Zoom Neurons in Visual Cortex: Receptive Field Enlargements with Near Fixation in Monkeys

The nervous system exhibits size constancy; that is, it is capable of computing a constant size for objects in visual space despite their angular size changes as a function of distance. Psychophysical studies have established that size constancy exists in animals including monkeys[1] as well as man. The neural activity at the basis of this perceptual phenomenon might be expected to be evident in receptive fields in the visual system. SHERRINGTON[2] initiated the receptive field concept in studies of the somatosensory system and HARTLINE[2] first defined and studied receptive fields in the visual system. Anatomically the concept may be described as a subset of first order neurons mapping a particular sensory space with convergent connections to subsequent, higher order neurons. The activity of these higher level neurons maps the events in that particular sensory space. Receptive fields in the mammalian visual system have been described in the monkey at the level of the retinal ganglion cells[3], lateral geniculate body[4], visual cortex[5] and in other cortical areas[6,7]. A visual receptive field without a neural scaling mechanism, limited by anatomical restraints at the level of rods and cones, might be expected to maintain a constant angular size at all fixation distances. The size relationship between a receptive field and the image of an approaching object would be expected to constantly change. If such a receptive field were to concomitantly enlarge in size during the enlargement of the retinal image of an approaching object, then a constant relationship could be maintained between receptive field and object image size. Size constancy might then be neurally encoded as a constant firing rate in a cell monitoring this constant stimulation of the receptive field. Such a neurological zoom system was proposed by MARG and ADAMS[8] after initial results from limited cortical single neuron recordings in human patient volunteers. Those results indicated a receptive field enlargement at the near fixation point in some cortical units. This zoom model also predicted eccentric displacement of receptive fields as a function of decreasing fixation distance. Our study originated to investigate this kind of proposed receptive field plasticity.

Two adolescent female Rhesus monkeys were trained, using operant techniques, to fixate on a light emitting diode (0.7° of arc at 0.33 m); their heads were restrained during this task by a technique following that of WURTZ[9] Craniotomies over the primary visual cortex were maintained and a small mechanical micromanipulator[10] was used to position tungsten recording microelectrodes[11]. All penetrations were in the primary visual cortex and all receptive fields were within 13° of the visual axis. There were no abrupt transitions in recorded receptive field sizes and positions from one cell to another. Therefore it is unlikely that any units were recorded from other than area 17. Water deprivation was used to motivate the monkeys to fixate on the light. The body weight of the animals was taken before and after recording sessions and supplemental water was given as necessary. A tangent screen was positioned at a near and a far distance within the range of 0.33 to 3.12 m (3.00 D to 0.32 D) from the eye. The background luminance of the screen was 0.4 cd/m^2; slit and spot stimuli of 300 cd/m^2 were moved across the screen by a handheld projector and by mirror galvanometers. Luminance of the screen and stimuli were controlled to be the same at all distances, the physical size of the screen and fixation spot were constant, and the angular size of the stimuli was held constant to within 15%. Cell activity was monitored by loudspeaker and cathode-ray oscilloscope. During the experiment the monkey sat in its primate chair in an electrically shielded cage facing a square translucent tangent screen 1.6 m^2 in area. The monkey pressed a button activating the fixation light for an unpredictable length of time ranging from 3 to 10 sec. If the monkey activated a second lever during a period of 1.0 sec after the light was extinguished, the monkey received a reward of $^1/_4$ to $^1/_2$ cm^3 of water. Successful trials were adjusted to occur 75% of the time by dimming the fixation light. Horizontal electro-oculographic recordings were obtained from each eye separately and simultaneously with a resolution of a quarter of a degree. These signals were recorded with a dc amplifier from stainless steel screws attached to the bony orbit. During fixation and receptive field plotting the recording indicated that the eye position varied no more than $\pm$ 1.0°. All eye movements with significant horizontal components are detected in this system. When the monkeys were not fixating on the target light, they exhibited a pattern of consecutive saccadic eye movements fixating various points for no longer than 1 to 3 sec. This eye movement pattern was clearly distinguishable from fixations on the target light.

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Representative receptive fields plotted

Cell	Distance (m)	Receptive field (degrees)			Measured scale factor (Near size/far size)		Predicted scale factor (Far distance/near distance)	Comparative scale factor (Near size/far size) −1/(Far distance/near distance −1	
		Height	Width	Distance from visual axis	Height	Width		Height	Width

The receptive fields were plotted and then redetermined at the same distance in 13% of the cases. Linear dimension differences of up to ±5% were found with the same experimenter. When there were differences, the measurements in the direction of the geometric expectations were always chosen to bias the data against the zoom model. All cells tested had a binocular response in that each eye, when separately stimulated, would give a response. All receptive fields were demonstratively rectangular. The microelectrodes were $^1/_4$ mm diameter tungsten wire sharpened to an abrupt taper with a 1 μm tip. It is likely that we recorded from cells rather than fibres. This coupled with the rectangular shape and the binocularity of the receptive fields makes it unlikely that we recorded from optic radiation fibres.

Cells were fully investigated in 1 to 2 h of recording. A third of the units encountered were lost before a complete study could be made. Only data from cells completely

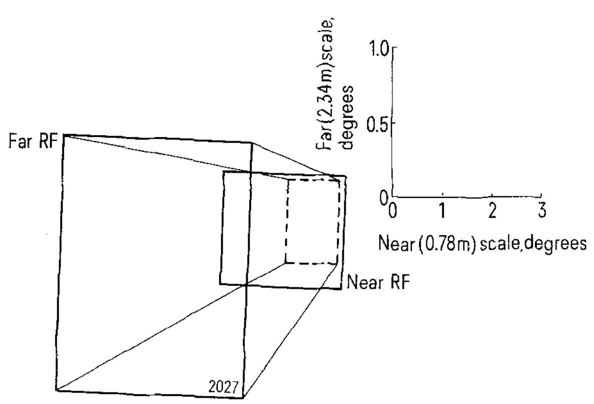

Fig. 1. A typical example of receptive field enlargement at near point fixation. The dark lines indicate actual receptive fields plotted at the near and far fixation planes. Geometric projection of the far receptive field to the near plane gives an expected receptive field sketched in dotted lines. There is a separate scale for each fixation distance. The two scales cross at the monkey's fixation point. These are the receptive fields of entry No. 4 in the Table.

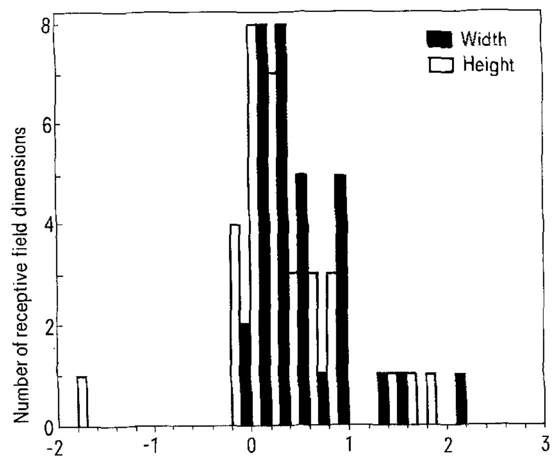

Fig. 2. The histogram shows the distribution of the comparative scale factor, for both the height and width of each cell recorded. The comparative scale factor (CSF) is a single number which incorporates the measured scale factor (MSF) (near angular size/far angular size) and the predicted scale factor (PSF) (far fixation distance/near fixation distance): CSF = (MSF)/PSF-1), and has been computed for both dimensions of each receptive field.

studied are included here. All cells were plotted for both eyes simultaneously under binocular viewing conditions. A receptive field was first plotted in 3 to 5 min by using a slit of light projected from a handheld lamp. Next the borders of the field were carefully verified in 15 to 20 min. At this time the corners of the field were stimulated with a spot of light to establish whether a rectangular or circular field was present. All borders of the receptive field were again checked and the screen was moved to the second fixation distance. Receptive fields were established where repeated stimulus movement regularly resulted in a burst of spike activity in the recorded cell. The same field was again plotted as described above but at the new fixation distance. 90% of the fields were classified as complex according to the HUBEL and WIESEL[5] nomenclature. We did not test for hypercomplex properties. 75% of the receptive fields were defined with horizontal and vertical borders; the remainder of the receptive fields, also rectangular, had various angular orientations. An example of our receptive field plots is shown in Figure 1.

Receptive fields for 32 cells were plotted at the 2 distances; 4 cells from one animal and 28 from the other. The ratios of the angular size of a near fixation field dimension from its expected size (the angular size at the distant fixation plane) are listed as the measured scale factors in the Table.

We have used a comparative scale factor (CSF) to compare the size scaling with geometric expectation and the zoom model prediction. For most of the receptive field dimensions, the CSF ranges between zero and one. A one indicates perfect correspondence with our zoom model and a zero indicates no size scaling of the receptive field for a different fixation distance, the geometric expectation. In a few cases, negative scaling occurs; that is, a receptive field dimension is reduced in angular size at the near fixation distance. It is interesting that a variability is seen in size constancy estimations in the psychophysical results reported by LEIBOWITZ[12]. This may correspond to our neuronal range of size scaling.

Only one cell exhibited no significant difference in scaling properties from geometric expectations, i.e., the measured scale factor was essentially one (No. 5, Table). The other 31 cells exhibited receptive field size changes in height and/or width that were different from those predicted by the geometric projection. In Figure 2 the comparative scale factor for both the height and width of each cell has been plotted as a histogram. The average comparative scale factor for receptive fields was for height, 0.40 ± 0.11 s.e., and for width, 0.50 ± 0.09 s.e.

Three cells matched out theoretical predictions closely. The enlargement of both dimensions of these cells at the near plane approached or exceeded the predictions of a zoom model of receptive field plasticity which would enable a single cortical neuron to track the apparent size changes of an object at different distances[8]. Entries 2, 10 and 15 in the Table are examples.

The comparative scale factors of the heights, widths and positions of the receptive fields were significantly different from zero (the geometric expectations) by the t-test: height, $N = 32$, $t = 3.56$, $p = 0.002$; width, $N = 32$, $t = 5.72$, $p < 0.001$ and position, $N = 12$, $t = 6.28$, $p < 0.001$.

The enlargement of retinal images of approaching objects is accompanied by an angular eccentric displacement unless the image is centered on the visual axis. Therefore our model predicts a compensatory eccentric displacement of receptive fields. This predicted displacement was not

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Representative receptive fields plotted

Cell	Distance (m)	Receptive field (degrees)			Measured scale factor (Near size/far size)		Predicted scale factor (Far distance/ near distance)	Comparative scale factor (Near size/ far size) −1/ (Far distance/ near distance) −1	
		Height	Width	Distance from visual axis	Height	Width		Height	Width
1.	0.95	4.09	0.66	11.52	1.99	1.14	1.55	1.80	0.25
	1.47	2.06	0.58	12.86					
2.	0.94	2.86	6.68	2.13	2.67	3.34	2.70	0.98	1.38
	2.54	1.07	2.00	0.94					
3.	0.78	1.61	0.88	0.88	1.56	0.78	3.00	0.28	−0.11
	2.34	1.03	1.13	0.95					
4.	0.78	2.49	3.01	1.03	1.78	2.74	3.00	0.39	0.87
	2.34	1.40	1.10	1.59					
5.	0.78	0.95	1.69	1.83	0.88	1.13	3.00	−0.06	0.06
	2.34	1.08	1.49	2.15					
6.	0.78	2.42	2.64	2.57	1.39	2.90	3.00	0.20	0.95
	2.34	1.74	0.91	2.08					
7.	0.78	0.88	0.88	0.80	0.92	1.28	3.00	−0.04	0.14
	2.34	1.74	0.91	2.08					
8.	0.78	3.45	1.91	5.72	1.56	1.30	3.00	0.28	0.15
	2.34	2.21	1.47	5.38					
9.	0.78	5.35	2.79	3.96	1.90	1.41	3.00	0.45	0.21
	2.34	2.82	1.98	6.87					
10.	0.33	5.21	14.48	11.28	2.57	1.84	2.00	1.57	0.84
	0.67	2.03	7.89	5.72					
11.	1.00	1.66	0.92	5.33	1.61	1.18	1.33	1.85	0.55
	1.33	1.03	0.78	5.13					
12.	1.00	6.25	3.50	11.17	0.44	1.48	1.33	−1.69	1.46
	1.33	14.18	2.37	13.57					
13.	0.92	1.62	1.19	3.69	1.07	1.49	1.09	0.06	0.45
	1.92	1.52	0.80	3.50					
14.	0.94	5.41	4.92	1.82	2.14	2.67	2.7	0.67	0.98
	2.54	2.53	1.84	0.72					
15.	0.94	3.77	6.62	3.52	2.67	2.42	2.7	0.98	0.84
	2.54	1.41	2.73	1.42					
16.	0.94	3.10	7.66	1.76	2.67	1.52	2.7	0.98	0.31
	2.54	1.16	5.05	1.28					
17.	0.78	1.61	4.69	1.47	1.87	2.52	3.0	0.44	0.76
	2.34	0.86	1.86	0.64					
18.	0.78	3.45	5.06	0.59	2.35	1.71	3.0	0.68	0.36
	2.34	1.47	2.96	0.86					
19.	0.78	3.67	3.00	1.32	1.83	1.46	3.0	0.42	0.23
	2.34	2.01	2.06	1.00					
20.	0.78	2.77	1.76	1.25	1.80	1.49	3.0	0.40	0.25
	2.34	1.54	1.18	1.05					
21.	0.78	1.69	2.05	0.44	1.15	1.33	3.0	0.08	0.17
	2.34	1.47	1.54	0.73					
22.	0.78	2.42	2.64	2.49	1.34	1.93	3.0	0.17	0.47
	2.34	1.81	1.37	1.81					
23.	0.78	2.05	2.27	0.66	1.53	1.47	4.0	0.18	0.16
	3.12	1.34	1.54	0.81					
24.	0.78	1.76	1.54	1.61	1.89	1.23	3.0	0.45	0.12
	2.34	0.93	1.25	2.40					
25.	0.78	1.54	1.69	2.79	1.75	0.99	4.0	0.25	−0.003
	3.12	0.88	1.70	2.42					
26.	0.78	1.21	2.35	1.03	1.26	1.65	3.0	0.13	0.33
	2.34	0.96	1.42	2.20					
27.	0.78	1.47	2.57	1.69	1.18	2.14	3.0	0.09	0.57
	2.34	1.25	1.20	2.42					
28.	0.78	1.10	2.49	1.98	1.59	1.64	3.0	0.30	0.32
	2.34	0.69	1.52	2.27					
29.	0.78	0.88	1.07	1.61	0.77	1.24	3.0	−0.12	0.12
	2.34	1.15	0.86	2.05					
30.	0.33	3.65	3.65	6.94	1.12	2.03	2.0	0.12	0.52
	0.67	3.26	1.80	5.99					
31.	0.33	2.60	3.65	6.42	1.66	3.15	2.0	0.66	2.15
	0.67	1.57	1.16	7.01					
32.	0.33	3.05	10.07	6.77	0.83	1.10	3.0	−0.09	0.05
	1.00	3.67	9.17	8.94					

All receptive field heights, widths and positions are in degrees. Measured scale factors indicate the decimal fraction of the near field angular size as compared with the size at far fixation. The comparative scale factor normalizes all size scaling for comparison with geometric expectations and the zoom model prediction. A comparative scale factor of zero indicates constant angular size of the receptive field at both fixation distances. A comparative scale factor of unity indicates size scaling in perfect accordance with the zoom model.

observed in an average of all 32 cells. The displacement was evident within a subgroup of the 12 best zoom cells. These cells were chosen based on the average near field enlargement of the two dimensions, with each cell having more than 70% of the enlargement predicted by the zoom model. The eccentric displacement of the near receptive fields of these cells was about 1 1/2 times the displacement of the far plane receptive field. The comparative scale factor averaged 0.36 ± 0.13 s.e.

The zoom effects we measured could not be attributed to optical accomodation. In the first place, accomodation could not account for a simultaneous magnification and minification of the two dimensions of a receptive field. Furthermore, using the Gullstrand schematic eye one can calculate that 3 diopters of accommodation result in only about 1% magnification[13]. All of our recording was done in response to binocular stimulation. It is reasonable to suggest that near field enlargement may result from fixation disparity and the shifting of two monocular receptive fields. This is ruled out as the sole explanation since the majority of receptive fields have changes in the vertical dimension.

It appears that in contradiction to indirect evidence, many cells in the primary visual cortex of the monkey exhibit zoom scaling that may subserve size constancy[14]. Our results support the zoom model predictions for near field enlargement of visual receptive fields. This receptive field zoom mechanism can provide a substrate for size constancy in the visual system[15].

Zusammenfassung. Rezeptive Felder von 32 Zellen im primärvisuellen äusseren Teil des Grosshirns unbetäubter, abgerichteter Affen wurden abgesteckt. Davon zeigten 97% der Zellen Vergrösserung der eckigen Abmessungen auf der nahen Fläche. Diese Grösse-Einstellung unterstützt unsere Vorstellung eines «Zoom-Modells» der Grössen-Konstanz.

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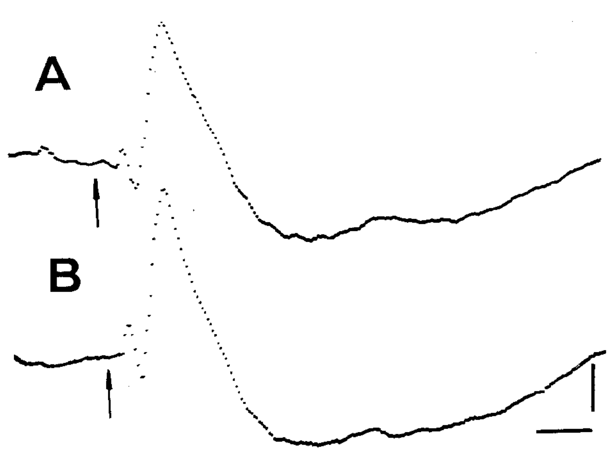
Influence of Superior Cervical Ganglion on Electroretinogram of the Rabbit

The present investigation was made to analyze the influence of the superior cervical ganglion on the ERG (electroretinogram) of the rabbit. Only a report deals with such a problem[1], while the effects of electrical stimulation of superior cervical sympathetic trunk or ganglion on the blood circulation in the eye[2,3], on the intraocular pressure, on the intrinsic eye musculature and the relation between autonomic nervous system and retina were investigated in previous works[4,5]. On the other hand, some authors analyzed the influences of variation of the blood circulation, pupillary diameter and intraocular pressure on the ERG[6–11].



Effect of the electrical stimulation of right superior cervical ganglion on the ipsilateral ERG. Each trace represents the average of 16 responses. A) normal ERG. B) ERG after sympathetic stimulation (10 V; 25/sec; 1 msec; train of 30 sec). Parameters: darkness adaptation, 30 min; light stimulation: 200 lux, 50 µsec, 1/sec. Time: 100 msec. Amplitude: 100 µV.

Thirty-five rabbits under Nembutal anaesthesia (33 mg/kg) were put in a stereotaxic apparatus in dorsal position, then were curarized and artificially ventilated. Subsequently the superior cervical ganglion was isolated. The ipsilateral eye was atropinized, the nictitating membrane was cut, an artificial pupil on the cornea limited the light input; however, 5 rabbits underwent iridectomy in order to eliminate any possible variation of the pupil diameter.

The ERG was elicited with a DC Galileo electronic flash. Each single flash lasted 50 µsec, the light intensity ranged from 20 to 800 lux and the flash frequency was 1/sec. The animals were maintained 30 min in darkness before beginning the photostimulation. The ERG was recorded by a Hewlett-Packard 5480 two channel input analyzer, which averaged usually 16 single responses. After numerous normal ERGs were recorded from the right eye, the ipsilateral superior cervical ganglion or the trunk (after proximal section) was electrically stimulated for 30 sec by means of silver bipolar electrodes with the following parameters: 25–100/sec, 8–15 V,

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