of 410 nm of β-naphthylamine released by enzymatic hydrolysis of amino acid β-naphthylamides was measured with the excitation light at 335 nm using an Aminco-Bowman Spectrophotofluorometer[8]. A blank without substrate was run for each sample. All values were corrected for spontaneous hydrolysis of amino acid β-naphthylamide[7] by substracting the value in a control solution containing water instead of the enzyme sample. Serum enzyme activities were measured colorimetrically. Incubation was stopped by the addition of 0.3 ml of 10% Tween-20 in 1 *M* acetate buffer pH 4.2 containing 0.45 mg of stabilized diazonium salt Fast Garnet GBC.

Results are shown in the Table. Although the activities in human parotid saliva were very low compared with those in serum, enzymes responsible for the hydrolysis of various kinds of amino acid β-naphthylamide were found in human parotid saliva. Substrate specificities of hydrolysis of various amino acid β-naphthylamides by human parotid saliva were similar to those by human serum. Naphthylamide derivatives of alanine, leucine, methionine, and norleucine were good substrates for both salivary and serum enzymes. The hydrolysis of lysine and arginine may be catalyzed by aminopeptidase B[9] in parotid saliva. This enzyme activity may have significance in the formation of bradykinin from kallidin-10[10] in saliva. Very low activity of the hydrolysis of α-L-aspartyl β-naphthylamide and α-L-glutamyl β-naphthylamide was detected in saliva only in the presence of Ca^{2+}. This activity may be catalyzed by aminopeptidase A[11] in parotid saliva. This enzyme in serum is responsible for the destruction of angiotensin II[12]. It is interesting that the hydrolysis of glycyl-prolyl β-naphthylamide in parotid saliva was relatively higher than those of other amino acid β-naphthylamides, indicating the presence of a newly described enzyme[13] in parotid salivary fluid[14].

Hydrolysis of amino acid β-naphthylamides by human parotid saliva and serum

Amino acid β-naphthylamide	Aminopeptidase activity (mean ± S.D.)	
	Parotid saliva mμmoles/min/l	Serum μmoles/min/l
Ala	87.0 ± 5.7	78.3 ± 19.0
Arg	7.5 ± 3.5	34.8 ± 18.0
Asp-NH_2	7.3 ± 3.0	0.9
α-L-Asp	0.8 ± 0.9	0.8 ± 0.5
β-Asp	0.0	0.0
Glu-NH_2	18.8 ± 4.5	20.0
α-L-Glu	1.2 ± 1.6	8.6 ± 3.6
D-Glu	0.0	0.0
γ-Glu	0.0	0.0
Gly	4.7 ± 6.4	9.8
Gly-Phe	10.0 ± 4.4	9.6 ± 4.5
Gly-Pro	1120 ± 692	25.1
Ile	23.7 ± 10.8	8.4 ± 3.5
Leu	94.3 ± 10.8	45.0 ± 18.4
Lys	16.8 ± 5.7	10.3
Met	101.3 ± 16.5	65.5 ± 27.2
Norleu	125.3 ± 71.9	34.0 ± 19.3
Norval	46.3 ± 19.8	26.6
Phe	65.0	34.0
Pro	6.8 ± 7.9	1.8 ± 1.9
Ser	0.0	4.6 ± 3.0
Val	5.5 ± 2.5	7.6 ± 4.1

Zusammenfassung. Die Aktivität der Aminopeptidasen im menschlichen Speichel von Ohrspeicheldrüsen wurde durch Fluoreszenzanalyse gemessen. Die Substratspezifität der Speichelaminopeptidasen war derjenigen der Serumenzyme ähnlich. Das Glycyl-Prolin β-naphthylamidspaltende Enzym war jedoch im Speichel von Ohrspeicheldrüsen in relativ grösserer Menge vorhanden.

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Receptive Fields of Cells in the Human Visual Cortex

Microelectrodes developed for neurosurgical use[1] were adapted for chronic implantation into the brain of patients with intractable seizures[2], in addition to the usual macro-electrodes of 'depth electrography'[3]. By means of these indwelling microelectrodes scores of single units in the visual cortex have been observed, many showing no change of activity to any of a wide range of stimuli. Many other units were responsive to general visual stimulation (by the movement of random sized discs and bars in various orientations on contrasting backgrounds), but in each of these we could not find a specific or key feature of the stimulus which would allow us to plot the receptive field. This is defined as a spatial plot of the visual stimuli which influence the firing of the unit under observation.

A number of receptive fields belonging to both cell bodies and axons were found in several patients. We had the opportunity to study 5 of them in 2 alert and co-operative patients. The patient viewed a 'grain of wheat' lamp or an ink dot accurately and without difficulty. Plotting was done directly on a large white or black sheet of cardboard at a distance of 1 m with the aid of various sized black and white discs and bars held on thin, stiff, wire handles (Fig. 1). Similar wands were used in 4 colors, red, yellow, green and blue. Spectrophotometric curves of these colors are unimodal, revealing good purity of hue.

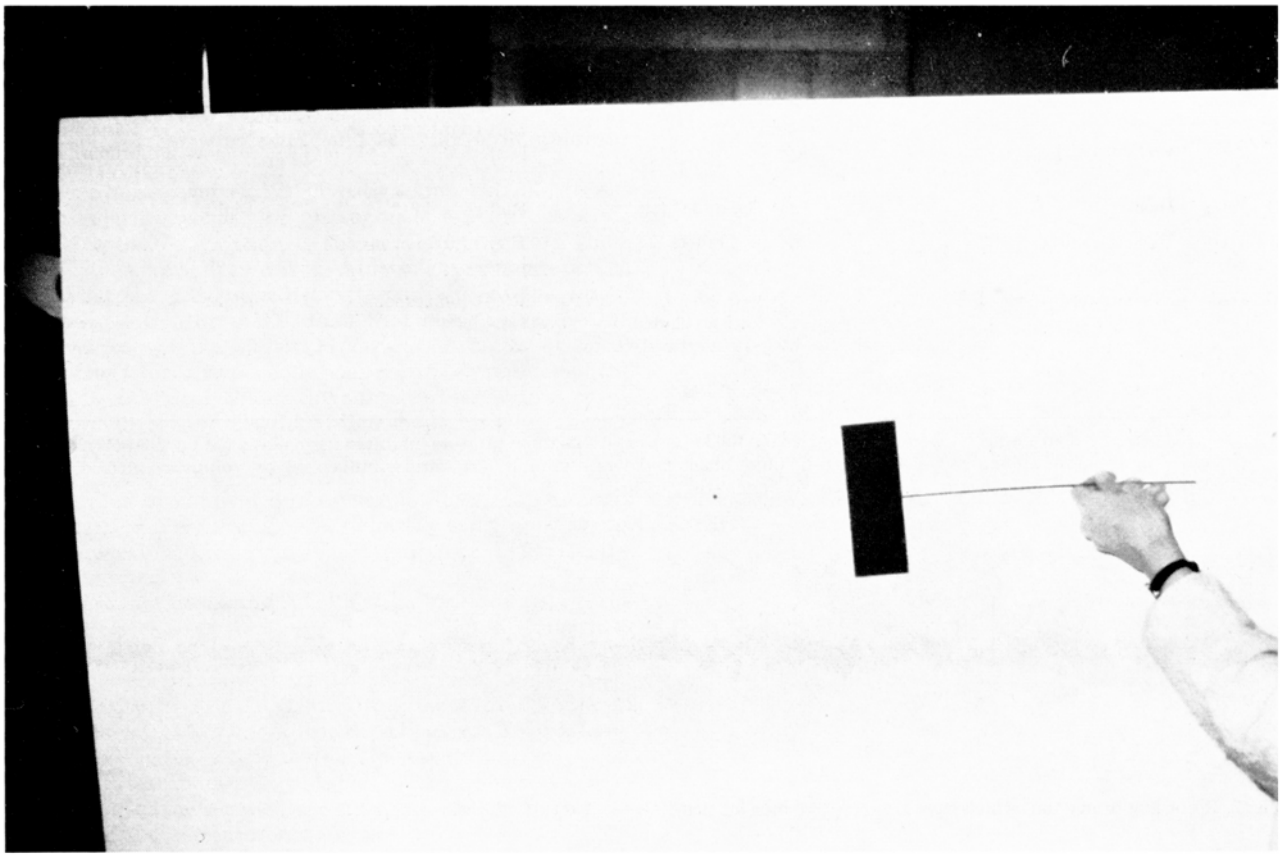

Fig. 1. The patient with indwelling microelectrodes is viewing an ink dot at 1 m distance while his visual field is being searched for the receptive field of a cell in the visual cortex whose spontaneous activity is being monitored through a loudspeaker and cathode ray oscilloscope. The receptive field was outlined in pencil on the background for measurement later.

The fields basically resembled those studied by HUBEL and WIESEL in cats[4], but differed in certain important details. The plotted receptive fields, labeled A to E inclusive, are described in the Table. Stimulus velocity was not critical. The exact location of the implanted microelectrodes in the visual cortex is uncertain since they were inserted freehand into the cortex through a burr hole 2 cm from the midline at the occipital pole. Unit A was probably in the striate cortex (area 17) and the rest in the para- or peristriate cortex (area 18 or 19).

One of the 5 units, D, responded to movement of the specific bar stimulus over a wide area of the visual field. Two receptive fields were circular or disc-shaped (B and E) and the rest were rectangular or bar-shaped. All projected from the left visual field to the right hemisphere except A which was $1-{}^1/_2{}^\circ$ from the fixation point. The receptive field of this unit projected from the left visual field to the left hemisphere. The projection is either directly through the primary visual pathways or indirectly via the corpus callosum. If it were the former it might account for clinical 'sparing of the macula' where the central visual area remains functional in hemianopsia.

The bar-shaped receptive fields were horizontal except for A which was almost vertical (95° from a right horizontal reference line through the fixation point). Two receptive fields, A and D, responded clearly only during movement of the target in the receptive field. We have seen no directional selectivity exhibited in our small sampling of individually plotted receptive fields, although apparent directionality was sometimes noted in other units when complex stimuli of random discs and bars were swept across the visual field. Some units were activated by stimuli presented to either eye in approximately corresponding areas of the visual field, others were mainly or totally monocularly stimulated.

All the units exhibited a slightly irregular or 'bursty' spontaneous rhythm. A record from 1 unit is seen in Figure 2. No influence on these receptive fields of non-visual sensory stimuli was noticed. The source of the irregularity of the spontaneous rhythm was not apparent.

Changes in room illumination or occlusion of the eyes by a large card did not noticeably affect the rhythm. The patient was instructed to close his lids, following which an inhibition of the rhythm was observed in all instances.

The units were all excitatory, that is, the cell's firing rate increased to stimulation within the receptive field. No manipulation of visual stimuli would decrease this rate. Inhibitory effects on the spontaneous rhythm could be demonstrated only by the closing of the lids and not by occlusion of the eyes. This would suggest that the

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Receptive fields from cells in the human visual cortex

Receptive field	Receptive field shape	Disc diameter or bar width	Field position from viewing point	Eye	Hemisphere	Remarks
A	Bar almost vertical (95°)	17 min arc	1–1/2° left	Left (right response less)	Left	Response primarily to movement
B	Disc	11°	23° down, 23° left	Right	Right	
C	Bar horizontal	1–2/3°	6° up, 11° left	Right (little or no response from left)	Right	
D	Bar horizontal	1–2/3°	Centred, 6° up, 17° left. Extended over 12° vertically	Right (no response from left)	Right	Response primarily to movement Plasticity
E	Disc	8–1/2°	8° up, 8° left	Right and left	Right	

All receptive fields or their units: (1) were in the left visual field; (2) were excitatory; (3) were inhibited upon closing of eyelids; (4) exhibited no difference in response among red, yellow, green, blue, black and white stimuli; (5) were uninfluenced by voluntary mental efforts; (6) exhibited no apparent influence from other sensory modalities.

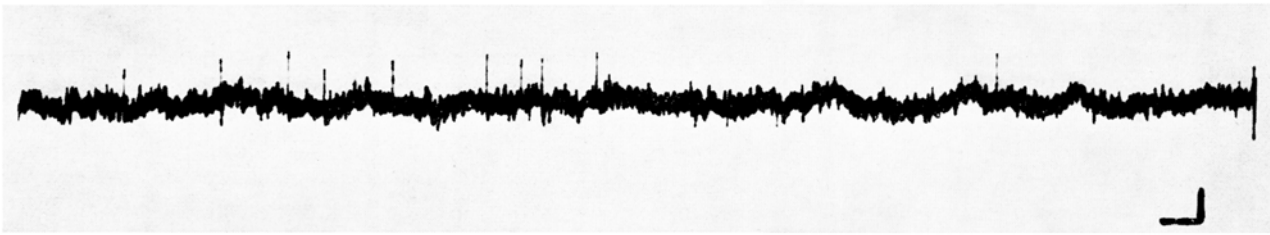

Fig. 2. Recording from a unit which gave the receptive field labeled E in the Table. Calibration: 50 μV, 5 msec, positive up.

sensation of black does not arise from this inhibition. We are not convinced of the absence in man of inhibitory areas surrounding these excitatory centers nor of inhibitory centers perhaps with excitatory surrounds as in the cat[4], but we have not yet found any trace of them. More refined plotting may ultimately reveal inhibitory influences.

Possibly most surprising of all in view of the rich representation of hue reported in the lateral geniculate body and visual cortex of the monkey[5], the different color of the stimuli (red, yellow, green, blue, black and white on contrasting backgrounds) elicited identical fields. Each cell responded to all colors equally without distinction.

One cell, D, had a receptive field in which a horizontal bar 1–2/3° wide elicited a response over a range of 12° vertically. It disappeared after some 10–15 min (although the unit's spontaneous rhythm was observed continuously). The phenomenon apparently was habituation without dishabituation since it could not be restored by extraneous stimuli[6]. Upon returning to the same microelectrode about 1/2 h later, the unit which appeared to be the same one as before had a change of the size and locus of its receptive field demonstrating a plasticity. It again disappeared even more rapidly than before. This phenomenon appears to be a decoupling of the unit from its visual input because the irregular spontaneous rhythm continues unchanged. It is possible, when time allows, to measure the receptive fields (visual grain) at different fixation distances, giving direct information about the size constancy mechanism[7].

Attempts to have the patient mentally control unit rhythms which he could hear over a loudspeaker were fruitless. Similarly, attempts at mental imagery, even of the effective target seen moments previously, did not noticeably influence the unit response. These cells seem to have no role in mental visual imagery.

Our preliminary results are of interest in themselves, but perhaps more important is the demonstration of the kinds of problems that can be solved only by this kind of investigation in conscious human patients. It seems entirely clear that this approach may help elucidate the complex psychological phenomena of the visual system and could be applied equally well to other sensory, motor, and integrative systems of the brain[8].

Résumé. Des microéléctrodes implantées dans le cortex humain visuel donnent des champs réceptifs de formes rectangulaires et circulaires qui ont des réponses d'excitation achromatiques, non influencées par les efforts mentaux volontaires ou par d'autres modalités sensorielles. Il y a inhibition quand les paupières sont fermées.

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