

HYPOTHALAMIC NEURONAL RESPONSES ASSOCIATED WITH THE SIGHT OF FOOD

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SUMMARY

Neurons in the lateral hypothalamic region are described which alter their firing rates when a monkey looks at food. The units responded when the monkey looked at different types of food, but not at non-food objects or simple visual stimuli. The units did not respond in relation to motor movements, intense arousal, nor when a salient aversive stimulus was shown, nor in relation to eye movements, and were thus shown to be different from units in the globus pallidus which did respond in some of these control tests. The neurons did not respond to olfactory stimuli and did not respond if the animal ate in the dark. Because of these findings it is suggested that the activity of these hypothalamic neurones is associated with the sight of food. It is of interest that these neurones which respond when food is shown to a hungry animal are found in a region thought to be involved in the control of feeding.

INTRODUCTION

While recording from single units in the monkey lateral hypothalamus to analyze the neural basis of eating and drinking^{14,15}, we have found not only neurones which fire during eating and drinking² but also neurones which fire prior to the onset of eating and drinking. Neurones which fire immediately before the onset of eating have also been described in the cat¹³ and rat⁷. We first describe an investigation of the responses of the neurones we found in the monkey which alter their firing rates before the animal eats or drinks. Experiments were performed to determine whether the activity of these neurones is associated with olfaction, movement including eye movement, arousal, or the sight of food. The results of this investigation suggest that the activity of these neurones is associated with the sight of food. A comparison of the responses of these hypothalamic units with the motor responses of neurones found just above in the globus pallidus strengthen the suggestion that the activity of the

hypothalamic neurones is associated with the sight of food, rather than with basic movements.

METHODS

Recording method

Seven squirrel monkeys (*Saimiri sciureus*) and two rhesus monkeys (*Macaca mulatta*) were implanted under Pentothal anaesthesia with a stainless-steel holder on which a Trent–Wells adapter for chronic single-unit recording could be placed during recording sessions. Stimulation electrodes aimed at a number of brain sites were also implanted during the same operation. After a recovery period of at least one week, daily recording sessions started. The monkey sat in a primate chair. Single unit activity was recorded extracellularly with a tungsten microelectrode⁸ driven by a hydraulic microdrive mounted on the permanently implanted holder using the Trent–Wells micropositioner. The microelectrode entered the brain through a stainless-steel guide tube which just penetrated the dura. This system provided good stability, so that single units could often be held for many hours. With this system and the relatively small tungsten microelectrodes used (shaft diameter was 0.005 in.) one or two tracks were made daily and brain damage as judged by presence of units in the hypothalamus, lack of hemiparesis and the histology was not usually significant. A FET pre-amplifier mounted on the microdrive connected the microelectrode to conventional amplifiers and an oscilloscope display. The single unit spikes and firing rate were also displayed on a polygraph, together with external event markers for visual presentation of food, and consumption of food. To ensure that a recording was being made only from a single unit the waveform of the action potentials was continuously monitored, and care was taken to show that the spikes were never coincident in time. The amplitude and waveform of the single unit activity suggest that the recordings were from cell bodies.

Presentation of stimuli

Different procedures were used as described below to determine whether the firing of a neurone was related to the sight of food, or to other factors such as the taste or smell of the food, reaching, and general excitement. The responses to the visual stimuli, which were presented in random order at 1–2-min intervals, were measured as the average firing rate over several 10-sec periods in which each stimulus was presented, or over the parts of these 10-sec periods in which the animal looked at the stimuli. The spontaneous baseline firing rates were measured in the interstimulus intervals and were constant throughout the experiments. Control recordings were made from single neurones in other brain areas to determine how well these procedures were able to distinguish between different types of neurone with activity associated with feeding.

During the experimental sessions the monkeys were hungry, and would reach for and eat food. Food was available overnight in the home cage but was removed early in the morning, so that the monkeys were about 4 h food-deprived when the first

hypothalamic units were recorded. Recording sessions typically lasted a further 6 h. In the home cages the squirrel monkeys consumed chow, orange, egg, banana, carrots, grapes, peanuts and mealworms. When sitting in the primate chair, they would accept and reach for peanuts, mealworms and glucose solutions; they would accept but not reach for carrots, bananas and mash; and they would not accept chow or egg. The rhesus monkeys showed slightly different preferences, preferring banana, peanuts, grapes and carrot in descending order, but were often willing to reach for all foods presented. These preferences varied and were checked prior to and during recording sessions. There were thus 3 classes of food in descending order of preference — those the animal would reach for and eat, those which he would not reach for but would eat when given, and those which he refused to eat.

Using the following tests it was possible to separate responses of units associated with seeing, seeing and tasting, tasting, smelling, reaching for, and consumption of food. The activity of the neurones was measured when food and non-food odours were presented on cotton swabs, when the animal reached for and chewed edible and inedible objects, when the food was shown to the monkey and then either given or not given to the monkey, and to assess somatosensory effects, when the animal was touched, especially on the face, eyes, mouth, throat and stomach. These procedures were repeated in the dark. When a food or non-food object was shown to the monkey, it was introduced rapidly into the visual field, and moved gradually over a 10-sec period from a distance of 1 m towards the monkey's mouth. The response of the unit was measured while the monkey looked at the object in this 10-sec period.

If in the above tests it was found that the response of the neurone was associated with the sight of food, then tests were performed to analyze this response. The magnitude of the response to the sight of each food normally available in the home cage, and to the sight of a syringe from which the animal was fed 5% glucose solution, was determined. Then the responses to food and to non-food visual stimuli were compared. The non-food visual stimuli used were black and white edges, and more complex stimuli such as common laboratory objects, the forceps used to present food to the animal, and the experimenter's hand which normally held the forceps. All visual stimuli were tested in different orientations, in different parts of the visual field, and moving with different velocities and in different directions. To assess the contribution of the shape of the stimulus to the response, food objects with different shapes were presented (e.g. a peanut and a banana), and paper and modelling clay models of the effective stimulus in which the shape, color, and contrast were separately varied, were presented to the animal. A further test was to show the animal a squeeze bulb from which it had previously received air puffs in the face. The air bulb first elicited fixation, then as it was moved towards the animal, reaching, arousal, lip and general body movements, and then eye closure. Further information on the effects of eye and eyelid movements was obtained by recording the eye movements and the unit response on video tape. The responses of some units were also measured when the monkeys grasped food in the dark and then ate it, to determine whether the responses of the units were associated with feeding even when the monkey could not see the food.

Observations on unit activity in other brain areas in the same test situation

When the above procedures had been performed on a number of units in the lateral hypothalamus which altered their firing rate when the monkey looked at food, it was found that changes in the activity of the neurones were associated with the sight of food, and not with the sight of other visual stimuli, or with motor movement, or with arousal. To obtain further evidence on the adequacy of these procedures, recordings were made using the same procedures from cells in the globus pallidus which also fired during feeding.

Localization of recording sites

The sites where the neurones described in this paper were recorded were located in 3 different ways. Lesions were made through the recording microelectrodes to mark selected units. This was done by passing an anodal current of 30–60 μA for 30–100 sec. Anterior and lateral X-ray photographs of the microelectrode at the recording site were taken. The unit position could then be calculated by reference to the X-ray which showed both the microelectrode, and the nearby chronically implanted stimulation electrodes the sites of which were determined when histology was performed. Some microelectrode tracks could usually be identified when histology was performed. After a lethal i.p. dose of Nembutal the animal was perfused with 0.9% saline followed by formal-saline. After equilibration in sucrose-formalin, serial frozen 50 μm brain sections were cut and stained with thionin. Lesions made through recording microelectrodes, microelectrode tracks, and the stimulating electrodes were located.

RESULTS

Recordings were made from 423 neurones in and lateral to the lateral hypothalamus in the 7 squirrel monkeys and from 341 neurones in the same region in two rhesus monkeys.

Responses of hypothalamic neurones

The response of one of the units which decreased its firing rate when the animal saw food is shown in Fig. 1, above. A peanut was introduced into the field of vision at a distance of 1 m from the monkey and then was steadily moved towards the monkey over the next 10 sec. On this trial when the peanut was several inches from the monkey it was removed from the field of vision. The spontaneous firing rate of the unit fell to a low value while the monkey looked at the peanut, and returned to its baseline firing rate when the peanut was removed. A small rebound in the firing rate of this unit occurred when the peanut was removed from the animal's field of vision. The firing rate of this unit when the animal looked at different stimuli is shown in Fig. 1, below. The spontaneous firing rate of the unit was 20 spikes/sec and fell to 7 spikes/sec during the presentation of a peanut ($P < 0.001$). There was only a small decrease in the firing rate when a carrot or a grape was shown, and these were less preferred foods. The unit decreased its firing rate to 7 spikes/sec when the monkey

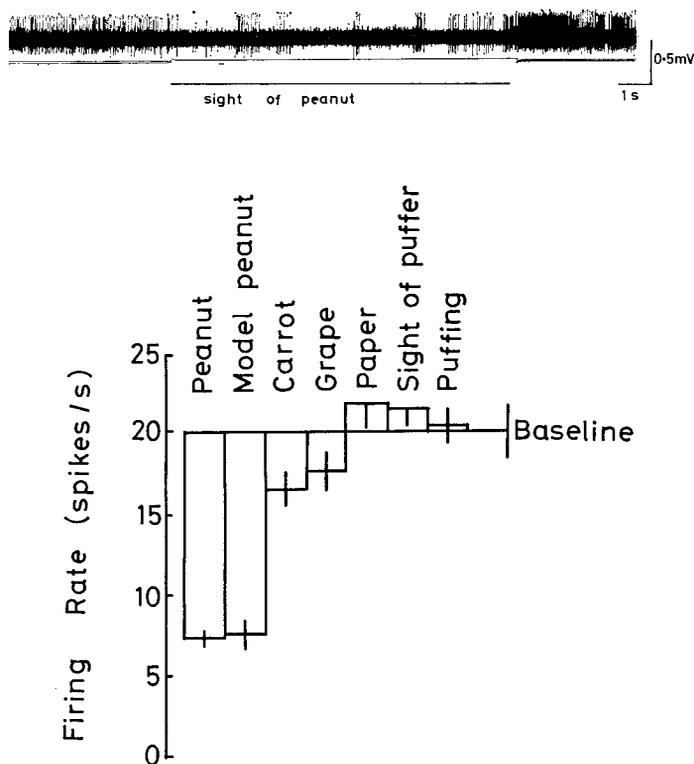


Fig. 1. Above: the firing rate of this lateral hypothalamic unit decreased when the squirrel monkey saw a peanut, which was initially at a distance of 1 m from the animal. The peanut was moved gradually towards the animal's mouth, but on this trial the peanut was not given to the monkey. The short bursts of action potentials occurred when the monkey glanced away from the peanut. Below: firing rate of a squirrel monkey lateral hypothalamic unit during a 10-sec period in which different visual stimuli were shown to the monkey. The histograms show how the firing rate changed (the vertical bars represent the standard error of the firing rate calculated over the 10-sec period in which the stimulus was shown) from the spontaneous baseline rate of 20 spikes/sec. The model peanut was made of modelling clay and was used as a control for olfaction. The paper had the same outline and colour as the peanut and was used as a control for shape. Air was blown from a squeeze bulb over the monkey's face to control for arousal and general movement (puffing). The squeeze bulb was shown to the monkey to test the effect of an aversive visual stimulus, and of a highly salient visual stimulus which was not food, on the unit.

looked at a realistic model peanut made from brown modelling clay which the monkey accepted and placed in its mouth. Thus an olfactory effect cannot account for the response of this unit. The unit did not respond to paper cut to the same outline shape as the peanut (see Fig. 1, below). Thus a simple feature such as shape cannot account for the responsiveness of the unit. Air blown onto the monkey's face from the squeeze bulb (Fig. 1, below, puffing) did not affect the firing rate of the unit. This procedure was aversive and produced arousal and vigorous movements which thus cannot account for the responses of the unit. The squeeze bulb was a salient stimulus which the animal looked at, yet it did not affect the firing rate of the unit. The response of this unit to the sight of the peanut did not depend on whether the monkey reached

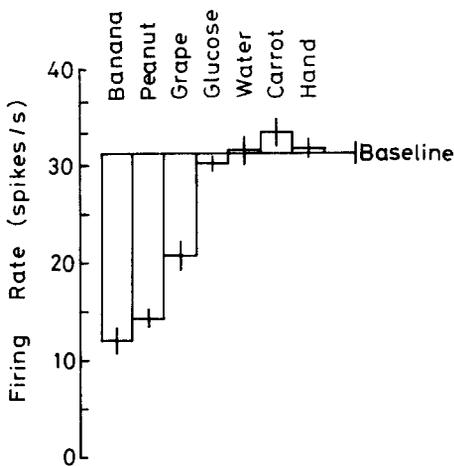


Fig. 2. Firing rate of a rhesus monkey lateral hypothalamic unit when different foods or the experimenter's hand were shown to the monkey. Conventions as in Fig. 1. The glucose and water were contained in black and white syringes respectively. For the trials illustrated the foods were only shown to the monkey, and he was not allowed to eat.

for the nut, nor did reaching for the squeeze bulb affect the firing rate of the unit. Thus the response of the unit was not dependent on these movements which sometimes occurred when the monkey was shown the peanut.

The firing rate of another unit during the period when different foods were shown to a monkey is seen in Fig. 2. The spontaneous baseline firing rate of this unit was 31 spikes/sec. During the presentation of a piece of banana, the rate fell to 12 spikes/sec ($P < 0.001$, Mann-Whitney U-test). Presentation of a peanut or of a grape also decreased ($P < 0.001$) the firing rate of the unit. The foods to which the unit responded were this monkey's preferred foods (see Methods). The experimenter's hand without any food, or a carrot, or syringes containing glucose (both of which were non-preferred foods) or water, did not produce any reliable change in the firing rate of the unit (see Fig. 2). Thus the unit decreased its firing rate only when preferred foods were shown to the animal.

The response of one of several units which was tested in the dark as well as in the light is shown in Fig. 3. The spontaneous baseline firing rate of the unit in the light and in the dark was 14 spikes/sec. The firing rate decreased to 7 spikes/sec when the animal looked at a mealworm in the light. There was no response to the mealworm in the dark, even when the animal grasped the mealworm, then moved it to his mouth, and then ate it. The other units tested in this way also had responses which were associated with feeding only if the animal looked at the food.

The response of a unit which increased its firing rate when the animal was shown food is illustrated in Fig. 4. The unit had a spontaneous firing rate of 1 spike/sec, which increased to 6 spikes/sec for several seconds when the animal was shown food (see Fig. 4). On the first trial on which a number of different objects were presented there was some response, but the response only occurred on later trials when the monkey was shown its preferred foods, which were banana, and glucose solution

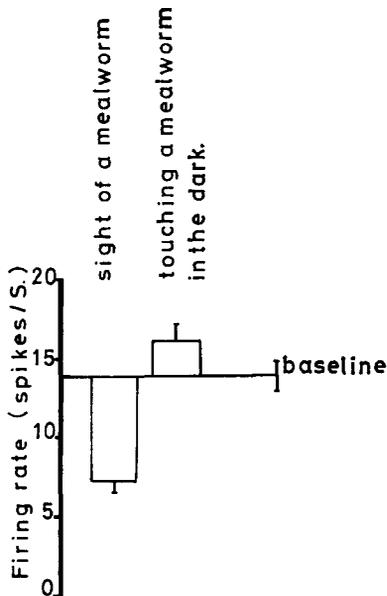


Fig. 3. The firing rate of a lateral hypothalamic neurone when the squirrel monkey saw a mealworm and when the animal held a mealworm in the dark. Conventions as in Fig. 1.

which was in a black syringe. Units which increased their firing rates were typically more variable in their responses. Further differences between these units and the units which responded by a decrease of firing rate remain to be investigated.

Twenty-four of the units classified in the squirrel monkey as responding to the sight of food responded with an increase in the spontaneous firing rate, and 12 with a decrease. In the rhesus monkey, 21 units responded with an increased and 14 units with a decreased firing rate. (Thus of these 71 neurones, 45 responded when the monkey looked at food with an increase in firing rate, and 26 with a decrease in firing rate.) Most of the units had a relatively low spontaneous firing rate of between 0 and 30 spikes/sec. This distinguished them clearly from the units directly above them in the globus pallidus, most of which attained higher maximum firing rates. The hypothalamic units usually responded maximally when the monkeys looked at their most preferred food (see Methods).

The tests, examples of which have been given, were performed on all the units described here. None of these units responded significantly in these tests to the presentation of the experimenter's hand alone or to the forceps alone, or to visual stimuli such as a paper outline of a peanut, or to lines or edges moved in different directions in the visual field. This was despite the fact that the monkey looked at these stimuli. None of these units responded significantly when the monkey tasted or smelled food, not when he reached for and tasted, or was touched by, food and non-food objects. Touching the body, face, eyebrows and eyelids did not affect the activity of the units. Nor did olfactory stimuli affect the units. In a few cases the spontaneous baseline firing rate of a unit changed when the monkey fell asleep, or when the monkey strug-

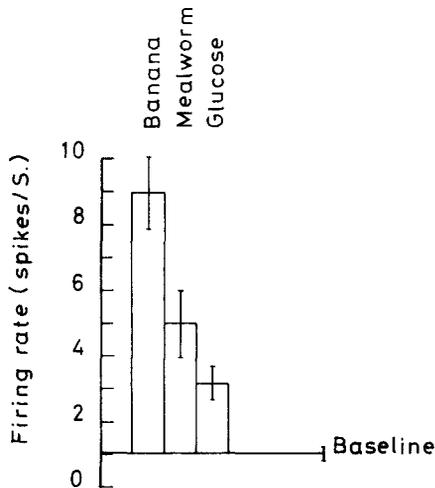


Fig. 4. The firing rate of a lateral hypothalamic unit which increased the firing when the animal was shown a piece of banana, a mealworm and a syringe containing glucose. Conventions as in Fig. 1 except that the firing rate was averaged over three 5-sec periods in which the foods were shown to the monkey.

gled, but this was not a regular finding, and the firing rate of the units was not correlated with eye movements during rapid eye movement sleep. Nor did the units respond when the squeeze bulb was shown, even though this was aversive and the monkeys looked at it steadily and then became excited. Using direct observation of eye position as well as analysis of the video recording by an independent observer, it appeared that the response of the units occurred during the period when the monkeys looked at food but not when they looked at non-food objects, so that eye movement or position did not appear to account for the responses of the units.

Observations on neuronal activity in other brain areas in the same test situation

As the microelectrode was angled towards the far lateral hypothalamus and the substantia innominata observations were made on single units in the medial part of the globus pallidus. Units in the globus pallidus were typically large and often reached firing rates greater than 50 spikes/sec. Units were found which altered their firing rates in relation to reaching (see example in Fig. 5) and grasping, or when the monkey's face was touched or puffed with air, but did not fire when the animal first looked at food. Other units were found which responded when the animal moved its eyes to an extreme position such as fully elevated, or when it moved its head to a stimulus. These observations show that the responses of these pallidal units, which respond when the animal moves, can be clearly distinguished in these test situations from the responses of the lateral hypothalamic cells which only respond when a hungry animal sees preferred foods, and suggest that the hypothalamic cells do not respond as a result of movements made by the animal.

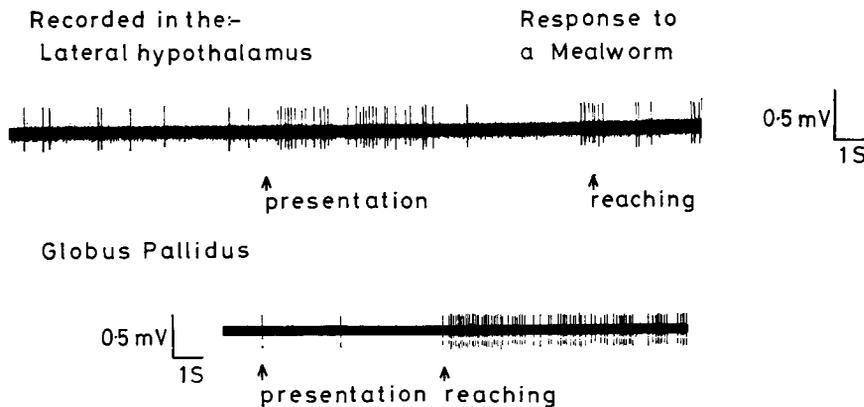


Fig. 5. Comparison of the response of a lateral hypothalamic unit (upper trace) with the response of a unit in the globus pallidus (lower trace). The lateral hypothalamic neurone responded when the animal just saw food and not in association with reaching for food, whereas the pallidal unit did not fire when the monkey first saw food, but only when he reached.

Recording sites

In this first study of these units recordings were made daily over many months, and only lesions made close to the time of histology could be identified. The recording sites of units marked by lesions made close to the time of histology, and the sites of other units reconstructed from lateral and anterior X-radiographs of a recording microelectrode at the site of a unit and of a nearby stimulating electrode in the lateral hypothalamus the exact site of which was found histologically, are shown for the squirrel monkey in Fig. 5. Examples of the lesions made through the recording microelectrode to mark the sites of similar units in the rhesus monkey are shown in Fig. 6. Some of the units were in the lateral hypothalamus. Others were found lateral to this in the general region of the substantia innominata in an area below the globus pallidus and above the main body of the amygdala. Some of the lesions which marked the recording sites were at the junction between the ventral border of the globus pallidus and the substantia innominata or lateral hypothalamus. We believe that the cells recorded here belong either to the region of this junction or to the substantia innominata or lateral hypothalamus, because the lesions were made at the first cell encountered which responded to the sight of food as the microelectrode was lowered, and because the cells recorded immediately above the lesions were typical of the cells which were found throughout the depth of the globus pallidus on angled tracks.

DISCUSSION

The neurones we describe here in the lateral hypothalamus alter their firing rate when a hungry monkey looks at food. The greatest response of these neurones was usually associated with the most preferred foods, and only small non-significant responses were found in the tests described to non-food objects or to foods which the

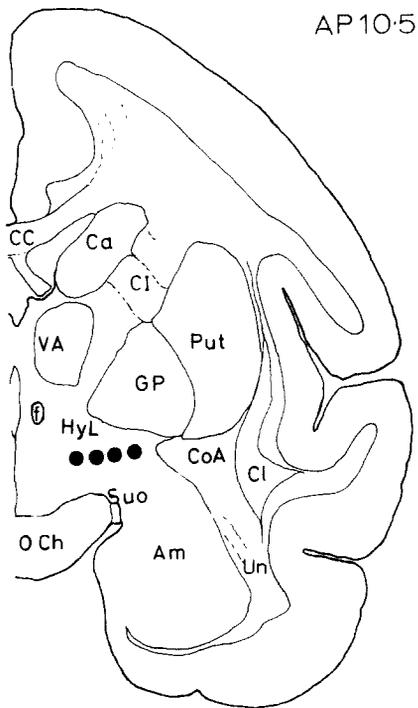


Fig. 6. In this transverse section of the squirrel monkey brain, 10.5 mm anterior to the ear bars, the filled circles indicate the region in the lateral hypothalamus and lateral to it in the substantia innominata in which neurones were recorded with activity associated with the sight of food. Am, amygdala; Ca, caudate; CC, corpus callosum; Cl, claustrum; CI, internal capsule; CoA, anterior commissure; f, fornix; GP, globus pallidus; HyL, lateral hypothalamus; OCh, optic chiasm; Put, putamen; SuO, supraoptic nucleus; Un, uncinate fasciculus; VA, nucleus ventralis anterior thalami.

monkeys would not eat when sitting in the primate chair. Thus the responses of these neurones are related to the motivational state of the monkey.

It is suggested that the response of these hypothalamic neurones is associated with the sight of food, rather than, for example, with the smell of food or with movements which occur during feeding or with simple visual stimulation, for the following reasons. The neurones are not olfactory, in that they do not respond when olfactory stimuli are presented, but do respond to a visual stimulus which looks like food but is made of modelling clay. The units are not low-level motor units in that their firing is not related to movement, and does not change when the monkey grasps and then eats food in the dark. In control recordings in the same test situation it was found that pallidal units did respond during movement, for example during reaching for food, or during opening of the mouth, or in some of the ways described previously by De Long⁴.

Fig. 7. Above: site of unit marked by lesions (and indicated by line) in the region of the lateral hypothalamus and substantia innominata which was activated by the sight of food in the rhesus monkey. Abbreviations as in Fig. 6, and OT, optic tract; St, stimulating electrode site in the lateral hypothalamus; SI, substantia innominata. Below: sites of units in and near the ventral border of the globus pallidus which had motor components to their responses occurring during feeding.

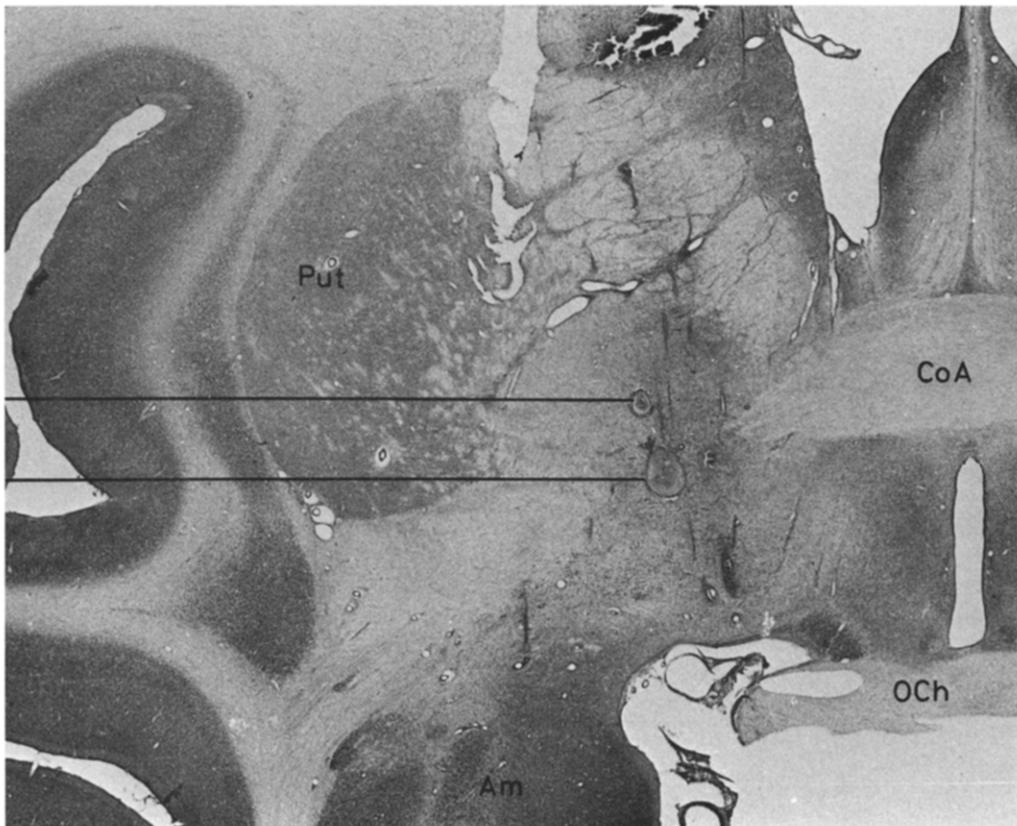
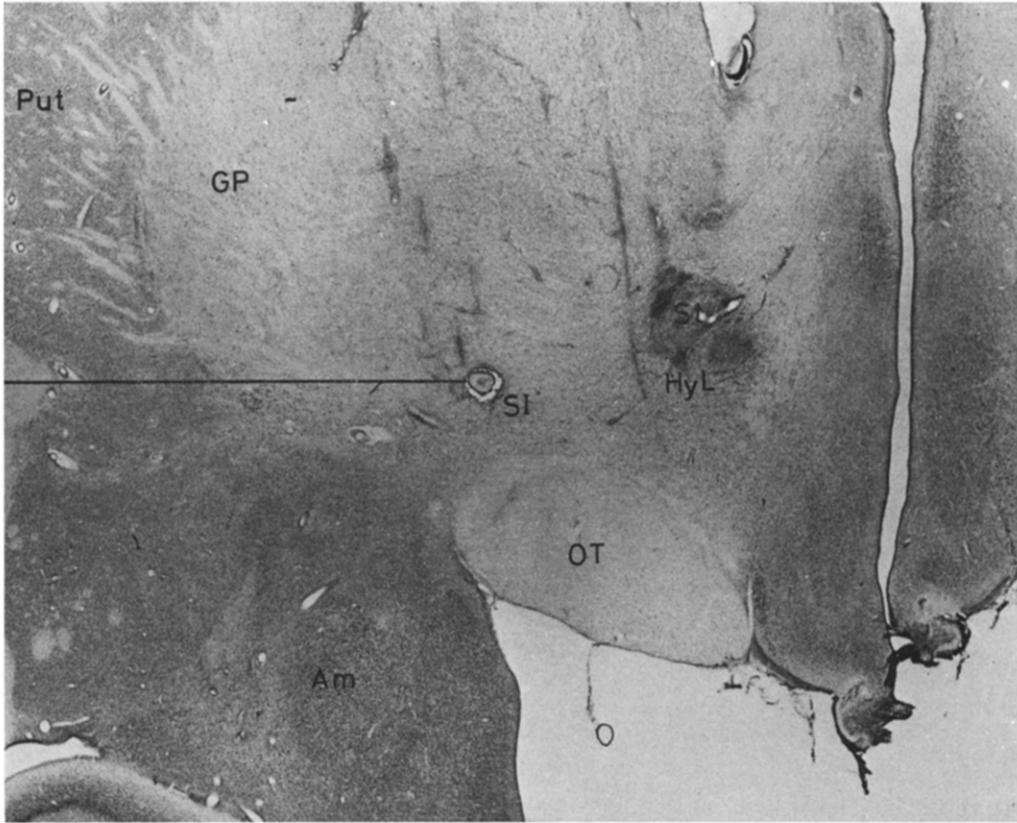


TABLE I

Numbers of neurones in the lateral hypothalamus and substantia innominata of the hungry rhesus and squirrel monkey with activity classified in the test situation as associated with the sight, taste, or sight and taste of food, or with other factors such as movement or touch of the face or body

<i>Numbers of neurones</i>	
Sight of food	71
Sight and taste of food	19
Taste	14
Other responses (see text)	128
Unclassified or unresponsive	532
Total	764

Also the hypothalamic units we describe here are different from some of the complex motor units described by Sparks and coworkers¹⁷⁻¹⁹ in the globus pallidus, which fired, for example if a monkey grasped food, even if the monkey could not see the food. The firing of the hypothalamic units described here did not depend on whether the monkey grasped the food, or even grasped then ate the food in the dark, but depended on whether the monkey could see the food. These same observations, that the hypothalamic neurones do not respond when the animal feeds in the dark, suggest that the responses of these neurones are not due to sensory input from other modalities, or to anticipatory responses such as salivation. Further evidence that the responses of these hypothalamic neurones are not related to taste or to salivation is that none of these neurones responded while the food was in the animal's mouth. Although further investigations using recordings of the electro-oculogram are in progress, the activity of the hypothalamic units does not appear to be due to eye movements, in that the units did not fire in relation to eye movements to other salient, non-food, visual stimuli. Nor is the activity of the hypothalamic neurones due to arousal, in that the units did not respond when a monkey became very excited by the sight of an aversive stimulus such as an air puffer. For these reasons it is suggested that the responses of these hypothalamic neurones are associated with the sight of food in an animal motivated to obtain the food, and as discussed below, this association could be because the neurones are involved in food reward or in initiating behaviour to obtain food.

It is possible that these hypothalamic neurones are involved in the control of food intake for the following reasons (see also refs. 15 and 16). First, these neurones respond when the animal looks at food but not at non-food objects (see above). Second, they only respond to food if the animal is hungry^{1,3}. Third, the magnitude of the response of these neurones depends on the preference which a monkey has for each food (see above). Fourth, these units only respond to the sight of food objects which the monkey has learned will be given to him, and do not respond to the sight of the food if it is no longer given to him (Mora, Rolls and Burton, in preparation). Fifth, there are other neurones in the same region which only respond to the taste or to the sight and taste of food if the animal is hungry¹⁻³. The numbers of neurones of

these different types recorded and analyzed in our sample of 764 neurones in the lateral hypothalamus and substantia innominata are shown in Table I. The neurones classified as showing 'other responses' during feeding included neurones which responded to body or mouth touch or movement, and to the sight of non-food as well as food objects. The presence of these neurones in this region meant that great care was necessary when classifying neurones in this region, and neurones not held long enough for classification or which did not respond during feeding were placed in the category 'unclassified or unresponsive'. Because of this, Table I should be used only as a description of the units we recorded and could analyze, not as a full classification of the responses of hypothalamic units active in feeding. Sixth, electrical stimulation in this region which excites these neurones can mimic the effects of food¹⁵. Seventh, lesions in this hypothalamic region produce aphagia, and also sensory neglect^{6,11}.

The results described here suggest that there are cells in a horizontal region which includes the lateral hypothalamus and the substantia innominata which respond when a hungry monkey looks at food. The first 4 points noted above suggest that the hypothalamic neurones described here respond when the animal sees food which he finds rewarding, measured by his willingness to work for the food. Whether the responses of these neurones are due to the sight of the food reward, or are related in some way to the initiation of feeding behaviour which occurs when food is shown to the hungry animal is not yet clear. In this context it is of interest that there are neurones in the parietal cortex which respond in relation to movements made to obtain for example food^{9,12}, and that there are connections from the basal forebrain areas in which we have recorded to the cortex^{5,10}. Although the responses of the hypothalamic units described here could be related to the initiation of motor behaviour made to obtain food, the responses do appear to be separable from the more low-level types of neuronal response associated with the execution of movements found in pallidal neurones in the same test situation (see above). In summary, the evidence described here and elsewhere^{15,16} suggests that these hypothalamic neurones respond when a hungry monkey sees a food reward and then initiates behaviour to obtain the food, and that the activity of these neurones could be related to these processes^{15,16}.

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