Effect of adaptation level on maintained firing and sensitivity in receptive field center of X and Y cells[1]

J. G. Pollack and R. W. Winters

Psychology Department, University of Miami, P. O. Box 248185, Coral Gables (Florida 33124, USA), 3 June 1977

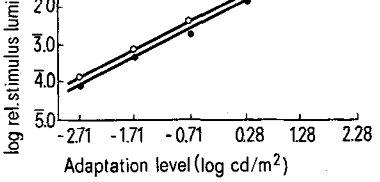
Summary. Maintained firing rates of X cells and Y cells were compared at 6 adaptation levels (AL) between -2.71 log cd/m^2 and 2.28 log cd/m^2 (10 mm^2 pupil size). X cell maintained firing was higher at all ALs and was statistically different at medium and high ones. Changes in AL had nearly identical effects upon X and Y cell suprathreshold sensitivity to a flashing spot in the center of their receptive fields; the Weber function had a slope of 0.744 for Y cells and 0.743 for X cells. These values are not statistically different.

Research over the past decade indicates that on-center retinal ganglion cells of the cat are of 2 types[2–8]. The 2 groups have been referred to as X and Y cells[2,8], type I and type II[3,6] cells sustained and transient cells[4,5] or as group I and group II cells[7]. Henceforth we will use the language, of Enroth-Cugell and Robson[2] and refer to these cells as X and Y cells. The criteria for classifying these cells has been described in previous papers[7,9,10]. Several papers published recently[11–13] suggest that differences between the responses of X and Y cells occurring at high adaptation (AL) levels are not found at lower background luminances. In the present study we compared 2 characteristics of X and Y cells at 6 ALs: a) the maintained firing rate, b) sensitivity to a flashing spot in the RF center.

Single cell recording were made from 37 on-center fibres (19 X and 18 Y cells) in lightly anesthetized cats. Details of the recording system, optical system, and animal preparation can be obtained by referring to Winters, Hickey and Pollack[9].

Statistical analysis of maintained activity for X and Y cells

AL log cd/m^2	Type	Mean ± SD	Range	Probability of t
-2.71	Y	25.8 ± 16.6	0–56	0.15
	X	34.1 ± 16.7	10–69	
-1.71	Y	27.4 ± 17.4	0–59	0.10
	X	42.4 ± 23.3	4–83	
-0.71	Y	34.9 ± 26.9	0–79	0.05
	X	59.1 ± 31.6	16–87	
0.28	Y	27.4 ± 23.3	0–66	0.05
	X	53.3 ± 39.9	11–85	
1.28	Y	22.0 ± 23.9	0–84	0.05
	X	43.3 ± 26.6	4–80	
2.28	Y	18.3 ± 19.9	0–54	0.025
	X	42.4 ± 24.1	8–93.2	



Mean equal-response plots for suprathreshold response criterion (about 10 times threshold for most ALs) for X cells (○—○) and Y cells (▲—▲).

Effect of AL on maintained activity. The table summarizes the relationship between AL and the maintained firing rate of X and Y cells. Maintained firing rate is defined as the average discharge rate of the cell in the absence of any stimulation other than a diffuse background (left hand column of table). X and Y cells show similar changes in maintained firing rate as AL was increased. The maintained firing rate was lowest at -2.71 log cd/m^2 and increased through the mesopic range. At higher levels (1.28 log cd/m^2) the maintained rate began to decrease for both X and Y cells. Other investigators[14–16] have also found nonmonotonic relationships between AL and maintained firing but they examined maintained firing of ganglion cells without first classifying cells in X and Y cell groups. The X cells had higher group means than Y cells at each AL and this difference was statistically significant at all backgrounds except the -2.71 and -1.71 log cd/m^2 luminances. The general conclusion made by other investigators[8] that maintained firing is higher in X cells than in Y is thus confirmed statistically for medium and high ALs but not low ones.

Effect of AL on sensitivity to spot in RF center. Intensity-response functions to a 0.5°, spot in the RF center were obtained at 6 ALs. Polynomial regression equations were then fitted to the data and equal response plots derived from the linear equations (semilog plots). Linear equations proved to be an adequate fit for all of the functions examined; second order coefficients did not differ from zero ($p > 0.15$).

[1] This research is supported by Public Health Service grant no. EY 00701.

[2] C. Enroth-Cugell and J. G. Robson, J. Physiol., Lond. *187*, 517 (1966).
[3] Y. Fukada, Vision Res. *11*, 209 (1971).
[4] B. G. Cleland, M. W. Dubin and W. R. Levick, J. Physiol., Lond., *271*, 473 (1971).
[5] H. Ikeda and M. J. Wright, J. Physiol., Lond. *227*, 769 (1972).
[6] D. I. Hamasaki, J. Fengel and L. R. Hazelton, Vision Res. *13*, 1421 (1973).
[7] T. L. Hickey, R. W. Winters and J. G. Pollack, Vision Res. *13*, 1511 (1973).
[8] J. Stone and Y. Fukuda, J. Neurophysiol. *37*, 722 (1974).
[9] R. W. Winters, T. L. Hickey and J. G. Pollack, Vision Res. *13*, 1487 (1973).
[10] R. W. Winters, T. L. Hickey and D. H. Skaer, Vision Res. *13*, 1499 (1973).
[11] R. W. Winters, J. G. Pollack and T. L. Hickey, Brain Res. *47*, 501 (1972).
[12] J. G. Pollack, R. W. Winters and T. L. Hickey, Br. J. Physiol. Optics, *28*, 175 (1973).
[13] H. G. Jakiela and C. Enroth-Cugell, Expl. Brain Res. *24*, 335 (1976).
[14] R. W. Rodieck, J. Physiol., Lond. *30*, 1043 (1967).
[15] H. B. Barlow and W. R. Levick, J. Physiol., Lond. *202*, 699 (1969).
[16] B. Sakman and O. D. Creutzfeldt, Pflügers Arch. *313*, 168 (1969).

The relationship between log background luminance and the luminance of the spot necessary to meet a criterion response was examined for the (transient first 80 msec) of the response of X and Y cells. The criterion response was the spike rate produced by a stimulus luminance 0.8 log units above threshold at the 0.28 log cd/m^2 AL. Equal-response curves were then generated by solving the intensity-response functions for this criterion spike rate. Regression lines were then fitted to the computed equal-response data. Linear equations provided a satisfactory fit ($p < 0.001$) to data for both cell types. The figure shows the equal-response plots.

The change in retinal sensitivity over the observed range of adapting luminances was smaller than that predicted by Weber's Law ($\Delta I/I_a = K$): I_a refers to AL and ΔI the intensity difference between test target and AL necessary to produce a criterion response; K is a constant. It has been demonstrated previously for ganglion cells considered as a single group (for threshold responses), that the test spot luminance required to yield a constant response does not rise directly with I_a, but is proportional to I_a^n, where n is smaller than 1[15]. The relationship between ΔI and I_a is given in the figure for X cells and Y cells. The values for the slope of the relationship is 0.744 for Y cells and 0.743 for X cells. No statistical difference could be found between these values ($p > 0.15$).

The meaning of this function is that the intensity-response curve generated at a given AL is shifted along the background luminance continuum by the relation $I = f(I_a)^n$. Sakmann and Creutzfeldt[16] reported similar findings with the exponent equal to 0.7. This is confirmed here for both X and Y cells considered separately.

Increased resistance to satiation in diazepam-treated pigs

R. Dantzer[1]

I. N. R. A., Station de Pharmacologie-Toxicologie, 180, chemin de Tournefeuille, F-31300 Toulouse (France),

20 June 1977

Summary. Sated pigs, having a previous history of operant responding according to a CRF schedule, resumed responding when put back in the Skinner box after 1 mg/kg diazepam. This effect did not appear to be related to the disinhibition of an extinction process.

Benzodiazepines have been reported to increase resistance to satiation in cats or rats under conditions in which emotional factors are not present[2,3]. This effect has been attributed to an interference of the drug with hunger or satiety mechanisms. However, in an extensive review of resistance to satiation, Morgan[4] has recently suggested that satiation is highly related to extinction, so that the effects of benzodiazepines may be viewed as another example of drug-induced resistance to extinction[5]. Using pigs, we have shown that diazepam is effective in increasing responding only in the early stages of the extinction procedure, when there is still some residual responding, but is no longer effective when responding is fully suppressed[6]. In studies of benzodiazepine effects on satiation, satiation was operationally defined by giving the subjects free access to food during the course of the experiment[3] or, during a limited time, just before the drug test[2]. It was found, in both studies, that control animals ate in the experimental situation, i.e. that satiation was not effectively reached. If satiation is governed by the same active inhibitory process as that which controls extinction, benzodiazepines would be expected to have no effect on the behaviour of fully sated subjects which do not eat in the experimental situation. Moreover, satiation should be 'disinhibited' by appropriate external stimuli[7]. The present experiments were initiated to test this assumption using pigs as experimental subjects.

Methods. Apparatus and general training procedures have already been fully described[6]; 5 pigs, 3–5 months old and weighing 25–50 kg were first put on a restricted

Number of responses and amount of food eaten in sated pigs submitted to a 15 min CRF session under different conditions

Subject	Control session Number of responses	Amount of food eaten	Drug session Number of responses	Amount of food eaten	Disinhibition session Number of responses a	b	Amount of food eaten
109	2	0	21	77%	–	–	–
110	7	0	38	53%	–	–	–
82	5	0	115	75%	2	0	0
73	5	0	26	82%	3	0	0
79	0	0	80	54%	6	2	0

* Percent of food delivered. a: total number of responses emitted; b: responses emitted during the stimulus presentations.

---

[1] Acknowledgment. Many thanks are due to the skillfull technical assistance of Ms R. M. Bluthé. This work has received financial support from Institut National de la Recherche Agronomique, Recherches Vétérinaires, and from Institut National de la Santé et de la Recherche Médicale (ATP 39. 76. 71).

[2] W. Fratta, G. Mereu, P. Chessa, E. Paglietti and G. L. Gessa, Life Sci. *18*, 1157 (1976).

[3] R. A. Wise and V. Dawson, J. comp. physiol. Psychol. *86*, 930 (1974).

[4] M. J. Morgan, Anim. Behav. *22*, 449 (1974).

[5] D. L. Margules and L. Stein, Excerpta med. Int. Congr. Ser. *129*, 108 (1967).

[6] R. Dantzer, Pharmac. Biochem. Behav. *6*, 157 (1977).

[7] C. J. Brimer, Learn. Motiv. *1*, 346 (1970).