J. Physiol. (1975), **250**, *pp.* 385–407
With 1 plate and 9 text-figures
Printed in Great Britain

RESPONSE OF VENTROBASAL THALAMIC CELLS TO HAIR DISPLACEMENT ON THE FACE OF THE WAKING MONKEY

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(*Received 29 January 1975*)

SUMMARY

1. In the unanaesthetized, moving monkey, single cell firing patterns in the region of the ventrobasal complex (VB) of the thalamus that respond to facial hair displacement were the basis for a statistical analysis of the effects of tactile, thermal and behavioural stimuli.

2. There were facial hair responses throughout the dorsoventral extent of the ventralis posterior medialis (VPM) nucleus of the contralateral thalamus over a rostro-caudal distance of about 2 mm (Fr. 5.1 to Fr. 7.1).

3. The three different anatomical types of facial hairs that activated thalamic neurones were common facial hairs, circumoral vibrissae and facial whiskers.

4. Displacement of the intermediate length, soft, yellow-brown common facial hairs on the central and lateral face from fields of 1–9 cm^2 produced a fast-adapting burst discharge in single thalamic cells in the upper half of the contralateral VPM.

5. Tactile stimuli applied to the short, stiff, white circumoral vibrissae in fields of 0·2–0·9 cm^2 along the margins of the upper and lower lips resulted in fast-adapting phasic firing of units in the lower half of the contralateral VPM. Engagement or disengagement of the interlocking hairs of upper and lower lips resulted in increased or decreased, respectively, firing of these thalamic units.

6. Bending a single, long, stiff, black facial whisker extending out from the side of the face resulted in a sustained increased firing of contralateral VPM cells with directional sensitivity.

7. Cells in the ventrobasal thalamus relay mechanoreceptor input from three specialized hair types on the face of the monkey. These somatotopically organized hairy receptive fields are unique, registering response patterns from tactile, thermal and behavioural stimuli. Facial hairs must play an important part in primate feeding, drinking, and oral-exploration.

INTRODUCTION

Sensory input from the face and oropharyngeal structures in mammals is important in the reflex organization of feeding, drinking and oral-exploratory behaviour. In the subprimates, the complex structure of the whiskers (Vincent, 1913; Patrizi & Munger, 1966), the large size and number of afferent nerve fibres supplying them (Vincent, 1913), the large volume of thalamus (Waite, 1973*a*) and cortex (Welker, 1968, 1971) involved in vibrissal responses and the involvement of vibrissae in tactile exploration and roughness discrimination (Vincent, 1912; Welker, 1964) indicate that in the rat the whiskers provide a particularly important sensory input. In the primate the whiskers decrease in size and number but there remains a complex organization of facial hair types (Hayward, 1974). Despite the physiological importance of facial hairs for oral behaviour, no systematic attempts, as far as I am aware, have been made to study the spontaneous and evoked activity of single cells in the somatosensory thalamus during displacement of various types of facial hairs in the conscious animal.

Using evoked potential technique Mountcastle & Henneman (1952) studied the tactile sensibility in the thalamus of the anaesthetized monkey. They demonstrated important sensory input from the facial region in VPM, but did not delineate the type of cutaneous receptors involved. In the anaesthetized animal tongue afferents to thalamic units involving tactile (Benjamin, 1963; Langdren, 1960*a*; Poulos & Benjamin, 1968), thermal (Benjamin, 1963; Langdren, 1960*b*; Poulos & Benjamin, 1968) and gustatory (Benjamin, 1963; Burton & Benjamin, 1971; Emmers, 1966; Frommer, 1961) receptors have been studied extensively. In the anaesthetized rat Waite and co-workers mapped the vibrissal area of the ventrobasal thalamus (Waite, 1973*a*), studied single thalamic cell discharge to precise whisker displacements (Waite, 1973*b*), and recorded the responses of thalamic vibrissal units to facial nerve stimulation (Brown & Waite, 1974). In their analysis of thalamic somatosensory neurones in the unanaesthetized monkey, Mountcastle and co-workers have studied the mechanoreceptor input from the body and extremities (Mountcastle, Poggio & Werner, 1963; Poggio & Mountcastle, 1963; Rose & Mountcastle, 1954) rather than from the facial hairs. Pubols (1968) studied the somatic sensory representation in the thalamic ventrobasal complex of the anaesthetized spider monkey (Ateles) but did not describe the facial hair input. Only in their study of the somatotopic organization of trigeminal ganglion neurones in the anaesthetized monkey did Kerr & Lysak (1964) describe unitary responses from common facial hairs, perioral vibrissae and facial whiskers.

In the present study I find the facial hair input to the thalamus of the

unanaesthetized monkey organized into two major classes, common hairs and vibrissae. The thalamic common facial hair units are rapidly adapting with larger receptive fields. The thalamic vibrissal units were divided into three groups, circumoral vibrissae, facial whiskers and eye-lashes. The latter were not studied. A small field of circumoral vibrissae could activate a single thalamic cell with rapidly or slowly adapting responses. A single facial whisker could activate a slowly adapting response from a thalamic unit. A preliminary account of some of this work has been published (Hayward, 1974).

METHODS

The subjects for the chronic recording techniques (Hayward & Jennings, 1973*a*, *b*; Hayward & Vincent, 1970) were four adult female rhesus monkeys (*Macaca mulatta*, 4·5–5·5 kg) previously conditioned to primate restraining chairs. The animals were anaesthetized with pentobarbitone (30 mg/kg) and prepared for aseptic surgery. Of the eight stainless-steel epidural bolts affixed to the calvarium, four were positioned laterally for head fixation (Evarts, 1968), four placed at the vertex to support an elevated lucite cranial platform (Baker *et al.* 1968; Findlay & Hayward, 1969). Without excising the dura mater, a mid line craniotomy adequate to accept a 10 mm o.d. stainless-steel cylinder was performed at Fr. 5·5 (Snider & Lee, 1961; Olszewski, 1952). The cylinder, which subsequently supported the recording electrode carrier, was fastened to the skull and the lucite platform with dental cement, and filled with bone wax in order to seal the cranium from pressure fluctuations and sepsis. Biparietal silver–silver chloride ball electrodes for electrocorticography (e.e.g.) recording and periorbital stainless-steel electrodes for eye movement (e.m.) were implanted. E.e.g. and e.m. leads were soldered to an eighteen-pin receptable previously attached to the platform. Two five-pin connectors fastened to the platform held a field-effect transistor amplifier, power input and unit output connexions.

When its eating at preoperative levels indicated recovery from surgery, the previously conditioned monkey was placed in a primate restraining chair situated within a light, temperature and sound-controlled recording chamber (Hayward & Baker, 1968). A vibration pick-up accelerometer attached to the primate chair indicated gross body movements (Move). The four protruding cranial bolts fastened to the frame of the primate chair steadied the animal's head during recording sessions. The monkey behaved in a normal fashion and dozed intermittently during unit recordings (Evarts, 1968; Hayward & Jennings, 1973*a*, *b*; Hayward & Vincent, 1970). A tungsten micro-electrode (tip capacitance, 50–80 pF) within a 22-gauge stainless-steel guide tube was stereotaxically lowered through the implanted bone-wax-filled cylinder to a level 4–5 mm above the ventrobasal thalamus (VB). Then, under the control of a calibrated hydraulic microdrive arrangement, the micro-electrode was lowered out of its guide tube through the ventralis posterior lateralis (VPL), ventralis posterior medialis (VPM) and adjacent thalamus. Extracellular single unit activity was amplified by the field effect transistor mounted on the platform, led through a high impedance probe, and into a high-gain a.c.-coupled pre-amplifier. This amplified activity was channelled into an oscilloscope and audio monitor, a magnetic tape-recorder for later computer and photographic analysis, and a pulse-height discriminator (Martin, 1969). An ink-writing polygraph recorded two outputs from the pulse-height discriminator, a one-to-one pulse output and an analogue output proportional to the rate of discharge. The cortical e.e.g., eye movement potentials (e.m.), skin and nasal thermocouple e.m.f.s (ice water reference

junction, 0° C), accelerometer and stimulus signal outputs were obtained simultaneously. Thus, a written record was provided. The investigator could correlate observed and recorded parameters of behaviour of the monkey with single unit activity in response to tactile, thermal and other sensory stimuli (Hayward & Jennings, 1973*a*, *b*; Hayward & Vincent, 1970).

While the tip of the micro-electrode was advancing toward the ventrobasal complex, the hairy and glabrous skin of the monkey was brushed, tapped, pressed, heated and cooled in order to activate quiescent units. On the basis of spike shape as observed on a storage oscilloscope, single units were isolated from background activity. The peripheral receptive field of each unit was determined by deflecting hairs gently, heating the skin and delimiting the skin area, which elicited a responsive phasic discharge or inhibition of the unit. During the recording, receptive field size and location were tested several times over periods as long as 1 hr, during different states of the animals' behaviour. Temperature of the skin of the face was measured with a fine copper-constantan arc-welded thermocouple taped to the skin in or adjacent to the receptive field of the thalamic cell under study.

After characterizing the location and size of the peripheral field for a ventrobasal thalamic unit and determining the modality of stimulus which drives a unit, I studied the responsiveness of the cell to tactile and thermal stimuli during waking and during slow-wave sleep. I characterized the states of sleep-waking behaviour in the monkey according to the criteria of Jouvet (1967). Two clearly distinct states were chosen for study. (A) *SS: slow wave sleep with e.e.g. high voltage slow waves.* The monkey sat with eyes closed, without gross body movement, with high amplitude slow waves in electrocorticogram. (B) *W: waking quietly with e.e.g. low voltage fast waves.* The monkey sat with eyes open, with some spontaneous body and eye movement, with low voltage fast waves in electrocorticogram. In this study no paradoxical (REM, activated or deep) sleep state was observed. A total of twenty-four experiments (3–4 per week), each varying from 6 to 8 hr in duration, were conducted on the four monkeys.

At the conclusion of a set of experiments on each chronically prepared monkey, a lesion was placed stereotaxically at several known levels along the recording tracks with either the tungsten recording electrode (15 μA for 30 sec, Baker, 1971) or a steel electrode (Hayward & Jennings, 1973*a*, *b*). In 1 week after the tungsten lesions and immediately after the steel lesions, the animal was terminally anaesthetized, its brain perfused through the carotid artery with isotonic saline containing 10% formalin. In addition, the steel lesions received 2% sodium ferri-ferrocyanide. Frozen sections were cut at 80 μM in a stereotaxic plane and stained with thionin. Individual cell locations and their relationship to the dense glial (tungsten lesions) or the Prussian-blue (steel lesions) spots were determined and placed on an expanded drawing of the monkey thalamus (Snider & Lee, 1961; Olszewski, 1952).

Analysis of data began with a review of those cells responsive or not to tactile or thermal stimulation of the hairs of the face. Periods of recordings which were to be analysed further were replayed from the magnetic tape and cell potentials displayed on a storage oscilloscope (Tektronix, Type R5103N) in order to establish the shape of the wave form, stability of the unit, and to make a photographic record. Single cell spike trains that were clearly separable from base-line activity and neighbouring units were led into the pulse-height discriminator (Martin, 1969), while short (0·5 msec) pulses triggered by the unit action potentials on magnetic tape were recorded.

We programmed the PDP-12 digital computer, using a sampling rate of 2000 samples/sec, to identify the times of occurrence of the spikes and record these times on a digital tape. The IBM 360/91 computer was utilized for the statistical

analysis of the interspike intervals, using a programme which calculated the mean firing rate, interspike interval mean, standard deviation, coefficient of variation and histogram of any desired order (Perkel, Gerstein & Moore, 1967). Firing patterns of a neurone during several periods of control and test activity could be analysed separately and the accumulated statistics and histogram presented (Findlay & Hayward, 1969; Hayward & Vincent, 1970; Hayward & Jennings, 1973*a*, *b*).

RESULTS

The hair on the face of an adult female rhesus monkey (*Macaca mulatta*) is not uniform. It presents a variety of lengths, tensile strength, mobility, pigmentation and distribution among the facial structures (see Pl. 1). Three basic types of facial hair emerge: common facial hair, circumoral vibrissae and facial whiskers. Much of the head, ears, side and front of the face is covered with common hairs of soft tensile strength, fine, yellow-brown in colour, ranging between 10 mm in length on the head to 10–20 mm in length along the sides of the face and jaw (see I, Pl. 1). Circumoral vibrissae, short, stiff, white hairs, project at right angles from the margins of the upper and lower lips with the shorter hairs (3 mm) projecting from the mucocutaneous junction and the longer vibrissae (10 mm) at the outer margin of this 5 mm strip. The upper and lower lip circumoral vibrissae interdigitate with their opposite number, thus enclosing the oral cavity in a hairy gate (see II, Pl. 1). Projecting from the orbital margins (mid line, upper, lateral, inferior), peri-nasal and perioral regions are thick, stiff, black 20–30 mm long facial whiskers which arch out and around the respective oriface (see III, Pl. 1). Light stroking of the common facial hair alerts the monkey, brushing the circumoral vibrissae causes reflex contraction of the ipsilateral corner of the mouth and cheek pouch, touching the various facial whiskers causes eye closure or head turning away from the tactile stimulus. Beyond such simple reflex responses what role these three types of facial hairs play in the activities of the monkeys is not known. We can speculate, however, that these hairs help recreate the external world for the monkey, acting as sensory guidance for feeding, drinking and oral exploratory behaviour.

In studying over 200 cells in the ventrobasal thalamus of four unanaesthetized monkeys, fifty cells were responsive to mechanical, thermal and behavioural stimuli in the trigeminal distribution. Over forty of these cells had peripheral receptive fields on contralateral-haired skin of the face. Recording sites were located by lesioning the brain with the recording tungsten micro-electrode during the experiment or with a steel micro-electrode at the termination of the experiments. Penetrations of the lateral parts of the ventrobasal complex (VPL) yielded units driven by tactile stimulation of the trunk, upper and lower extremities. In the medial thalamus vertical tracks passed first through the medial extension of VPL

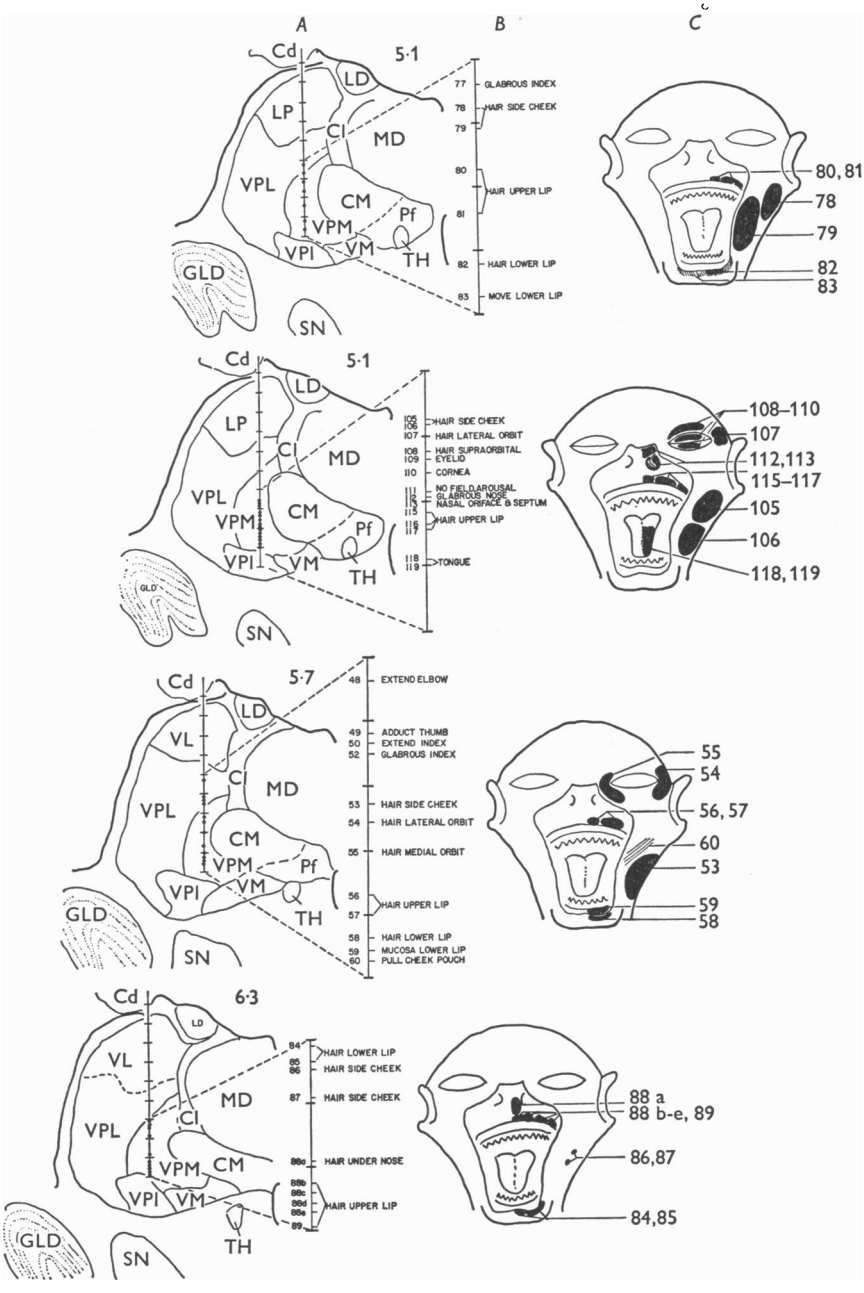


Fig. 1. For legend see facing page.

where neurones were sensitive to movements of the forelimb and tactile stimulation of the glabrous skin of the hand (see Text-fig. 1). In the nucleus ventralis posterior medialis (VPM), neurones sensitive to facial and oral stimulation were found in the following sequence, from above downward: hair side cheek, hair periorbital, eyelid and cornea, glabrous nose, nasal orifice and septum, hair upper lip, hair lower lip, mucosa lower lip, movement lower lip and tongue (see Text-fig. 1).

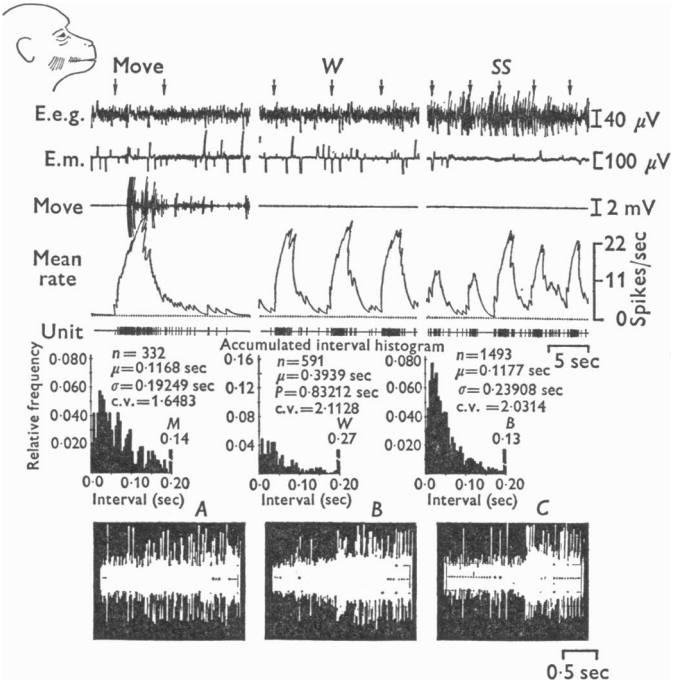
The presence of hairs on the highly mobile monkey face which drinks, eats, yawns, grooms, threatens, ogles, winks, and vocalizes raises the question: did each behavioural event include in its circuitry the feed-back effect of afferent discharges triggered by the activation of facial hairs? Is the effect reversed? Is the hair receptor discharge modified centrally by the behavioural state? Our current studies of thalamic unit activity during drinking may elucidate some of these answers.

Common facial hair thalamic units

Light, tactile bending of the common facial hair of the perioral, periorbital and lateral cheek and face areas in fields from 1·2–9·0 cm^2 produced fast-adapting burst discharges in thalamic neurones in the upper half of the nucleus ventralis posterior medialis (VPM) (see Text-figs. 1–4). In nine of these thalamic cells the mean field size was 3·7 cm^2, with the resting mean firing rate 16·1 spikes/sec and mean burst discharge upon hair displacement of 36·1 spikes/sec or mean 207 % acceleration change (see Table 1). Of the total of seventeen VPM cells responsive to mechanical stimulation of common facial hairs, three were unaffected by changes in behaviour, five showed altered firing patterns during behavioural events and the remaining nine cells were not adequately tested for such responsiveness.

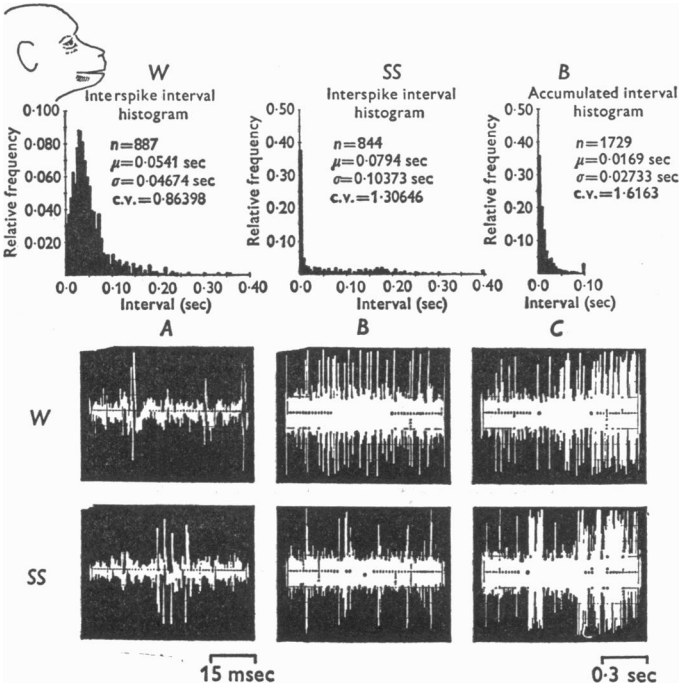
Text-fig. 1. Reconstruction of four micro-electrode penetrations into the thalamus at three frontal levels (Fr. 5.1, upper two, 5·7, third down, and 6.1, lower) in two monkeys. In *A* (left) the location of VB cells (dots) is indicated on an outline drawing of the thalamic nuclei (adapted from Olszewski, 1952). In *B* (centre) the peripheral receptive field and/or the adequate stimulus is indicated on an expanded track with appropriate cell numbers. In *C* (right) the size and location of receptive fields for VPM cells are indicated on the monkey figurine. Labels: Cd, nucleus caudatus; Cl, nucleus centralis lateralis; CM, nucleus centrum medianum; GLD, nucleus geniculatus lateralis dorsalis; LD, nucleus lateralis dorsalis; LP, nucleus lateralis posterior; MD, nucleus medialis dorsalis; Pf, nucleus parafasicularis; SN, substantia nigra; TH, tractus habenulo-interpeduncularis; VL, nucleus ventralis lateralis; VM, nucleus ventralis medialis; VPI, nucleus ventralis posterior inferior; VPM, nucleus ventralis posterior medialis; VPL, nucleus ventralis posterior lateralis. Calibrations: *A*-transverse lines = 1 mm; *B*-heavy transverse lines = 1 mm.

All these cells were spontaneously active, showed rapidly adapting responses to common facial hair displacement (see Text-fig. 2) and five showed sustained changes in firing rates during behavioural events.



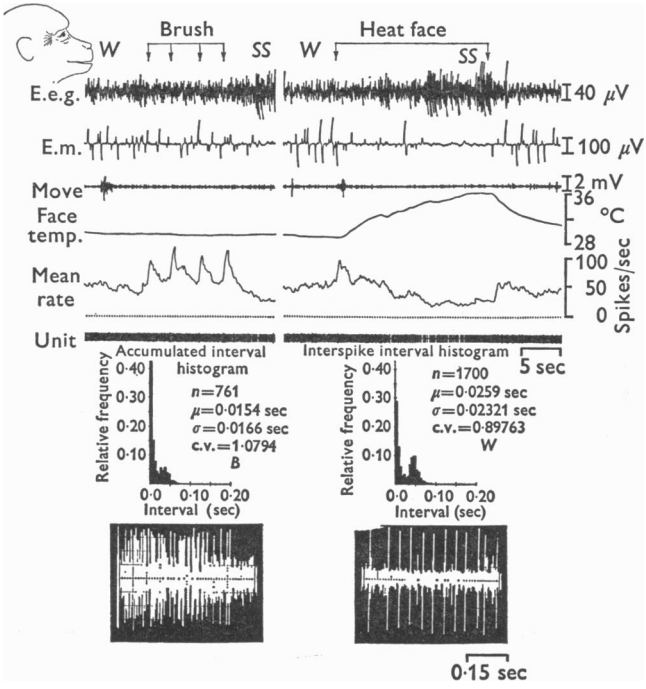
Text-fig. 2. Effects of sleep-waking behaviour and spontaneous body movements on the firing patterns of a ventrobasal thalamic cell with the receptive field on 6 cm² of common facial hairs of the contralateral posterior upper lip, side of the cheek and chin (see Figurine, upper left). During quiet waking this cell discharges slowly and irregularly at 2·5 spikes/sec as shown in the paper record (upper), 'asymmetrical' interspike interval histogram (middle, *W*), and the photograph of the spikes (lower, initial 1·0 sec of *B* and *C*). Spontaneous movement of the face produced accelerated cell discharge (upper, left, move) to 8·6 spikes/sec as seen in photograph (lower, *A*) with a shift of the 'asymmetric' interval histogram to the left (middle, *M*). Displacement of these common facial hairs produces rapidly adapting burst discharges at 8·5 spikes/sec during waking (upper centre, *W*; lower, *B*) and during slow wave sleep (upper, right, *SS*; lower *C*). This 'asymmetric' accumulated interspike interval histogram shifts to the left (middle, *B*). The moderate decline in amplitude of burst discharges, during slow wave sleep was a variable finding. Labels: e.e.g., biparietal electrocorticogram; e.m., eye movements; Move, accelerometer measure of body movements; Mean rate, analogue output proportional to the mean rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number of intervals; μ = mean interspike interval; σ = S.D.; c.v. = coefficient of variation.

Chewing, drinking, pursing or licking the lips and yawning are movements of the face and lips which may cause burst discharges of thalamic neurones with receptive fields situated in the common hair of the contralateral face (see Text-fig. 2). These burst discharges are identical during waking and slow-wave sleep (see Text-fig. 2). Cells with a steady firing rate during waking consistently slowed, during spontaneous (see Text-fig. 3) or thermally induced (see Text-fig. 4) slow-wave sleep, a reduction of cell



Text-fig. 3. Activity of a ventrobasal thalamic neurone during displacement of 1·2 cm² of common facial hairs on the contralateral, posterior, lower chin (see Figurine, upper left) during sleep-waking states. Spontaneous cell discharge during waking was at 18·5 spikes/sec with an unimodal 'asymmetric' interspike interval histogram (upper left, *W*) and with an irregular spike discharge (see *W*, upper photographs, *A* and *B* at different time base). During slow-wave sleep cell firing slowed to 12·6 spikes/sec with the presence of clusters of 4–6 spikes at 400–800/sec with gaps of 10–20 msec between clusters (see *SS*, lower photographs, *A* and *B*). Brushing the soft, yellow-brown, intermediate length hair of the contralateral, lower, posterior chin produced a rapidly adapting, phasic discharge at 59 spikes/sec with an 'asymmetric' interspike interval histogram (upper, right, *B*) during slow-wave sleep and during waking as shown in photographs (see *W* and *SS*, upper and lower *C*). Labels: *W*, quiet waking; *SS*, slow-wave sleep; *B*, brush common facial hairs: n = number of intervals; μ = mean interspike interval; σ = S.D.; C.V. = coefficient of variation.

discharge rates with a greater number of longer interspike intervals and the development of 'clusters' of four to six spikes at 400–800 spikes/sec separated by gaps of 10–20 msec (see Text-fig. 3). Slow-wave sleep occurred



Text-fig. 4. Influence of tactile-induced and heat-induced slow-wave sleep on the activity of a common facial hair unit in the ventrobasal thalamus with a receptive field on 2·0 cm² of the contralateral, lateral orbit (see Figurine, upper left). During quiet waking the cell fires spontaneously at 39 spikes/sec (upper, left) with a 'bimodal' interspike interval histogram (middle, *W*) and a regular spike discharge (photo, lower, right). Displacement of the soft, short, yellow-brown periorbital common facial hairs of the face produced rapidly adapting burst discharge at 65 spikes/sec (upper, Brush) with a shift of the 'bimodal' histogram to the left and increased spike density (photo, lower, left). Slow wave sleep induced by brushing the face (upper, left, *SS*) or heating the face (upper, right, Heat face, *SS*) produced a marked drop in VPM cell firing from the waking level of 39 spikes/sec to 12 spikes/sec without any change in response to hair displacement. Any thermal influences on cell firing activity appeared to be mediated by changes in the level of arousal. Labels: e.e.g., biparietal electrocorticogram: e.m., eye movements; Move, accelerometer measure of body movements; Face temp., temperature of the skin of the right anterior face; Mean rate, analogue output proportional to the rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number of intervals; μ = mean interspike intervals; σ = S.D.; c.v. = coefficient of variation; *W*, quiet waking; *SS*, slow-wave sleep.

'spontaneously' (see Text-fig. 3) and could be induced by repeated stroking of the face (see Text-fig. 2) or by radiant heating the face (see Text-fig. 4). In any of these situations cell discharge rates declined and remained slower as long as the slow-wave sleep persisted. With arousal, cell firing returned to control levels despite an elevated temperature of the receptive field (see Text-fig. 4) or persistent tactile stimuli.

Circumoral vibrissae thalamic units

Displacement of the short, stiff, white circumoral vibrissae (see Pl. 1) produces burst discharges in thalamic units in the lower half of the VPM (see Text-fig. 1). These VPM thalamic neurones fired spontaneously at 29 spikes/sec and with mean stimulated rates of 45 spikes/sec or an 85% increased firing (see Table 1). Peripheral receptive fields averaged 0·8 cm^2. Mechanical stimulation of the circumoral vibrissae showed three different repsonses in thalamic neurones: fast-adapting units; lip alignment units; and inhibitory units.

The majority of the thalamic neurones driven by displacement of circumoral vibrissae (16/21) were of the simple, excitatory, fast-adapting type as shown in Text-fig. 5 and the Table 1. Under resting conditions ten of these cells fired continuously at a mean steady, irregular rate of 29 spikes/sec (range 17–46 spikes/sec). During light tactile stimuli applied to the small (0·8 cm^2) peripheral receptive field, these cells gave a mean burst discharge of 50 spikes/sec (Table 1 and Text-fig. 5). Lifting the lips apart or placing them together did not change firing rates of these thalamic cells. Pressure on or around the receptive field did not inhibit cell firing. During puckering or licking of lips, chewing or body movement these thalamic units were driven by displacement of the circumoral vibrissae associated with such activity. Cell discharge decreased during both 'spontaneous' and radiant heat induced slow-wave sleep. During slow-wave sleep, these VPM cells exhibited 'cluster' discharges similar to those seen with the common facial hair thalamic units (see Text-fig. 3). In addition, those vibrissae displaced during slow sleep produced burst discharges in the thalamic cells identical to that produced during waking.

A few (3/21) of the circumoral vibrissae units were of the complex, excitatory 'lip-alignment' type as shown in Text-figs. 6 and 7 and Table 1. Under resting conditions with the circumoral vibrissae 'disengaged', two of these thalamic units had mean regular firing rate of 21 spikes/sec which increased to 54 spikes/sec with vibrissae 'engagement'. Vibrissae 'engagement' could be produced by spontaneous movement of the lips, brushing the upper or lower vibrissae to one side or other in relation to their opposite number (see Text-fig. 6). Such thalamic cells would continue to discharge at a high rate until the circumoral vibrissae in the receptive field were

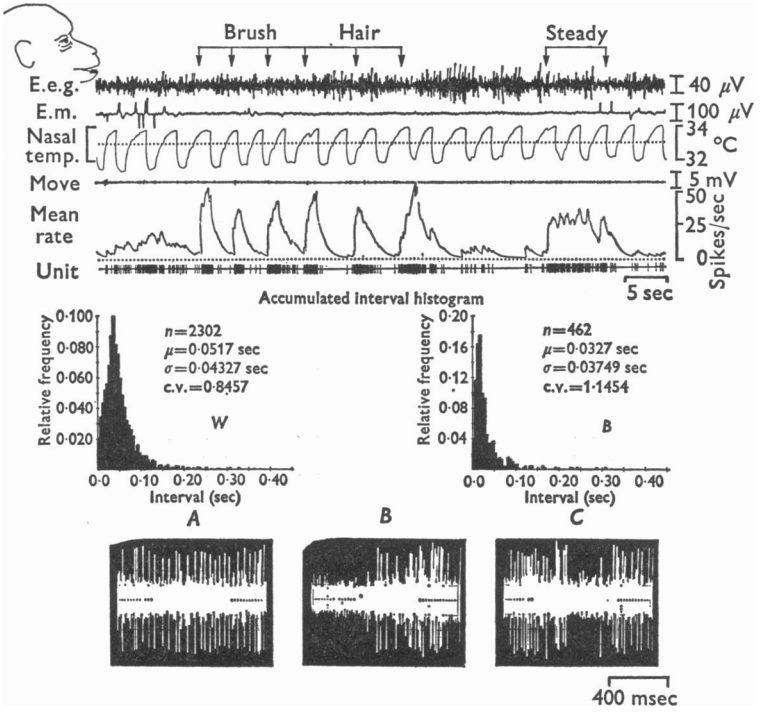
TABLE 1. Response of ventrobasal thalamic cells to hair displacement on the face of the waking monkey

Cell no.	Hair type	Field location	Field size (cm^2)	MFR* (control) (spikes/sec)	MFR (displacement) (spikes/sec)	% change in MFR (Δ %)
			Common facial hairs			
22	F.A.	Perioral	9·0	5·827	28·567	390·3
55	F.A.	Periorbital	2·0	33·816	52·848	56·3
64	F.A.	Lateral chin	3·0	8·752	16·279	86·0
66	F.A.	Perioral	2·8	3·821	28·676	650·5
78	F.A.	Lateral face	4·0	11·099	11·800	6·3
79	F.A.	Lateral cheek	6·0	2·539	8·497	234·7
85	F.A.	Perioral	1·2	18·485	58·558	216·8
106	F.A.	Lateral cheek	4·0	21·861	54·584	149·7
107	F.A.	Periorbital	2·0	38·678	64·999	68·1
Mean n = 9			3·7	16·098	36·090	206·5
			Circumoral vibrissae			
56	F.A.	Upper lip	0·9	46·564	139·871	200·4
57	F.A.	Upper lip	0·8	38·177	35·143	−8·6
58	F.A.	Lower lip	0·8	34·394	53·027	54·2
61	F.A.	Upper lip	0·9	25·807	29·726	15·2
63	F.A.	Lower lip	0·9	19·342	30·549	57·9
67	L.A.	Lower lip	0·8	14·061	18·990	35·1
70	F.A.	Upper lip	0·8	17·436	21·308	22·2
71	F.A.	Upper lip	0·8	19·666	37·566	91·0
80	I	Upper lip	0·8	24·116	0·000	−100·0
84	F.A.	Lower lip	0·8	31·869	49·452	55·2
88b	L.A.	Upper lip	0·2	27·311	88·557	224·3
89	I	Upper lip	0·8	48·244	22·829	−111·3
115	F.A.	Upper lip	0·8	19·444	32·339	66·3
116	F.A.	Upper lip	0·3	31·963	67·161	110·1
Mean n = 14			0·7	28·457	44·751	84·72
			Facial whiskers			
87	S.A.	Lateral face	1 hair	27·359	68·816	151·5
93	S.A.	Lateral face	1 hair	23·018	51·999	125·6
Mean n = 2			1 hair	25·189	60·408	138·6

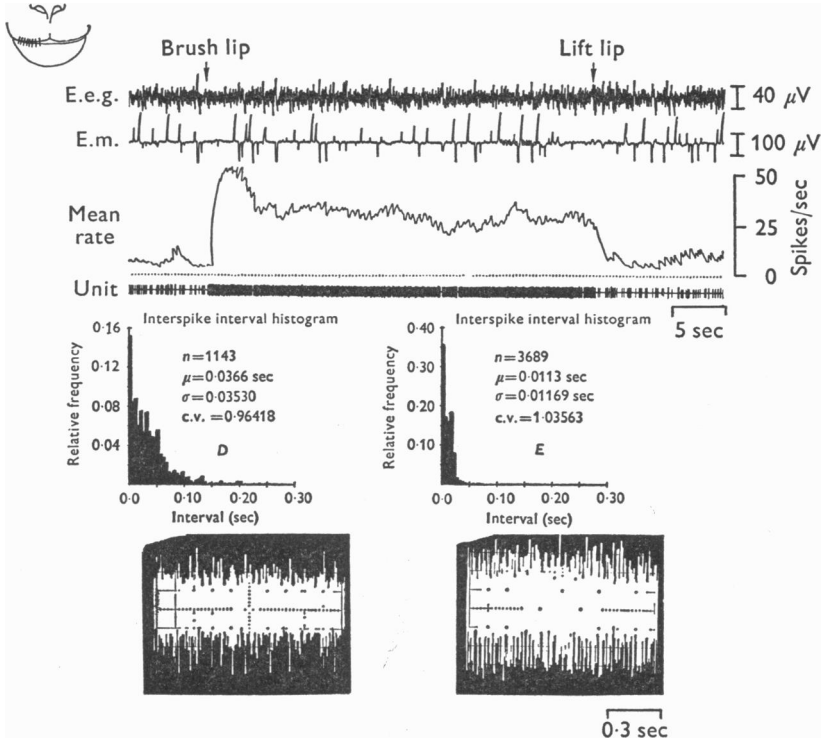
MFR, mean firing rate; F.A., fast-adapting hair unit; L.A., lip alignment hair unit; I, inhibitory hair unit; S.A., slow-adapting hair unit.

disengaged either by separating the lips (see Text-fig. 6) or by spontaneous movements (see Text-fig. 7). Radiant heating induces a reduction of cell activity. This may be the consequence of a relaxed lip motor tone (see Text-fig. 7). In one of these thalamic units the 'engaged' circumoral vibrissae apparently reflected a rhythmic movement of the lips, a micro-

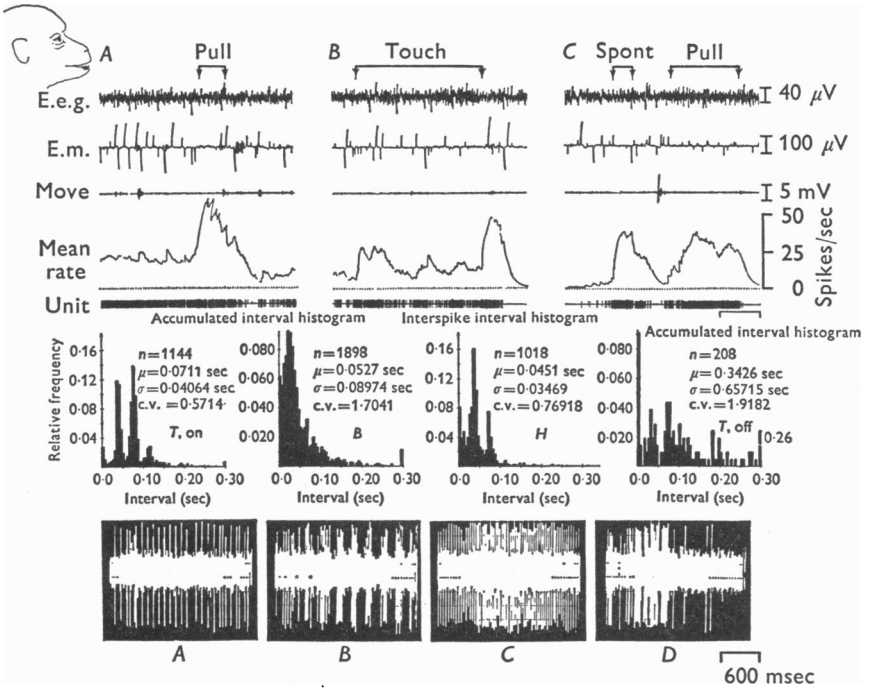
tremor with oscillations in simple harmonics of 40, 80 and 120 msec (see Text-fig 8). In these circumoral vibrissae-thalamic units displacement of the receptive field produced a fast-adapting burst discharge, pressure produced a transient phasic discharge without any inhibitory effects.



Text-fig. 5. Firing patterns of a circumoral vibrissae unit in the VPM of the unanaesthetized rhesus monkey. Displacement (*B*) of a 0·9 cm² field of short, stiff, white, vibrissae at the mucocutaneous junction of the rostral, contralateral lower lip (see Figurine, upper left) increased cell firing from a control, quiet, waking level of 19 spikes/sec to a rapidly-adapting phasic discharge of 30·6 spikes/sec as seen in oscillograph record (upper, Brush hair), 'asymmetric' interspike interval histograms (middle, *W* and *B*) and photographs (lower, *A* and *B*), respectively. Steady back and forth brushing of the receptive field (upper, steady), produced a sustained cell discharge of 26 spikes/sec with repetitive burst discharges (photograph, lower, *C*). Note the tendency of the monkey to quietly doze with absence of eye and body movements and higher voltage, slower e.e.g. during the rhythmic, repetitive cutaneous stimulation. Labels: E.e.g., biparietal electrocorticogram; e.m., eye movements; Nasal temp., temperature of the air in the nasal cavity; Move, accelerometer measure of body movements; Mean rate, analogue output proportional to the mean rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number of intervals; μ = mean interspike interval; σ = S.D.; c.v. = coefficient of variation.

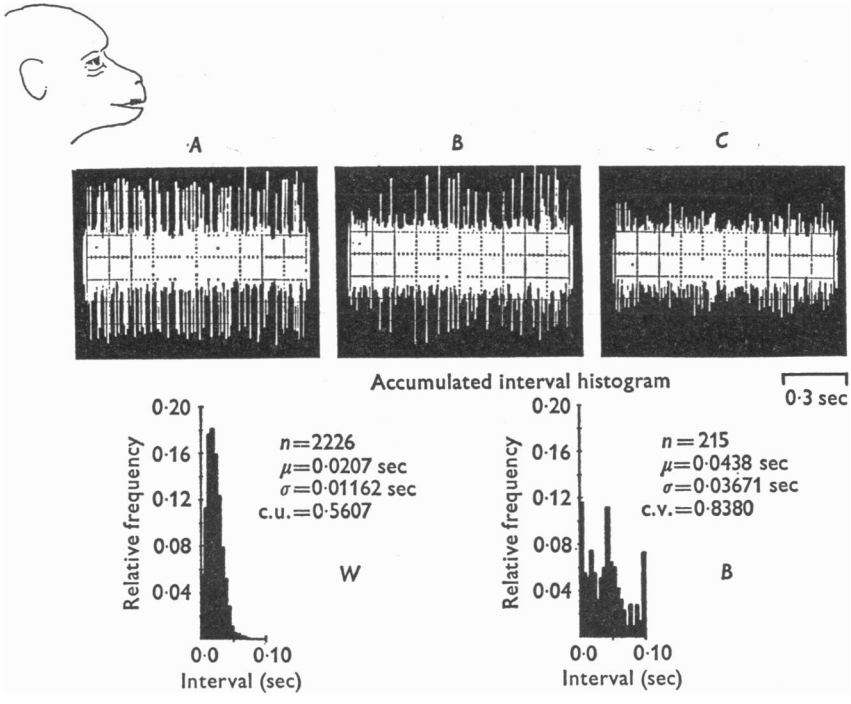


Text-fig. 6. Activity of a ventrobasal thalamic cell during 'engagement' and 'disengagement' of a 0·2 cm² field of circumoral vibrissae at the mucocutaneous junction of the contralateral upper lip (see Figurine, upper left). During 'disengagement' of the short, stiff, white, circumoral vibrissae from their opposite number on the lower lip, this VPM discharge at 27·3 spikes/sec as shown in the oscillograph writeout (upper, beginning and end), in the 'asymmetric' interspike interval histogram (centre, *D*) and in the photograph (lower, left). After spontaneous lip movement, our brushing the hairs from side-to-side with a brush, or other manoeuvres, these circumoral vibrissae 'engaged' the vibrissae of the lower lip, setting off a high level discharge at 88·6 spikes/sec in the ventrobasal thalamic cell (upper left, Brush lip), with the 'asymmetric' histogram shifting left (middle, *E*) and an accelerated cell discharge (photograph, lower, right). This sustained 'engaged' cell activity continues unabated until the circumoral vibrissae are 'disengaged' either by spontaneous movement or by lifting the upper lip away from the lower lip (upper, lift lip), with return of thalamic cell firing to the 'disengaged' level of activity. Labels: e.e.g., biparietal electrocorticogram; e.m., eye movements; Mean rate, analogue output proportional to the rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number; μ = mean interspike interval; σ = S.D.; c.v. = coefficient of variation.

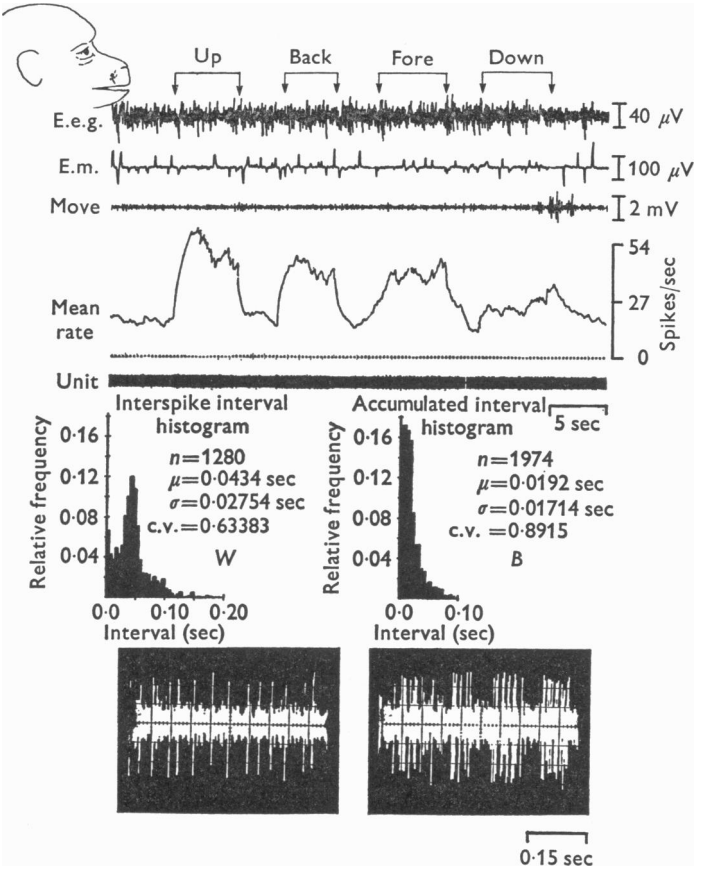


Text-fig. 7. Pattern of responses of a circumoral vibrissae unit in the thalamus to changes in position of the lips in the unanaesthetized monkey. During 'engagement' of a 0·8 cm² field of short, stiff, white hairs on the rostral lower lip with those of the upper lip, this VPM cell fires with a rhythmic discharge (upper *A*), of 14 spikes/sec with interspike intervals grouped at 40, 80 and 120 msec as shown in the multimodal histogram (middle, *T*, on) and in the oscilloscope photograph (bottom, *A*). Heating the receptive field during 'engagement' accelerates cell firing with a shift of more intervals into the 40 msec group as shown in histogram (centre, *H*) and photograph (lower, *C*). A downward pull, a touch and release, a spontaneous movement of the lower lip can each 'disengage' these circumoral vibrissae. As a result the VPM neurones slow (upper, *A*, *B*, and *C*) to 2·2 spikes/min with a shift in the intervals toward 80 msec and further to the right (histogram, centre, *T*, off, and in the photograph, lower, *D*) or cease activity. Steady brushing of the circumoral vibrissae of the lower lip produces burst discharges of this VPM cell, an unimodal 'asymmetric' accumulated interval histogram at a mean firing rate of 19 spikes/sec and rhythmic spike pattern (photograph, lower, *B*). Labels: e.e.g., biparietal electrocorticogram; e.m., eye movements; Move, accelerator accelerometer measure of body movements; Mean rate, analogue output proportional to the mean rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number of intervals; μ = mean interspike interval; σ = S.D.; c.v. = coefficient of variation.

Two (2/21) of these thalamic units were totally inhibited when the responsive field of circumoral vibrissae was firmly pressed, thus the designation of inhibitory type (see Text-fig. 8 and Table 1). In the thalamic neurone shown in Text-fig. 8, the spontaneous activity (48 spikes/sec) was halved (22 spikes/sec) when hairs were lightly displaced and firing completely inhibited by sustained firm pressure on the 0·8 cm² peripheral receptive field of circumoral vibrissae. In another of these thalamic cells light displacement of the vibrissae inhibited firing completely from control levels of 24 spikes/min (Table 1).



Text-fig. 8. Inhibition of ventrobasal thalamic cell activity during deflexion of an 0·8 cm² field of circumoral vibrissae of the contralateral upper lip in the conscious monkey. During quiet waking the VPM cell activity was irregular and fast at 48 spikes/sec (upper, *A*) with an interspike interval histogram of the 'asymmetric' type (lower, *W*). Brushing these short, stiff, white upper lip hairs partially inhibited cell firing (upper, *B*) with a reduction of firing rate to 22·8 spikes/sec and a 'multimodal' interspike interval histogram (lower, *B*). Light pressure applied to the circumoral vibrissae field completely inhibited firing of this thalamic cell (upper, *C*). Firing resumed when pressure was removed. Labels: n = number of intervals; μ = mean interspike interval; σ = S.D.; c.v. = coefficient of variation; *W* = quiet waking; *B* = brushing hairs.



Text-fig. 9. Spontaneous and evoked activity of a ventrobasal thalamic cell exclusively responsive to displacement of a single facial whisker in the conscious rhesus monkey. During quiet waking this facial vibrissal unit firing spontaneously at 23 spikes/sec (upper, left) with an 'asymmetrical' interspike interval histogram (middle, *W*) and irregular spike discharge (photograph, lower left). Upward displacement of this single, long, stiff, black hair which arched forward, out and down from the side of the face toward the mouth (see Figurine, upper left) produced a slowly adapting, maximal cell acceleration of 52 spikes/sec (upper, 'UP'), with the 'asymmetric' interval histogram shifting left (middle, *B*), 'clusters' of spikes (photograph, lower, right). Note the directional sensitivity of this facial whisker, with optimal slowly-adapting discharge in the 'UP' direction, opposing the natural curve of this vibrissa at the right angles. There is little or no change in firing with 'Down' displacement and intermediate degrees of change with 'Back' and 'Fore' displacements (upper). Labels: e.e.g., biparietal electrocorticogram; e.m., eye movements; Move, accelerometer measure of body movements; Mean Rate, analogue output proportional to the rate of unit discharge; Unit, pulse output from pulse height discriminator triggered by action potentials of the spike in the window; n = number of intervals; μ = mean interspike intervals; σ = S.D.; c.v. = coefficient of variation; *W*, quiet waking; *B*, whisker displacement; up, displacement upward; back, displacement backward; fore, displacement forward; down, displacement downward.

Facial whisker thalamic units

Facial whiskers, the long, black, stiff, single, hairs projecting out beyond the others around the mouth, nose, eye and lateral face appear to relay a one-to-one excitatory input to single cells in the ventrobasal thalamus. Deflexion of a single facial whisker produces a slow-adapting acceleration of thalamic cell discharge with directional sensitivity (see Text-fig. 9 and Table 1). Cell spontaneous activity of 25 spikes/sec increased to 60 spikes/sec with lateral facial whisker displacement upward (see Text-fig. 9 and Table 1). This upward displacement is directly opposed to the gentle, outward, downward and forward arch of these perioral facial whiskers (see III, Pl. 1; Text-fig. 9). Displacement of these facial whiskers in the direction of hair arch produced little response in the thalamic cell (see Text-fig. 9). Other bending directions were of intermediate effect. During waking and slow-wave sleep deflexion of these facial whiskers produced similar acceleration of these thalamic cells. Spontanous facial movements such as chewing, pursing the lips, and yawning result in accelerated thalamic unit discharge.

DISCUSSION

In mammals facial hairs evolve into specialized types, three of which are common facial hair, circumoral vibrissae and facial whiskers. In the present study probing the somatosensory nucleus of the thalamus in the conscious monkey, we found forty spontaneously active VPM units activated by mechanical displacement of facial hairs. The common facial hair is intermediate in length, soft, yellow-brown. Upon displacement of receptive fields of 1–9 cm^2 in the central and lateral face, this hair type produced fast-adapting bursts in single thalamic cells in the upper half of the contralateral VPM. The circumoral vibrissae, dense fields of short, stiff white hairs projecting at right angles from the mucocutaneous margins of the upper and lower lips, can drive the contralateral lower half VPM units from receptive fields of 0·2–0·9 cm^2 with fast and slow adapting responses. Facial whiskers are the long, stiff, black vibrissae extending out in gentle arcs from the side of the face. When bent, a single hair produces slow-adapting acceleration of the contralateral VPM units with directional sensitivity.

In the trigeminal ganglion of the barbiturate-anaesthetized monkey, Kerr & Lysak (1964) describe four types of spontaneously silent units which developed phasic discharge from tactile stimuli applied to the monkey face. Their twelve wide-field, fast-adapting hair units over the scalp and anterolateral face (see H, circle, in Figurine maps, Figs. 4 and 5, Kerr & Lysak, 1964) clearly correspond to the fast-adapting, common facial hairs

of the present study. The six, slow adapting vibrissae with directional sensitivity in the supraorbital and antero-lateral facial area (see V, dot, in Figurine maps, Figs. 4 and 5, Kerr & Lysak, 1964) undoubtedly represent the classical facial whiskers of this study and others (Waite, 1973*a*, *b*; Brown & Waite, 1974). In the margin of the upper lip Kerr & Lysak (1964) describe a variety of mechanoreceptor units in the trigeminal ganglion with discrete receptive fields that include vibrissae, hair pressure and touch (see H,P,V,P, circle, in figurine maps, Figs. 4 and 5, Kerr & Lysak, 1964) In view of the dense field of circumoral vibrissae covering the margin of the upper and lower lip in the rhesus monkey (see Pl. 1) and the possible effects of anaesthesia and immobilization of the lips, it seems likely that many of the circumoral tactile responses from discrete receptive fields described by Kerr & Lysak (1964) resulted from displacement of the circumoral vibrissae.

If the relative volume of neural tissue related to a particular skin area reflects the importance of that area for the animal, then the circumoral region is of prime importance for the rhesus monkey. In Mountcastle's & Henneman's (1952) study of thalamic evoked potentials from light tactile stimulation of facial cutaneous receptors in the barbiturate anaesthetized monkey, there was a large area of the dorsoventral extent of VPM responsive to stimulation of the perioral area (see their Figurine maps of Figs. 2–4, 7). This area featured dense circumoral vibrissae (see Pl. 1) and equals that representing intra-oral structures (Mountcastle & Henneman, 1952). Since their evoked potential technique could not distinguish cutaneous mechanoreceptor type, we can only speculate upon the possible contribution of circumoral vibrissae to their studied responses. Kerr & Lysak (1964) describe approximately one third of their mapped facial cutaneous receptors in the monkey trigeminal ganglion along the margins of the upper and lower lips (see Figs. 4 and 5, Kerr & Lysak, 1964).

In tactile evoked potential studies in rabbit thalamus, the large areas of VPM involved with tactile somatosensory input from the circumoral area equals that in the monkey (see their Figurine maps in Figs. 4, 6, 8, 10, and 14, Rose and Mountcastle, 1952). Circumoral tactile representation in the cat thalamus is much less extensive (see Figurine maps in Figs. 16, 17 and 19, Rose & Mountcastle, 1952). In the rat one third to one half of the dorsomedial part of the ventrobasal thalamus throughout its rosto-caudal extent is occupied by facial whisker responses (Waite, 1973*a*). The rat uses its whiskers for exploration of the surroundings and roughness discrimination (Vincent, 1912; Welker, 1964). These results are in marked contrast to the scant number of facial whiskers (see Pl. 1) and the paucity of facial whisker responses in the monkey thalamus (see Figs. 1 and 9; Table 1).

The importance of the circumoral vibrissae in other species is not known at the present time. Phylogenetically, apparently, as the whiskers decreased in size, number and importance from the nocturnal rodent to the diurnal primate, the animal depended less upon whiskers and hearing and more on the hand and vision for exploration of the environment. The apparent simultaneous increase in the discriminatory capacity of the circumoral region, as reflected by the rich field of circumoral hairs (see Pl. 1) and the increased perioral thalamic representation (see Fig. 1), perhaps relates to the increased use of the lips and oral structures for selecting food and drink, for grooming and for vocalization. This circumoral specialization reaches its evolutionary peak in man (Weinstein, 1968). The detailed examination of the functional role of circumoral vibrissae in these orofacial activities in the monkey awaits further electrophysiological studies in the conscious monkey.

In the waking monkey thalamic facial hair units were spontaneously active, firing at a mean overall rate of 23 spikes/sec. The common facial hairs with their less complex innervation (Munger, 1971) and their location on the less mobile areas of the face fired spontaneously at 16 spikes/sec and 36 spikes/sec bursts during tactile stimulation or a 200% change in MFR (see Table 1). The circumoral vibrissae with their more complex innervation (Munger, 1971) and their location on the highly mobile lip area fired spontaneously at 29 spikes/sec and at 45 spikes/sec bursts during tactile stimulation or a 85% change in MFR (see Table 1). The facial whiskers, besides receiving complex innervation (Munger, 1971) and being involved in facial twitching on the antero-lateral face, perinasal and periorbital areas, had spontaneous firing rates of 25 spikes/sec which rose to 60 spikes/sec with hair bending or a 138% change in MFR (see Table 1). Movements of the face and lips produced a greater change in cell firing in the circumoral vibrissae units and the facial whisker units than in the common hair thalamic units (see Text-fig. 7). If the common hair receptive field was accidentally rubbed against the primate chair, then head and face movement would elicit an enhanced burst discharge (see Text-fig. 2).

During spontaneous- (see Text-fig. 3), thermal- (see Text-fig. 4) or touch-induced (see Text-fig. 2) slow-wave sleep, cell firing decreased in all three types of thalamic facial hair units with development of 'cluster' or 'burst' discharges (see Text-fig. 3) and characteristic 'asymmetric' interspike interval histograms (see Text-fig. 3). These findings confirm previous work in the cat lateral geniculate (Hubel, 1960), rabbit mid-line thalamus (Findlay & Hayward, 1969) and cat somatosensory thalamus (Baker, 1971). Thalamic cell responses to hair deflexion remained the same during waking and slow-wave sleep with no change in receptive field size (see Text-fig. 2). Baker (1971) found constant receptive fields and

mechanoreceptor responses in cat VPL. Whether the silent facial whisker cells in the thalamus of the anaesthetized rat (Waite, 1973*b*) indicate a decrease in facial motor tone (Brown & Waite, 1974) or a depression of a central brainstem reticular activation remains a question. It is quite clear, that facial muscle activity can modify the activity of lip alignment circumoral vibrissae units (see Text-fig. 6) and rhythmic firing patterns of certain thalamic units suggest the influence of facial microtremors (see Text-fig. 7). The importance of peripheral motor activity in the modulation of facial hair receptor input to the thalamus requires further study in the waking mammal. While these richly innervated and specialized facial hairs help recreate the external world for the monkey and act as sensory guidance for feeding, drinking and oral exploratory behaviour, the movements of these receptive fields by facial muscles and the reticular bias on somatosensory neurones makes interpretation of the thalamic activity complex. In our current studies of gustatory and somatosensory input during drinking we hope to approach these questions.

This work was supported in part by Grants from NINSD (NS-10129 and NS-11443). The Data Processing Laboratory of the Brain Research Institute performed analogue to digital conversion, while the Health Sciences Computing Facility, sponsored by NIH Grant FR-3, performed the computations. The UCLA Brain Information Service, with support from contract PH-43-66-59, provided bibliographic aid. I thank Ms B. Bedard, S. Curtis, K. Koithan & R. Lawrence for valuable technical assistance and Ms A. Hastings for help with the manuscript.

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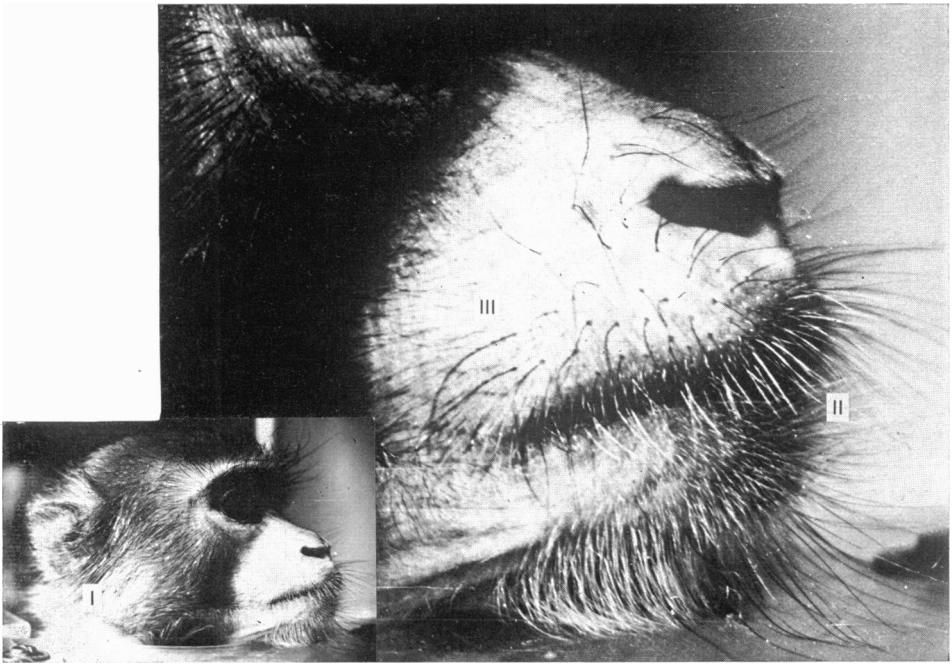

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EXPLANATION OF PLATE

Photograph of three types of hairs on the face of the monkey (*Macaca mulatta*). Type I (I, left) are soft, intermediate-length, yellow-brownish common hairs which lie along the lateral nose, face and head. Type II (II, right) are short, stiff, white circumoral vibrissae which project out from the margins of the upper and lower lips and interdigitate with their opposite number. Type III (III, centre) are single, isolated, stiff, long, black whiskers projecting in graceful arcs around the oral, nasal and orbital cavities and in the lateral facial region.