used is given at the right. Bar: black stripe on white background, stripes width = 1.5 cm. Grating: black/white alternating stripe pattern, stripe width = 1.0 cm. The upper histogram gives the total number of action potentials (sum) occurring in each 10 ms time bins for all the trials displayed. (See text for description of response characteristics).

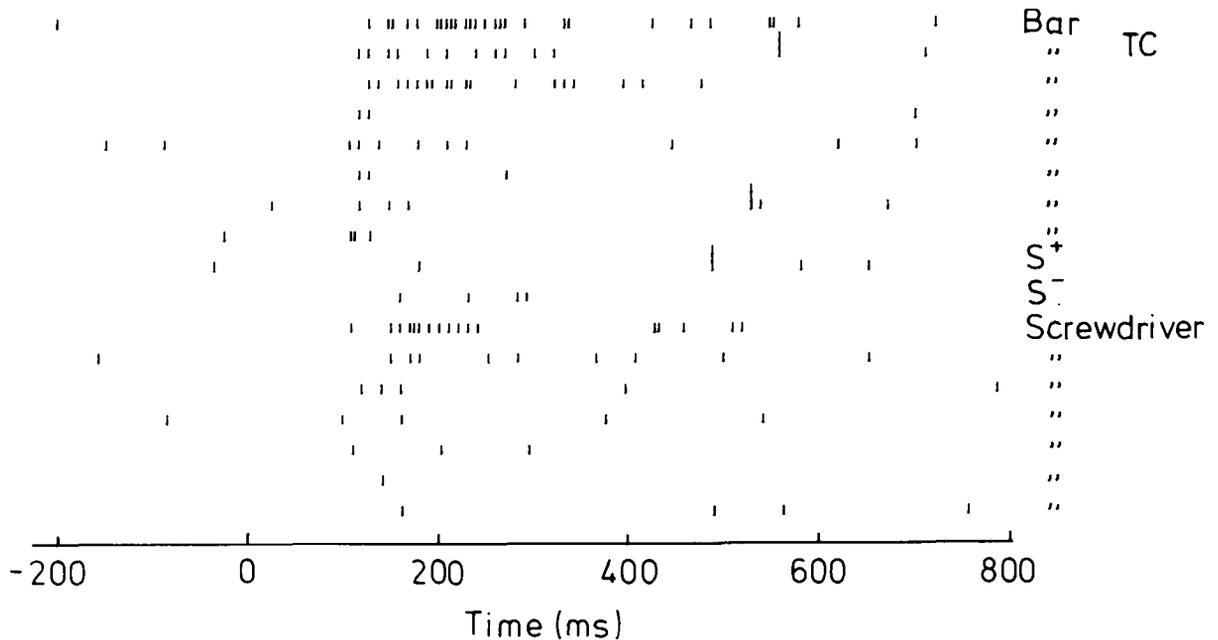


Fig. 4. Habituating responses of a tail of caudate neuron to visual stimuli. The cell responded to the bar on the initial trials but its responses quickly habituated. A similar habituating response was elicited by a screwdriver (lower trials). For further details, see text. Conventions are as in Fig. 3. S+ indicates a trial on which the reward-associated discriminative stimulus was shown, and S- a trial on which the saline-associated discriminative stimulus was shown. A long vertical bar represents a lick response made by the monkey.

the stimulus was repeatedly presented. A second example of the habituation process is illustrated in Fig. 4. It is shown that the cell was responsive to a vertical black bar on the first few trials, and that the responsiveness rapidly declined. That the monkey was attending to the stimuli presented was indicated by his correct lick response (L) given on trial 9 to the S+ stimulus. The cell was visually selective in that it did not respond to the S+ or S- stimuli (despite the vertical edges present in these stimuli). The cell had not simply become generally unresponsive by trial 9 since on trial 10 when a new stimulus was presented the cell responded vigorously, but again habituated over the following trials.

The responses for different stimuli and for different cells habituated at slightly different rates. It was found that the larger the initial response to a stimulus, the longer cells took to habituate to a minimal baseline, which was usually the spontaneous firing rate. The minimum number of trials for cells to habituate to baseline ranged between 1 and 3, and the maximum ranged from 3 to 20, with the average maximum number of trials for habituation equal to 4.8 for the whole population of cells.

Dishabituation

Dishabituation with altered views of objects. One feature of the responses of neurons in the tail of the caudate nucleus which relates both to their visual selectivity and to the process of habituation, was that changing the viewing conditions of an object renewed the cells' responsiveness. Though the cells became unresponsive when the same object was repeatedly presented, simply changing the orientation of the object between trials resulted in another large response in 80% of cells tested. This effect is illustrated in Fig. 5. Here, neuronal responses to stimuli on successive trials have been displayed in histogram form. The response rate was calculated from the number of spikes occurring in the 0.5 s period starting 100 ms after the stimuli were presented. A black bar (2 cm width) was used as a stimulus throughout and was simply rotated on trials 7 and 11. The response to the black bar when it was vertical declined markedly after the second trial. When the stimulus was rotated to the horizontal the cell's response was elevated but again quickly diminished when the same horizontal bar was repeatedly presented. Rotation of the bar

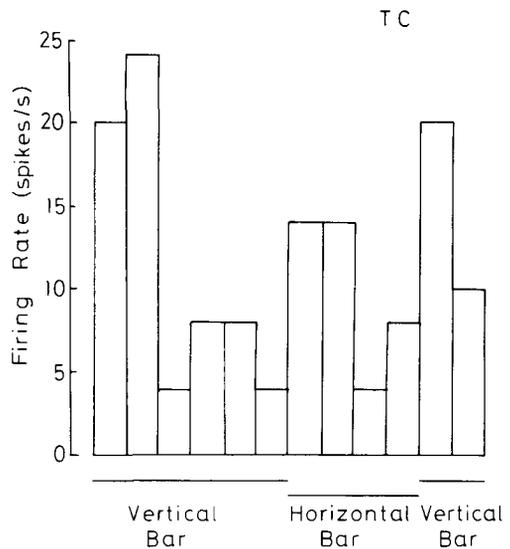


Fig. 5. Dishabituation induced by stimulus rotation of the responses of a tail of caudate neuron. Each histogram bar gives the response (spikes/s) to a bar stimulus for one trial. The response rate was calculated from the total number of action potentials occurring to the sight of a stimulus on a given trial in the period 100–600 ms after the onset of the stimulus presentation. The orientation of the stimulus is indicated at the base of the figure. For further details, see text.

back to the original vertical orientation restored the response which once again diminished.

A change in orientation was found to reinstate habituated responses in 20 cells, but was ineffective for 5 cells. This dishabituation by rotation could be observed not only with elongated stimuli such as bars and gratings, but also with junk objects isomorphically rotated.

Other types of changes in the stimuli or alteration of the viewing conditions were less extensively studied, but were also shown to produce recovery of habituated responses. Changing the direction of contrast in single bar stimuli (i.e. replacing a white bar by a dark bar of equivalent size) produced response recovery in 2 cells tested. Changing the size of a bar from 2 mm width to 2 cm width produced a dishabituation in 1 cell tested. Placing colored filters in front of stimuli or changing the color of filters, produced dishabituation for 3 cells.

Dishabituation from intervening visual stimuli. The habituation of neuronal responses in the tail of the caudate nucleus was not a durable phenomenon in that the habituated responses to particular stimuli recovered if the stimulus was retested after a few (often

as little as one) intervening trials with different stimuli. An example of this has already been given in Fig. 5, where the habituated response to a vertical bar returned to the original unhabituated level after 4 intervening trials with horizontal stimuli presented. Recovery of habituated responses for particular stimuli was observed in 28 of 32 cells tested. It was found that dishabituation could occur even when the intervening stimuli were not responded to. The remaining 4 cells showed little response recovery for old stimuli despite intervening stimuli, but these cells would respond to other new stimuli.

Dishabituation from non-visual stimuli. Incidental observations of 4 habituating cells suggested that alerting stimuli might produce dishabituation since on trials following an event such as the telephone ringing, or the shutter failing to open, habituated responses recovered unexpectedly. Formal tests with auditory and tactile arousing stimuli (loud noises, or touching the monkey's legs) did not, however, prove particularly effective and failed to produce consistent dishabituation for 7 cells studied (e.g. Fig. 6). Interestingly, the auditory and tactile stimuli themselves did not produce cell responses. This indicated that

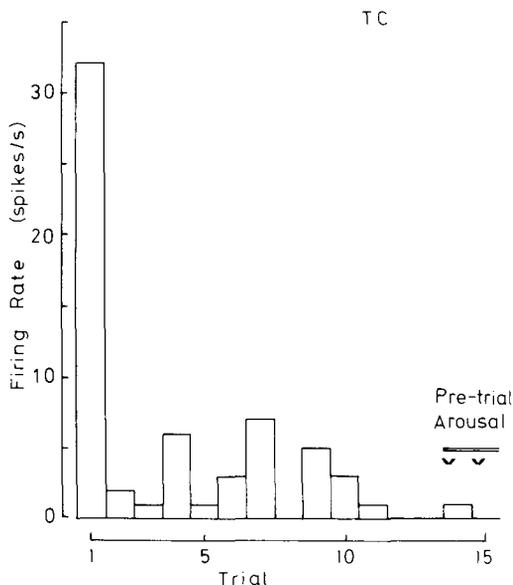


Fig. 6. Habituation of visual responses despite pretrial arousal. Ordinate; firing rate (spikes/s); abscissa: trial number. The same visual stimulus was used throughout. Each histogram bar gives the firing rate calculated from the total number of action potentials occurring to the sight of a stimulus on a given trial in the period 100–600 ms after stimulus presentation onset. The response habituated rapidly and remained at a low level despite arousal by a loud noise prior to trials 14 and 15.

the cells received specifically a visual input, rather than general multimodal inputs, and that the cells were not responding because of arousal per se.

When the monkey was simply left untested for periods of up to 30 s, only one-third of the cells studied (6/20) was observed to dishabituate. Thus, a short interval of time by itself was not necessarily sufficient for cell responses to recover. A cumulative effect of visual stimulation was evident when cells were repeatedly habituated to particular stimuli in that the speed of rehabituation following dishabituation tended to be more rapid than the rate of original habituation. Further, the magnitude of the initial response following dishabituation was often lower than the original responses prior to any habituation.

Although the major tendency for all of the 41 cells categorized as habituating was to become less responsive on repeated testing, there were instances for at least 10 cells where, during a long series of presentation of the same object, responses would unpredictably recover somewhat for 1 or 2 trials but then the cells would become unresponsive again. These 'spontaneous' recoveries were sometimes related to environmental stimuli as noted before, but at other times could not be related to any obvious cause.

Clinical testing

The very transient and small responses of most cells in the tail of the caudate nucleus made it difficult to quantify responses outside the shutter testing situation in the more clinical situation where objects were simply shown to the monkey. For 6 cells, however, it was possible to demonstrate clear habituation to visual stimuli presented clinically. The rate of habituation and magnitude of initial responses for these cells in the clinical situation was comparable to that in the shutter situation. This indicated therefore that the habituation process was not restricted to the shutter testing situation.

Visual discrimination performance

During task performance, many of the tail of caudate cells remained silent, not responding during trials with either of the discriminative stimuli (see Fig. 4). Responses of tail of caudate neurons could sometimes be observed at the beginning of a block of discrimination trials, but after a few trials, responses usually habituated and disappeared. Fig. 7 gives an

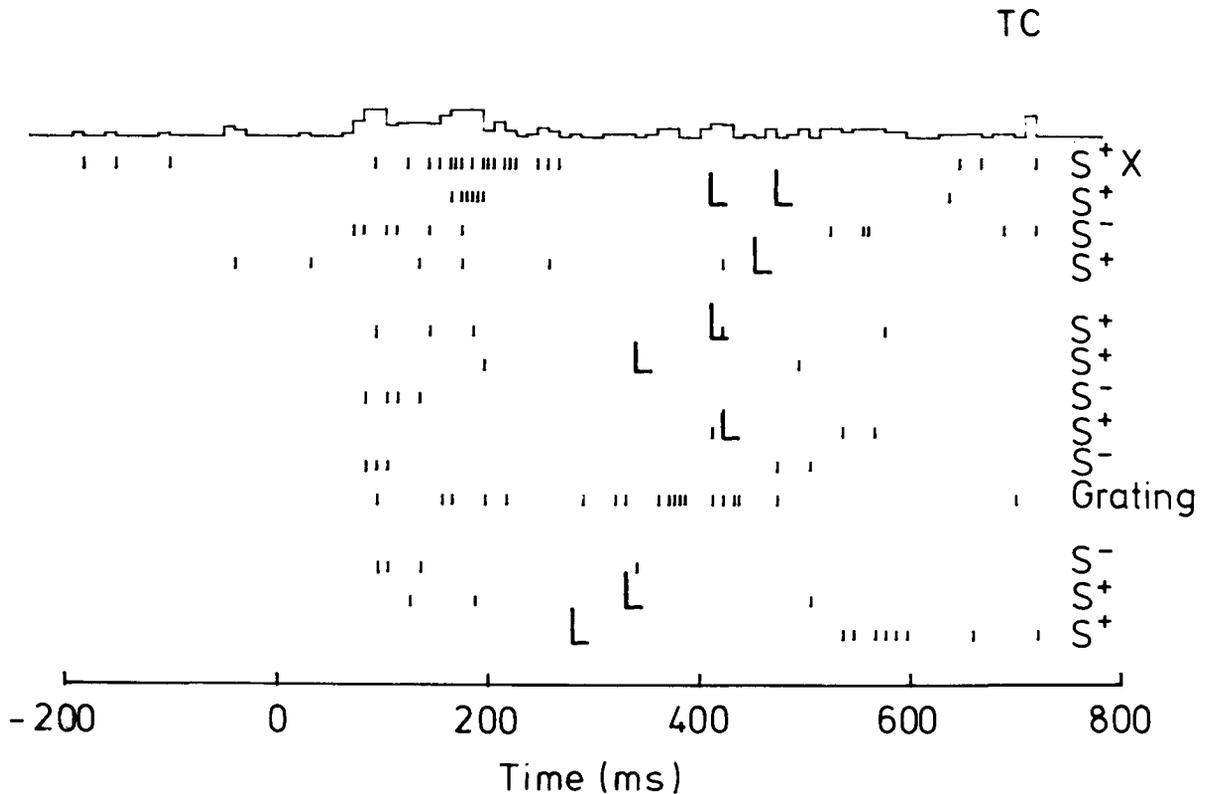


Fig. 7. Activity of a neuron in the tail of the caudate nucleus during visual discrimination performance. Conventions as for Fig. 3. Licks are indicated by an L, S+ denotes a reward-associated visual stimulus for which lick responses were rewarded with fruit juice, S— denotes a saline-associated stimulus for which lick responses were punished with saline delivery. For details, see text.

illustration of the habituation of responses to the discriminative stimuli. On trials 1–4, the monkey was presented with the S+ and S— stimuli. The neuronal response was present initially, but quickly declined despite the fact that the monkey settled down to accurate performance after an omission error on trial 1. The cell did not become simply unresponsive since it responded well to a vertical grating, but the response to this stimulus also habituated (not shown). When the S+ and S— were used again after trials with other stimuli the cell showed little recovery and continued to be relatively unresponsive despite correct discrimination performance (last 3 trials).

During discrimination task performance, both S+ and S— stimuli were presented in a standard orientation and against a uniform matt white background. As with other visual stimuli, presenting the S+ and S— stimuli in novel orientations or against unusual colored or patterned backgrounds would often produce dishabituation of responses of neurons in the

tail of the caudate nucleus. It was interesting that this occurred despite continuing correct performance of the visual discrimination task, so that there was a dissociation between the response of this neuronal system, which occurred to the changed physical nature of the stimulus, and the reward value of the stimulus, which was interpreted correctly despite the change in its normal appearance.

From these results it is evident that the responses of neurons in the tail of the caudate nucleus are more related to changes in the visual stimuli between trials than to the learned association of the stimuli with reward. Furthermore, these results showed that the responses of these neurons were not related to motor responses made in the task or to the accuracy of performance of the task.

Ventral putamen

Of 48 cells recorded with the ventral and posterior

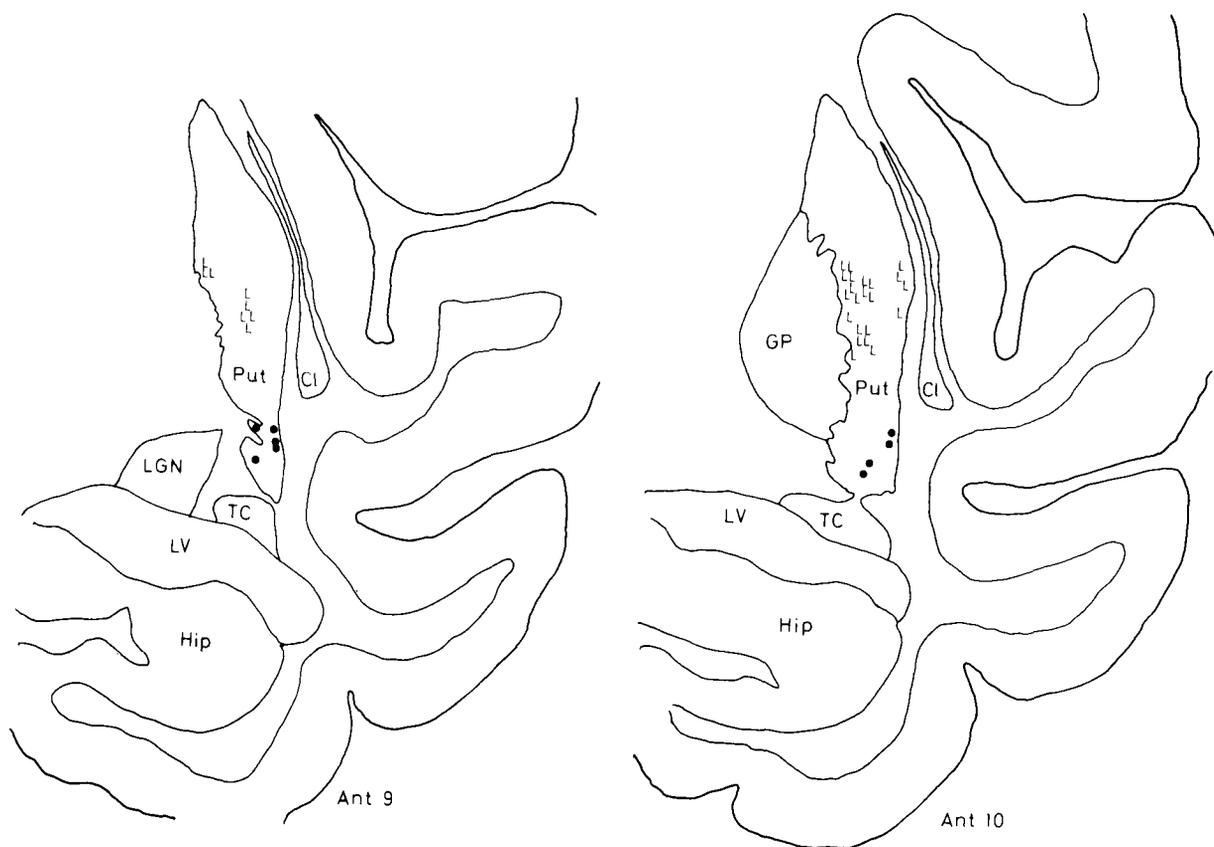


Fig. 8. Reconstructions of the positions of cells recorded in the putamen of one monkey. Outline drawing of structures evident in coronal sections (of the left hemisphere) 9, 10 and 11 mm anterior to the interaural plane. Abbreviations: Put, Putamen; TC, tail of the caudate nucleus; GP, globus pallidus; Cl, claustrum; LV, lateral ventricle; Hip, hippocampus; LGN, lateral geniculate nucleus. The positions of cells in the ventral putamen with habituating visual responses are marked by dots, and the position of cells in the lateral and medial putamen active during movements of the tongue made during lick responses are marked by L.

part of the putamen (see Fig. 8), a large proportion (69%, 33 cells) was found to have visual responses. Of 26 visual cells tested repeatedly with particular stimuli, most (17) responded similarly to neurons in the tail of the caudate nucleus in that they showed a marked tendency for their responses to habituate. Four cells (2 of which were motion sensitive) had non-habituating visual responses, and 5 cells had variable visual responses with no particular habituating pattern.

Visually habituating cells of the ventral putamen were very similar to those studied in the tail of the caudate nucleus, in that many had very low or zero spontaneous activity, gave transient visual responses at latencies ranging from 90 to 150 ms, were selectively responsive to particular stimuli, and showed rapid habituation which could recover with intervening visual stimuli. Fig. 9 illustrates these response

characteristics for one ventral putamen cell. Responses to the stimulus presented on trials 1–3 quickly habituated but recovered (dishabituated) with the intervening trials (4 and 5). Responses again quickly habituated over trials 6–8. The cell gave similarly habituating responses to a second visual stimulus (trials 12–14), but remained unresponsive when a variety of other stimuli were tested on trials 4, 5, 9, 10, 11 and 15. The stimulus used on trial 15 was a picture of a face which evoked considerable interest from the monkey but did not produce cellular responses, indicating a lack of correlation between discharges to stimuli and general interest evoked by them. The horizontal electro-oculogram recordings made during this series of trials confirmed that the monkey had maintained fixation (in the horizontal plane) of the stimuli even on trials where responses were absent. Thus the absence of responses was not likely to be be-

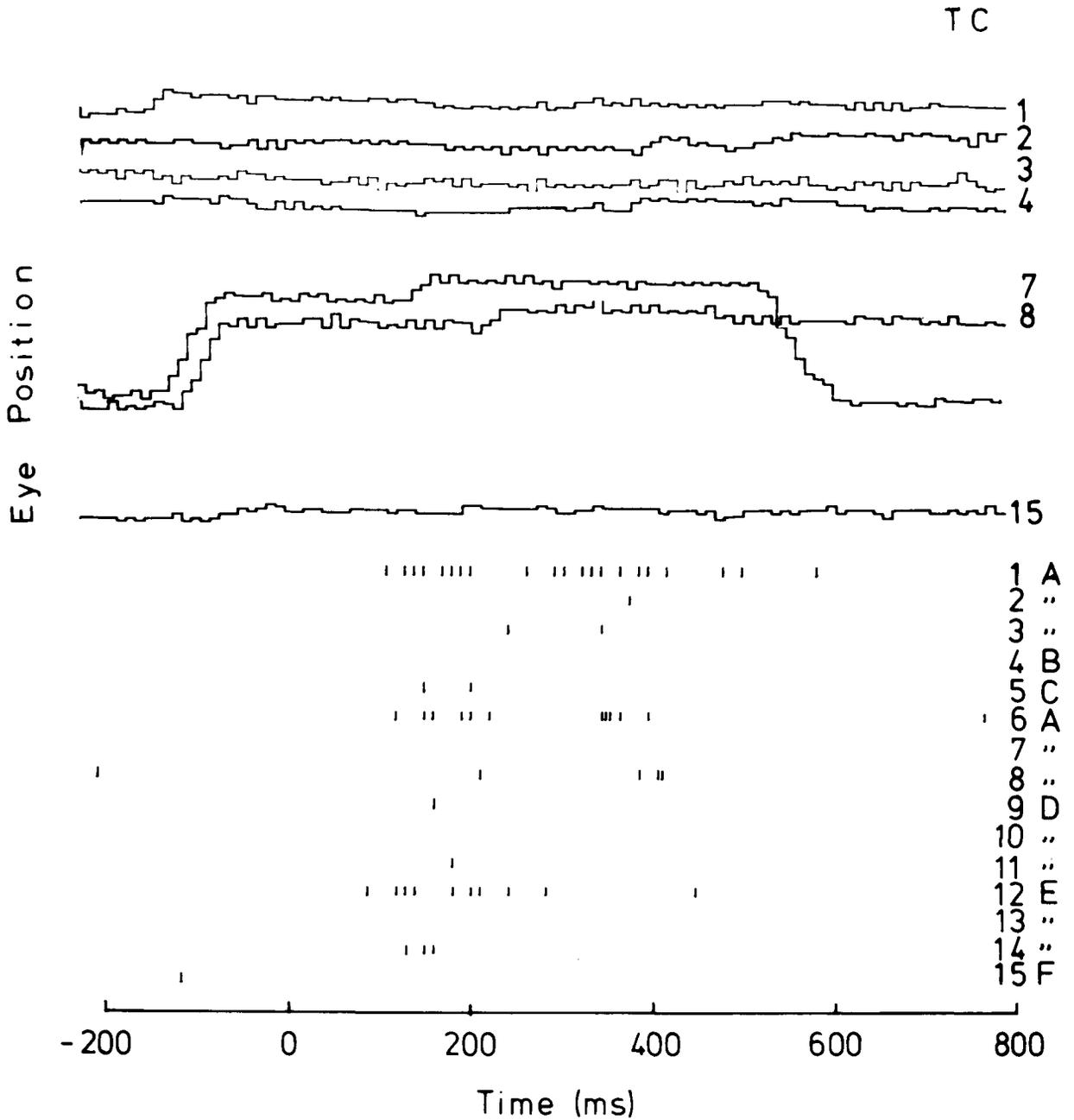


Fig. 9. Responses of a ventral putamen cell to different visual stimuli with electro-oculogram (EOG) records. The upper part of the figure gives horizontal EOG records during representative trials (the trial number is given at the right). EOG records from trials 7 and 8 are included to indicate that the recording sensitivity was sufficient to detect horizontal eye movements, which on these trials of approximately 30 degrees, and were made to fixate the shutter in the 200 ms period before the shutter opened. Fixation on the other trials (and normally) was made prior to 200 ms before the shutter opened at time 0 and was maintained throughout the presentation of the visual stimulus. Conventions for the lower part of the figure as for Fig. 3. The different visual stimuli used are labeled by letter. For details see text.

cause the monkey was not looking at the stimuli.

These visually habituating cells of the ventral putamen were not observed to respond in any exceptional or differential way to the S+ or S—, and many cells

did not respond to either stimulus at all. These cells then behaved in an essentially similar manner to visual stimuli as habituating cells studied in the tail of the caudate nucleus.

Three neurons in this part of the putamen with habituating responses to several visual stimuli were observed to respond without habituation to particular stimuli. This behavior was not observed in the tail of caudate, which may constitute a difference between the processing of the two areas, but the very small number of observations on such maintained responses does not warrant at present a firm conclusion on this.

DISCUSSION

The results of this recording study show that neurons in both the tail of the caudate nucleus and the ventral putamen are selectively responsive to particular visual stimuli, and that the neurons rapidly become unresponsive to these stimuli when they are repeatedly presented. Recovery from the habituated state is a relatively quick process and one or two trials with different stimuli usually restore responsiveness to stimuli for which habituation has taken place. We discuss how these properties might arise and what their functional role may be.

Visual input to the caudal neostriatum

The visual input from the occipital and temporal cortex to the caudal neostriatum has some topographical organization, with each cortical area projecting strongly to the part of the neostriatum lying beneath it^{15,39,40}. Since the recordings described here were mainly from the more anterior part of the tail of the caudate nucleus and adjoining part of the putamen, on anatomical grounds it is likely that the cells studied receive inputs directly from the inferior temporal cortex but not directly from the prestriate cortex. The stimulation studies of Reitz and Pribram¹⁹ also shown that the inferior temporal cortex anterior to the inferior occipital sulcus (but not posterior to it) gives rise to a direct input to the anterior part of the tail of the caudate nucleus and ventral putamen.

The properties of the neurons recorded in this study also suggest that they received inputs from the inferior temporal visual cortex. Thus these neostriatal neurons responded with latencies which were mainly between 100 and 150 ms, and these latencies are similar to the latencies of the responses of neurons in the inferior temporal visual cortex recorded in the same testing conditions²⁵. Moreover, the finding

that these neostriatal cells responded while the monkey fixated effective stimuli shown through the shutter also suggests that they receive inputs from inferior temporal cortex neurons, for these cortical neurons also respond in this way in the same testing conditions²⁵, probably because they have large receptive fields which include the fovea^{9,11,13}.

In the present study the majority (80%) of neurons in the tail of the caudate nucleus was found to respond to objects (including bars and edges) irrespective of orientation, and to habituate independently to stimuli shown in orthogonal orientations. Orientation selectivity in the caudal neostriatum appears to be lower than in the inferior temporal cortex where Gross et al.^{11,12} report that 50% of the cells display orientation selectivity when tested with bars and edges. This orientation tolerance and independent habituation to different orientations of caudal neostriatal neurons suggests that they receive a converging input from several inferior temporal cortex cells with different orientation sensitivities, so that they are able to respond to a complex patterned visual stimulus when it changes, even in orientation.

Visual habituation

The condition which affects responses of neurons in the tail of the caudate nucleus most predictably was found to be the change of visual stimuli. The general properties of the habituation observed conform well to the features of habituation reviewed by Thompson and Spencer³⁴. The difference between the habituation observed in the present study and that of most other studies concerns the stimuli to which habituation occurs, in that it occurs to complex patterned visual stimuli in the tail of the caudate nucleus. Rapid habituation to such complex visual patterns has only rarely observed previously⁹.

Habituation to specific visual stimuli could arise from a decline of responsiveness of neurons in the inferior temporal cortex, or from a decrease in the efficacy of the connections from the inferior temporal cortex neurons onto neurons in the tail of the caudate nucleus. The habituation does not reflect a general desensitization of neurons in the tail of the caudate nucleus, since habituation to one stimulus may not affect responses to a different stimulus. Nor is it likely that the habituation in the tail of the caudate nucleus reflects rapid and complete habituation of neurons in

the inferior temporal cortex, for under similar recording conditions Rolls et al.²⁵ found that neurons in the inferior temporal cortex which responded to stimuli used in a visual discrimination continued to respond even though these stimuli had been shown on thousands of previous occasions. Also, in the present study a number of tracks were made into the anterior inferior temporal cortex of the monkeys from which neurons were recorded in the caudal neostriatum in order to compare directly the neuronal responses in these two connected regions, and it was found that the inferior temporal cortex cells that were studied did not habituate markedly compared to the neostriatal cells, and in some cases were shown to respond for more than 120 consecutive trials. Further, neurons in other structures which receive from the inferior temporal cortex, as indicated by anatomical connections and the types of cell response found²¹, in many cases do not show pronounced habituation in the same testing conditions (and sometimes in the same animals). Such structures tested include the amygdala³³, the cortex in the anterior part of the superior temporal sulcus¹⁸, the rostral midline thalamic region²⁹, and the orbitofrontal cortex³⁵. Thus it is improbable that marked habituation of the types described here for the caudal neostriatum is a general property of the inferior temporal cortex. The most likely sites for the process causing neural habituation are the synaptic junctions of the inferotemporal cell inputs to the neostriatal cells, although some role of the subcortical inputs is also a possibility.

Possible functions of the visual habituation

The main characteristics of the responses of these neurons in the tail of the caudate nucleus and adjoining part of the putamen were rapid habituation to specific visual patterns, their sensitivity to changes in visual pattern, and the relatively short-term nature of their habituation to a particular pattern, with dishabituation occurring to one stimulus by even one intervening trial with another stimulus. Given these responses, it may be suggested that these neurons are involved in short term pattern-specific habituation to visual stimuli. This system would be distinguishable from other habituation systems (involved for example in habituation to spots of light) in that it is specialized for patterned visual stimuli which have been highly processed through visual cortical analysis mechanisms, as shown not only by the nature of the

neuronal responses, but also by the fact that this system receives inputs from the inferior temporal visual cortex. It may also be suggested that this sensitivity to visual pattern change may have a role in alerting the monkey's attention to new stimuli. This suggestion is consistent with the changes in attention and orientation to stimuli produced by damage to the striatum. Thus, damage to the dopaminergic nigrostriatal bundle produces an inability to orient to visual and other stimuli in the rat¹⁶, and damage to the neostriatum itself can lead to compulsive attention to stimuli with a failure to habituate normally in the cat³⁸ and monkey⁸.

Visual discrimination performance and caudal neostriatal function

Lesions to the caudal neostriatal structures can produce a mild but significant impairment of visual discrimination performance. It could therefore be the case that the responses of the neostriatal neurons receiving input from the inferior temporal cortex depend more on the learned significance of visual stimuli than the responses of inferotemporal cells, which are themselves predominantly visual in nature^{13, 20-22, 25}. No clear relation was found, however, between cellular activity in either of the caudal neostriatal structures, and reward contingencies or behavioral performance in a visual discrimination task. Many cells in the tail of the caudate nucleus and ventral putamen simply did not respond at all to the visual stimuli used in the discrimination task. The data we present suggest that the caudal neostriatum is not directly involved in the development and maintenance of reward associations to stimuli but may aid discrimination performance by its sensitivity to change in visual stimuli. As a population, these neurons could indicate whenever the stimulus on a given trial is different from that of the previous trial. It is clear that a brain system such as the caudal neostriatum which can detect change in visual stimuli over a short time scale can provide a mechanism for one form of visual short-term memory and may participate in a variety of cognitive operations in different behavioral situations.

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