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Neuronal responses in the ventral striatum of the behaving macaque*

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To analyse the functioning of the ventral striatum, the responses of more than 1,000 single neurons were recorded in a region which included the nucleus accumbens and olfactory tubercle in 5 macaque monkeys. While the monkeys performed visual discrimination and related feeding tasks, the different populations of neurons found included neurons which responded to novel visual stimuli; to reinforcement-related visual stimuli such as (for different neurons) food-related stimuli, aversive stimuli, or faces; to other visual stimuli; in relation to somatosensory stimulation and movement; or to cues which signalled the start of a task. The neurons with responses to reinforcing or novel visual stimuli may reflect the inputs to the ventral striatum from the amygdala and hippocampus, and are consistent with the hypothesis that the ventral striatum provides a route for learned reinforcing and novel visual stimuli to influence behaviour.

INTRODUCTION

Since the paper of Heimer and Wilson[14], great interest has focussed on the anatomy of the ventral striatum, which includes the nucleus accumbens, the olfactory tubercle (or anterior perforated substance of primates), and the Islands of Calleja. They showed that the ventral striatum receives inputs from limbic structures such as the amygdala and hippocampus, and projects to the ventral pallidum[11]. The ventral pallidum may then influence output regions by the subthalamic nucleus/globus pallidus/ventral thalamus/premotor cortex route, or via the mediodorsal nucleus of the thalamus/prefrontal cortex route[12]. The ventral striatum may thus be for limbic structures what the neostriatum is for neocortical structures, that is a route for limbic structures to influence output regions. The dopamine pathways are at a critical position in these systems, for the nigro-striatal pathway projects to the neostriatum, and the mesolimbic dopamine pathway projects to the ventral striatum[25]. This pattern of connections of the ventral striatum appears to occur not only in the rat[11], but also in the primate[15]. In addition, it is now clear that the olfactory tubercle is in the anterior perforated substance in the primate[13], and that while a small part of it related to the olfactory tract does receive olfactory projections, a much larger part of it receives a strong projection from the inferior temporal visual cortex[46,47], and could thus provide a link from temporal lobe association cortex to output regions.

In Parkinson's disease, there is marked depletion of dopamine in the nucleus accumbens, as well as in the putamen and caudate nucleus[1]. It is thus of importance to understand the functions of the ventral striatum. There is also some pharmacological evidence which links the ventral striatum to schizophrenia[21]. There is also evidence linking the ventral striatum and its dopamine input to reward, for manipulations of this system alter the incentive effects which learned rewarding stimuli have on behaviour[8,24]. Further evidence linking this system to some types of reward is that rats will self-administer amphetamine into the nucleus accumbens, and lesions of the nucleus accumbens attenuate the intravenous self-administration of cocaine[23]. Further evidence links the ventral striatum to responses to novel stimuli, for locomotor activity can be influ-

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enced by manipulations of the nucleus accumbens[17], particularly when this is in response to novel stimuli[10].

Although our understanding of the functions of the ventral striatum is now starting to develop, there have so far been no studies of what signals reach the ventral striatum, as shown by recording the activity of single neurons in the striatum. We have therefore analysed the activity of neurons in the ventral striatum of the behaving monkey, as described here. Preliminary results have appeared elsewhere[41,42].

In this investigation made to analyse the functioning of the ventral striatum, the responses of more than 1,000 single neurons were recorded in a region which included the nucleus accumbens and olfactory tubercle in 5 macaque monkeys. The neurons were recorded in test situations in which lesions of the amygdala, hippocampus and inferior temporal cortex produce deficits, and in which the responses of neurons in these brain regions which provide afferents to the ventral striatum have been analysed[31,32,33,34,35]. The test situations also included some in which the responses of neurons in other parts of the striatum have been analysed[30,38,39,40,41,42,44], so that comparisons of neuronal responses in different parts of the striatum can be made.

MATERIALS AND METHODS

Subjects, stimulus presentation and behavioural tasks

Five male cynomolgus macaques (*Macaca fascicularis*) (weight 3–4 kg) were trained to perform a visual discrimination task for the delivery of fruit juice. During the experiment the monkeys sat in a chair, the top, front and sides of which were enclosed by metal shielding. Their view of the laboratory was limited to a circular aperture in the shielding. Visual stimuli were presented with a fast (~ 10 ms) rise time 6.4 cm diameter electromagnetic shutter mounted over the aperture. The shutter was removable, allowing the presentation of objects and the delivery of foods to the monkey through the aperture.

The stimuli were presented individually, one per trial, with an intertrial interval of 6 s. Each trial began with a 0.5 s tone cue followed by the opening of the shutter for 1.5 s. During the stimulus presentation, the monkey was able to respond by licking a tube through which either fruit juice or saline was delivered, depending upon the learned meaning of the stimulus.

Training in the task began by familiarising the monkeys with two distinctive syringes differing in shape and colour. One syringe was used to deliver juice (the S +) to the mouth, the other being used to deliver saline (the S –). The monkeys rapidly learned to discriminate the valence of these syringes, and would reach for or turn away from the approaching S + or S – .

Formal training in the visual discrimination task began by using the shutter to present the S + and S – syringes to the monkeys. They learned to lick the tube at the sight of the S + for which juice was delivered, and to refrain from licking at the presentation of the S – , thus avoiding the delivery of saline.

In addition to the visual discrimination task, a novelty/familiarity task was run in which novel and familiar stimuli could be interspersed between the S + and S – stimuli. The task was similar to a serial recognition memory task[37], except that the novel and unfamiliar stimuli were unreinforced. Reinforcement was available if the S + was shown, and because this occurred randomly, the monkey did look at the shutter on every trial when the tone sounded just before it opened. Each such novel/familiar stimulus was shown only twice per day. Approximately 2,000 objects were used as stimuli, varying in size, colour and shape.

The presentation of a familiar stimulus in the novelty/familiarity task could occur immediately (6 s) after the first, novel presentation, or later in the series after a number of other stimuli had been presented. The novelty/familiarity task was run with the numbers of intervening trials between the two sucessive presentations of the stimuli ranging from 0 to 2, or from 0 to 8, or from 0 to 16. An example of part of one sequence (the 0 to 8 version) is shown below: N1→N2→F2→N3→N4→F1→N5→F4. The novel stimulus (N1) shown on trial 1 was shown again after four intervening trials as familiar (F1) on trial 6, while the novel stimulus (N2) shown on trial 2 was repeated with no intervening trials on trial 3.

Clinical tests

After the responses of neurons had been determined in the tasks, it was often possible to assess the effects of presenting foods, the S + and the S – syringes, and novel and familiar objects through the aperture in the primate chair. These presentations were done using a standard protocol in which counts of mean firing rate for a 2-s period were made by computer during the steps in the protocol. The protocol (see[39] for more details) consisted of (1) the presentation of the experimenter's arm viewed through the aperture; (2,3) reaching movements to and from the stimulus to be presented, with the stimulus still out of view; (4,5,6) the sight of the stimulus, its approach, movement of the stimulus close to the mouth and touching the mouth to elicit mouth movements and to test for somatosensory input, and finally (7) delivery of the stimulus into the mouth

to produce taste. The stimuli were presented without a preceding tone cue and the delivery of foods to the monkey was not contingent upon a lick response.

Experimental procedures and testing protocols

The monkeys became very proficient at the tasks, such that novel and familiar stimuli, the S + and S −, and other stimuli such as foods and faces were presented in pseudorandom order during the experiments, and the monkeys performed the tasks with a high degree of accuracy (> 90%). This procedure enabled a great many stimuli varying in their valence and familiarity to be presented to the monkeys.

After the monkeys were trained, they were prepared for the neurophysiological experiments, in which recordings were made from single neurons during the performance of the tasks. Details of this preparation, the microelectrodes, amplification, on-line computing, electro-oculogram, methods for determining the location of the neurons, etc. were conventional and have been described in detail elsewhere[9,39].

Data analysis

The computer sampled the occurrence of neuronal spikes every 10 ms, starting 200 ms before the onset of the visual stimulus and 700 ms after its presentation. The number of spikes emitted in a 500-ms period starting 100 ms after stimulus presentation was counted and used as the measure of the neuronal response. These data were subsequently treated to statistical analysis, in which the trial by trial responses to the novel and familiar stimuli, the S + and S − were entered into a computer which carried out a one-way analysis of variance. In order to determine which stimulus group was responsible for a significant result in the ANOVA, the Tukey test[4] was applied to test the significance of any difference between the means of the various groups.

The latencies at which neurons responded differentially to the S + and S − were determined with the use of cumulative sum techniques[50] implemented on a computer. Peristimulus time histograms were computed for each type of trial and subtracted from each other; the cumulative sum of this difference array was then calculated to allow estimation of the differential response latency.

RESULTS

It was possible to analyse the responses of more than 1,000 single neurons in a region which included the nucleus accumbens and olfactory tubercle in the 5 macaque monkeys.

TABLE I

*Neuronal responses in the ventral striatum**

		Ventral striatum		
		n	1,013	%
1	Visual, recognition related			
	novel	39		3.5
	familiar	11		1.1
2	Visual, association with reinforcement			
	aversive	14		1.4
	food	44		4.3
	food and S +	18	1,004	1.8
	food, context dependent	13		1.3
	opposite to food aversive	11		1.1
	differential to S + or S − only	44	1,112	4.0
3	Visual			
	general interest	51		5.0
	non-specific	78	1,112	7.0
	face	17		1.7
4	Movement-related, conditional	50	1,112	4.5
5	Somatosensory	76	1,112	6.8
6	Cue related	177	1,112	15.9
7	Responses to all arousing stimuli	9	1,112	0.8
8	Task-related (non-discriminating)	17	1,112	1.5
9	During feeding	52	1,112	4.7
10	Peripheral visual and auditory stimuli	72	538	13.4
11	Unresponsive	608	1,112	54.7

* The sample size was 1,013 neurons except where indicated. The categories are non-exclusive.

The following types of neuronal response were found. The numbers of neurons of each type are shown in Table I. The sample size was 1,013 neurons, unless otherwise stated in Table I.

Neuronal responses to novel visual stimuli

First, a population of neurons was found that responded to novel visual stimuli. An example of one such neuron is shown in Fig. 1. The neuron increased its firing rate to novel visual stimuli. If the same stimulus was presented as familiar, with 0 intervening stimuli, then the neuron did not respond to that visual stimulus. As an increasing number of intervening trials occurred between the novel and familar presentations of a stimulus, the neuron responded more and more to the familiar stimulus, until after 5–14 intervening stimuli, the neuronal response was not significantly different from that to a novel stimulus.

Another example of a neuron which responded more to novel than to familiar stimuli is shown in Fig. 2. On the right of Fig. 2 it is shown that the response to novel stimuli, an increase in firing rate to 25 spikes/s from the spontaneous rate of 10 spikes/s, in this case habituated only over repeated presentations of the stimulus. The lack of response shown in the left panel of Fig. 2 to the

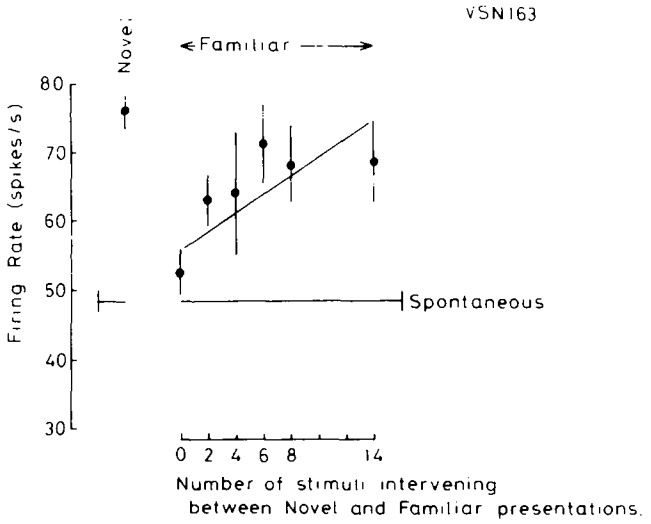


Fig. 1. An example of a ventral striatal neuron that responded to novel visual stimuli. The neuron increased its firing rate to novel visual stimuli. If the same stimulus was presented as familiar, with 0 intervening stimuli, then the neuron did not respond to that visual stimulus. As an increasing number of intervening trials occurred between the novel and familar presentations of a stimulus, the neuron responded more and more to the familiar stimulus, until after 5–14 intervening stimuli, the neuronal response was not significantly different from that to a novel stimulus.

familiar stimulus was thus achieved only after habituation produced by 4–7 presentations of the stimulus. It is also shown in Fig. 2 that the effect of novel stimuli on such neurons was not produced just because the novel stimuli produced arousal, for the neuron responded to aversive stimuli when they had not been seen for more than 1 day (Aversive (novel) in Fig. 2), but did not respond to aversive visual stimuli (such as the sight of a syringe from which the monkey was fed saline, Aversive (familiar) in Fig. 2), even though the latter produced arousal. Different neurons in this category show pattern-specific habituation over 1–10 trials, and show retention of this habituation over 1–14 intervening trials.

The number of neurons responding to novel visual stimuli is shown in Table I. The majority of these neurons responded to novel stimuli by an increase in firing rate. A smaller number of neurons responded to familiar rather than to novel visual stimuli (see Table I).

This first group of neurons thus has responses related to recognition memory, responding differently to novel and to familiar stimuli. They may receive their inputs from the amygdala and hippocampus, in both of which there are small numbers of neurons which respond differently to novel as compared to familiar visual stimuli[34,35,36,44,49].

Neuronal responses related to reinforcers

Second, other neurons respond to visual stimuli of emotional or motivational significance, that is to stim-

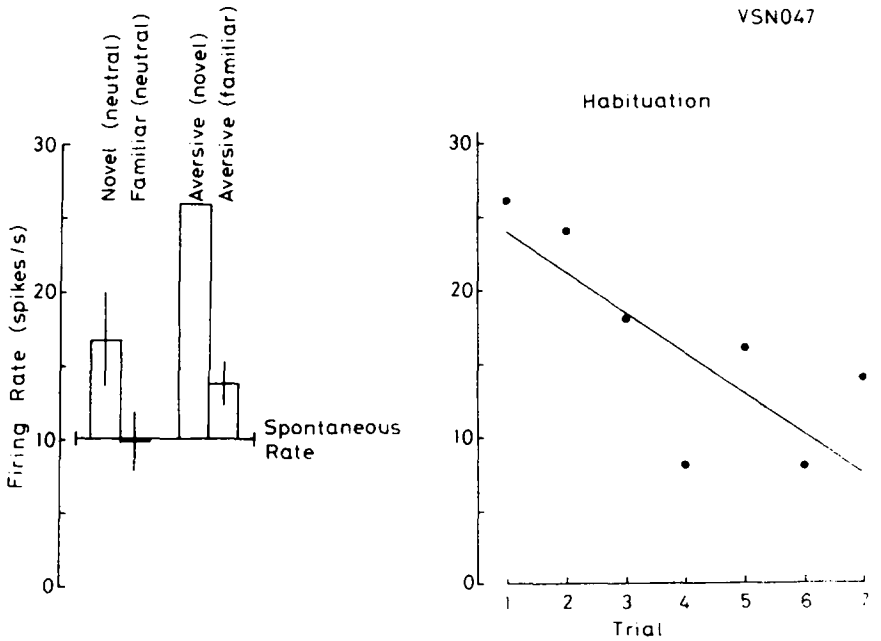


Fig. 2. The responses of another ventral striatal neuron to novel visual stimuli. On the right it is shown that the response to novel stimuli, an increase in firing rate to 25 spikes/s from the spontaneous rate of 10 spikes/s, habituated over repeated presentations of the stimulus. The lack of response shown in the left panel to the familiar stimulus was thus achieved only after habituation produced by 4–7 presentations of the stimulus. It is also shown the neuron responded to aversive stimuli when they had not been seen for more than 1 day (Aversive (novel)) but did not respond to aversive visual stimuli (such as the sight of a syringe from which the monkey was fed saline, Aversive (familiar)), even though the latter produced arousal.

uli which have in common the property that they are positively or negatively reinforcing[31]. (Reinforcers are stimuli which if their occurrence, termination or omission is made contingent upon the making of a behavioral response, alter the future emission of that response.) The responses of an example of a neuron of this type is shown in Fig. 3. The neuron increased its firing rate to the S − on non-food trials in the visual discrimination task, and decreased its firing rate to the S + on food reward trials in the visual discrimination task. The differential response latency of this neuron to the reward-related and to the saline-related visual stimulus was approximately 150 ms (see Fig. 3), and this value was typical.

Of the neurons which responded to visual stimuli which were rewarding, relatively few responded to all the rewarding stimuli used. That is, only few ventral striatal neurons responded both when food was shown and to the positive discriminative stimulus, the S +, in a visual discrimination task, as shown in Table I. Instead, the reward-related neuronal responses were typically more context or stimulus-dependent, responding for example to the sight of food but not to the S + which signified food (food in Table I), differentially to the S + or S − but not to food, or to food if shown in one context but not in another context. Some other neurons responded to aversive stimuli (see Table I). These neurons did not respond simply in relation to arousal, which was produced in control tests by inputs from different modalities, for example by touch of the leg.

These neurons with reinforcement-related responses represented 13.9% of the neurons recorded in the ventral striatum, and may receive their inputs from structures such as the amygdala, in which some neurons with similar responses are found[34,35].

Neuronal responses to other visual stimuli

Third, other neurons with visual responses had activity which occurred primarily to objects which the monkey paid attention to in the environment (Visual, general interest, in Table I), or which occurred to all visual stimuli presented (Visual, non-specific, in Table I).

In addition, some neurons responded more selectively to visual stimuli, in particular when the monkey looked at faces (see Table I). An example of such a neuron is shown in Fig. 4. This neuron decreased its firing to a low rate when the monkey was shown a face through the shutter. In contrast, when food was shown when the shutter opened, the neuron did not decrease its firing rate. (There was a small increase in firing to the food, as shown in Fig. 5. The face, food, the S +, and the S − were presented in random order during such testing.) The responses of these neurons to faces were not just due to arousal elicited by a face, in that they did not respond for example to touch to the leg which elicited arousal (see e.g. Fig. 5).

Altogether, the neurons with visual responses, defined according to the criteria of Sanghera, Rolls and Roper-Hall[45], represented 32.2% of those recorded in the ventral striatum (categories 1–3 of Table I). Their responses probably reflected the inputs received from the inferior temporal cortex as well as from the amygdala and hippocampus by the ventral striatum[32,34].

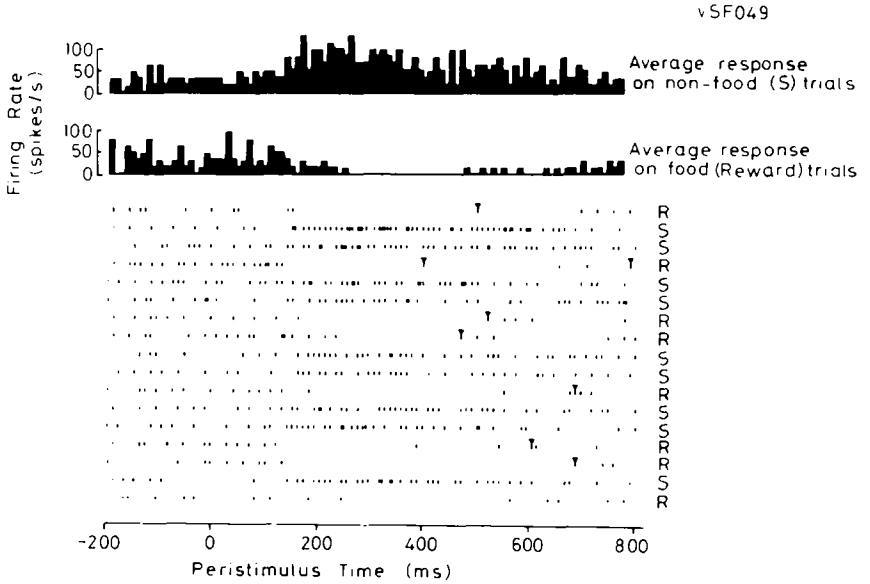


Fig. 3. Responses of a neuron in the visual discrimination task. The neuron increased its firing rate to the S − on non-food trials, and decreased its firing rate to the S + on food reward trials. Rastergrams and peristimulus time histograms are shown.

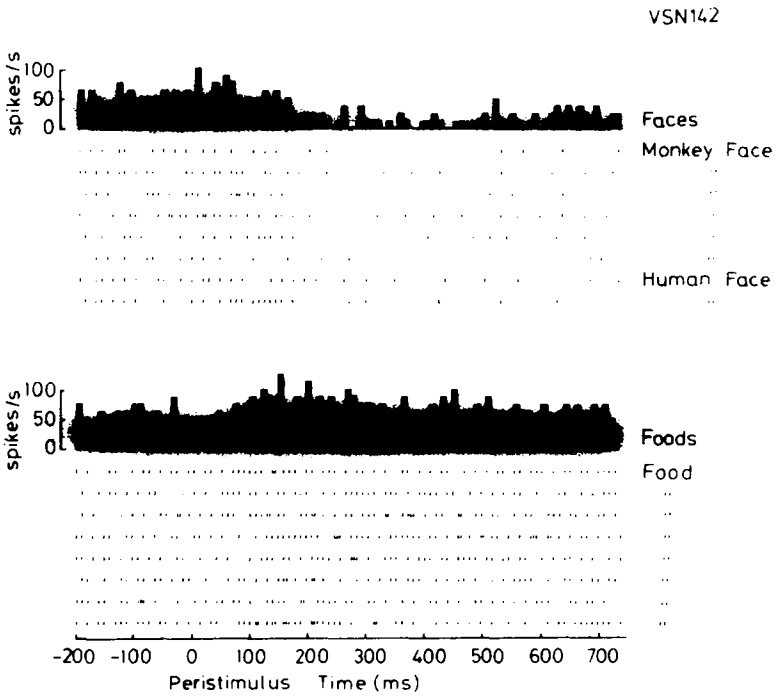


Fig. 4. Responses of a ventral striatal neuron to faces. The neuron decreased its firing to a low rate when a face was shown through the shutter. In contrast, when food was shown when the shutter opened, the neuron showed some increase in firing rate.

Neuronal responses related to somatosensory stimuli or movement

Fourth and fifth, other neurons responded in relation to movement or somatosensory stimuli, for example during licking or arm movements (see Table I). Some neurons appeared to have larger responses when the monkeys reached for food than when they reached towards other objects, and these are described as conditional movement-related in Table I.

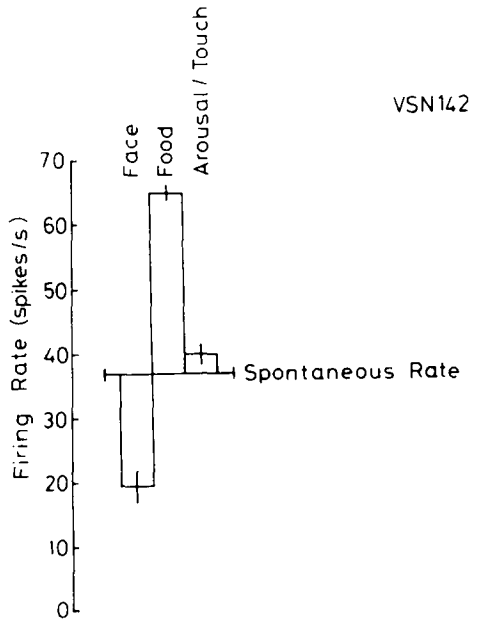


Fig. 5. Responses of the same neuron shown in Fig. 4, showing in addition that the neuron did not respond to arousal, produced by touch.

Neuronal responses related to signal cues

Sixth, other neurons responded, as in the head of the caudate nucleus[39], to cues such as a 0.5-s tone which the monkey used to prepare for the performance of each trial of the visual discrimination task (see Table I).

Neuronal responses related to arousal

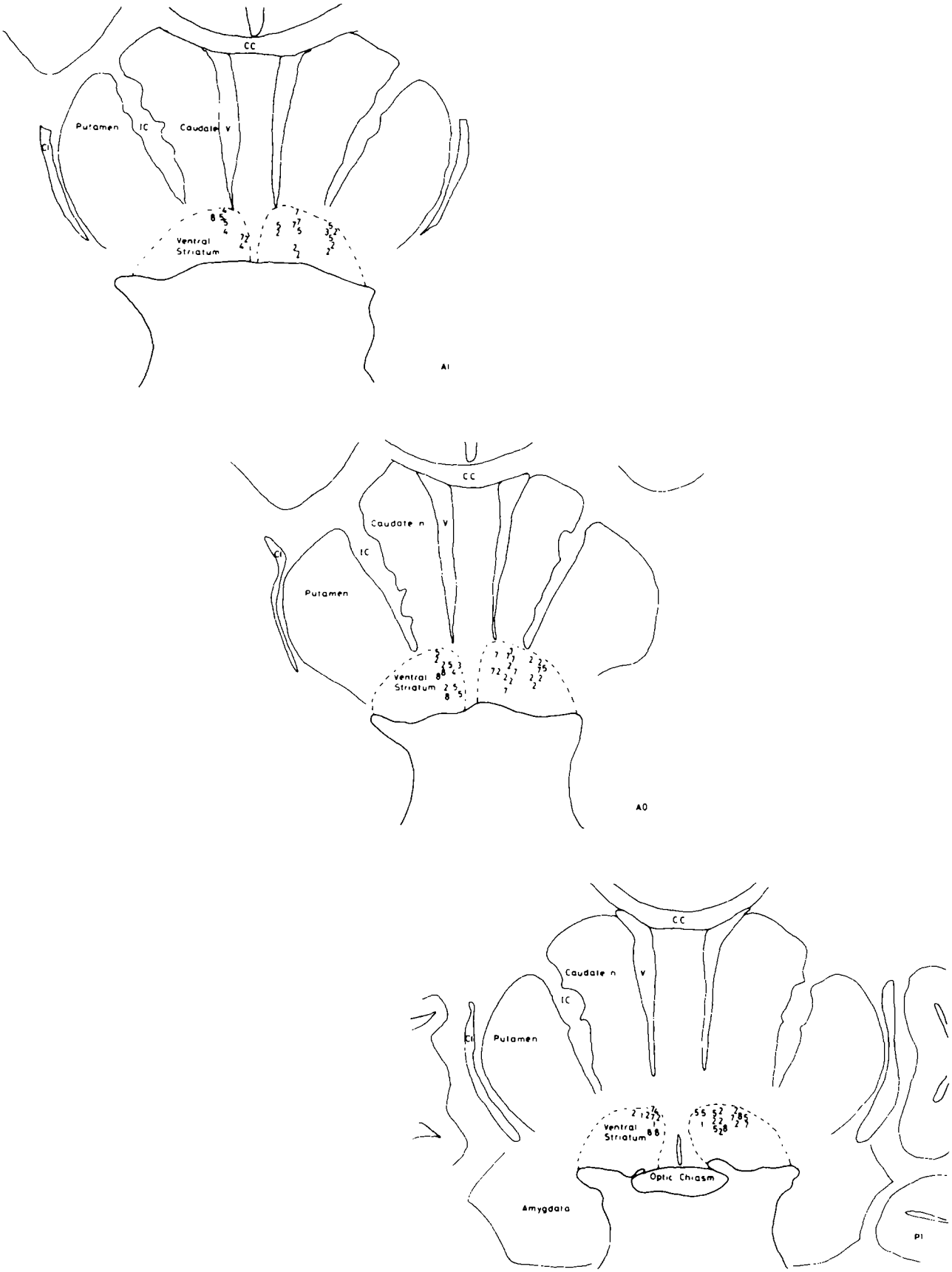
Seventh, other neurons responded in relation to arousal, however this was produced (see Table I). Such neurons always responded for example to touch to the monkey's leg.

Task-related neuronal responses

Eighth, some neurons responded while the monkey performed the visual discrimination task, but did not have differential responses to the rewarding and aversive stimuli in the task, and could not be shown to have visual or movement-related movements outside the task. These neurons are shown as task-related in Table I, and are similar to some neurons in the head of the caudate nucleus[39].

Neuronal responses occurring during feeding

Ninth, some neurons responded when the experimenter fed the monkey either just before or during the



ig. 6. The sites in the ventral striatum at which the neurons were recorded. The neuron types indicated on this figure correspond to the type numbers used in Table I and in the description of the results.

eating (see Table I). These neurons could have been influenced by olfactory and gustatory stimuli[29].

Tenth, some neurons responded to visual or to auditory stimuli in the periphery of the monkey's field of vision.

Recording sites

The sites at which the neurons were recorded in this study are shown in Fig. 6. The neuron types indicated on this figure correspond to the type numbers used in Table I and in the description of the results. The histological reconstruction of the recording tracks, based on the microlesions and the X-radiographs, was used to ensure that only neurons in the ventral striatum, and not neurons in the head of the caudate nucleus, were included in Table I.

DISCUSSION

These neurophysiological findings show that novel, motivational, and emotion-provoking visual stimuli influence the activity of neurons in the ventral striatum. These inputs probably reach it from limbic structures such as the amygdala and hippocampus, which project into the ventral striatum and are involved in these motivational, emotional and memory functions[30–32,34–36], and in which neurons that respond to similar reinforcing and novel visual stimuli are found[31,32,34,35,44,48,49]. Further the neurons which respond to faces are probably part of a system of neurons important in the recognition of individuals by their faces and in social and emotional responses to faces. Neurons in this system are found in the cortex in the superior temporal sulcus of the macaque monkey, and in the amygdala, which receives from the temporal lobe cortex and projects to the nucleus accumbens[3,20,26,35,36]. It is thus likely that the ventral striatum is one system which provides a route for this system to influence behavior.

In that the majority of these neurons did not have unconditional sensory responses, but instead the response typically depended on memory, for whether the stimulus was recognised, or for whether it was associated with reinforcement, the function of this part of the striatum does not appear to be purely sensory. Rather, it may provide one route for such memory-related, and emotional and motivational, stimuli to influence motor output. This is consistent with the hypothesis that the ventral striatum is a link for learned incentive (e.g. rewarding) stimuli[8,24], and also for other limbic-processed stimuli such as faces and novel stimuli, to influence behaviour[22,27,28,30,41–43]. It will thus be of interest to determine whether there are changes in responses to such stimuli in Parkinson's disease, or in monkeys with selective depletion of dopamine in the ventral striatum.

Segregation of function within the striatum

These neurophysiological investigations indicate that there are differences between neuronal activity in different regions of the striatum, and that the inputs which activate these neurons are derived functionally from the cortical region or limbic structure which projects into each region of the striatum[43]. Thus the majority of neurons in the main part of the putamen[40] had responses related to movements made by the monkey[6,7]. This is consistent with the inputs to these regions from sensorimotor cortex, areas 3,1,2,4 and 6[2,6,18,19]. In contrast, though the same testing methods were used, neuronal activity related to visual stimuli and which showed rapid habituation was found in the tail of the caudate nucleus and adjoining part of the ventral putamen, which receive from the inferior temporal visual cortex[5]. Also, neuronal activity related to the preparation for and initiation of behavioral responses in response to environmental cues was found in the head of the caudate nucleus[38,39], whereas such neurons were relatively rare (10%) in the putamen, and instead neurons with activity unconditionally associated with movements made in the same test situations were common (29%) in the putamen. This is again consistent with the inputs to the head of the caudate nucleus. This region of the striatum receives projections from the prefrontal cortex, in which neurons which respond to the same environmental cues are found (experiments of E.T. Rolls and G.C. Baylis, 1984). In the posterior and ventral part of the putamen, which receives from temporal lobe visual cortex, we have shown that neurons may respond during the delay in a visual delayed match to sample memory task, but not when instead an auditory delayed match to sample task is being performed[16,43]. The responses of these neurons are thus not related to movements made in the memory task, but instead have activity which is closely related to the responses of cells known to exist in the inferior temporal visual cortex, to which the posterior putamen is connected. In the study described here, we have shown that the activity of some neurons in the ventral striatum, which receives inputs from limbic structures such as the amygdala and hippocampus, occurs to stimuli related to reinforcing and novel environmental events.

The importance of this at least partial segregation of neuronal response types in different major parts of the striatum for our understanding of striatal function is that it shows that there is at least partial segregation of function within different regions of the striatum, and that it is not functionally homogeneous[43]. A conse-

quence of this is that damage to different regions of the striatum (including for example regional depletion of dopamine) would not be expected to necessarily lead to the same type of disorder. For example, in view of the results described here, it might be expected that movement disorders might be produced by depletion of dopamine in the putamen, but that other more complex, cognitive, sensory or emotional, disorders would result if there were depletion of dopamine in other regions of the striatum, such as the head of the caudate nucleus, the tail of the caudate nucleus, or the ventral striatum. The possibility that the architecture of the basal ganglia allows this segregated information to be brought at least partly together within and beyond the globus pallidus, ventral pallidum, and substantia nigra, and the implications this has for understanding the functioning of the basal ganglia, are considered further elsewhere[27,28,41–43].

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