

国家自然科学基金重大项目

# 视觉信息加工研究

(一九八八年十月——一九九二年十月)

## 论文集

下 册

项目学术领导小组

一九九二年十月

## 前 言

国家自然科学基金重大项目《视觉信息加工研究》经过全体参加者四年的努力，已经按计划并超额完成，取得了一系列基础理论成果和一些有实际应用前景的成果。据初步统计，在此项基金的支持下，在国内外学术刊物和学术会议上共发表/撰写研究论文 267 篇。获中国科学院自然科学二等奖二项、三等奖一项、省级自然科学一等奖二项及本单位奖多项、获国家专利二项。另有待申报国家自然科学基金成果奖二项、院级奖一项及国家专利二项。这批成果达到了国际水平或为国际领先，为了解视觉信息加工的神经基础和理论描述提供了丰富的资料，受到国内外同行的高度评价和重视。

本研究工作总结包括四部分内容分五册出版。第一部分在简述本项目研究的主要成绩之后，依次说明各个子课题研究所取得的进展，并列出研究论文目录；第二部分是 176 篇论文的摘要，它们是我们研究工作的缩影；第三部分是获奖成果简介；第四部分是分上、下二册出版的论文集。承担此项研究的全体同事谨以此献给予我们以有力支持的国家自然科学基金委员会及其生命科学部，献给各位参与评审的专家和所有关心、支持我们的同事和朋友。

项目学术领导小组

组 长 王书荣

一九九二年十月

项目负责人：王书荣

中国科学院生物物理研究所

子课题及其负责人：

一·中脑视觉神经回路中的信息加工

王书荣（中国科学院生物物理研究所，北京）

二·视觉信息加工中空间—时间相互作用及其神经机制的研究

寿天德（中国科技大学生物系，合肥）

三·视觉感受野空间相互作用与复杂图象的加工处理

李朝义（中国科学院生理研究所，上海）

四·胼胝体传递视觉信息的特征

刁云程（中国科学院生物物理研究所）

五·视觉图象识别中眼动对图象特征提取作用的研究

孙复川（中国科学院生理研究所，上海）

六·蜜蜂模式识别及平行加工机理研究

张少吾（中国科学院生物物理研究所）

七·视觉信息处理中基本神经网络的算法理论描述

汪云九（中国科学院生物物理研究所）

## 目 录

### 视觉图象识别中眼动对图象特征提取作用的研究

1. Human pupillary response to ramp changes in light intensity George K. Hung and Fuchuan Sun	2
2. 视觉信息处理: 阅读中文和英文时眼动模式的对比研究 孙复川 L. Stark	12
3. A switching process controls dual mode accommodation responses to ramp inputs: experimental and modeling evidence Fuchuan Sun and Lawrence Stark	18
4. Sampling or quantization in saccadic eye movement control Joseph Terdman, Fuchuan Sun, and Lawrence Stark	20
5. Static accommodation response: stigmatoscopic method to measure development of presbyopia Katsuya Matsunaga, an H. Nguyen, Fuchuan Sun, Corina Vandepol, and Lawrence Stark	23
6. Apple II 用于生物学实验---产生刺激信号、数据采集与处理 宋小军 翁为民 袁 锋 孙复川	27
7. Changes in accommodation with age: static and dynamic Fuchuan Sun, Lawrence Stark, an Nguyen, James Wong, Vasudevan Lakshminarayanan, and Elizabeth Mueller	31
8. 高抗干扰性的红外光电反射眼动测量仪 张名魁 孙复川	38
9. Frequency analysis of accommodation: single sinusoids Fuchuan Sun, Stephan Brandt, an Nguyen, Margaret Wong and Lawrence Stark	43
10. 运动图象刺激的视动振荡(OKN) 眼动反应的速度跟踪特性 朱惠敏 孙复川 梅镇彤	49
11. 在双脉冲光刺激下瞳孔系统的采样控制特性 孙复川 赵信珍	58
12. Switching control of accommodation: experimental and simulation responses to ramp inputs Fuchuan Sun and Lawrence Stark, Fellow, IEEE	66
13. 瞳孔控制系统非线性的频率特性与固有频率 杨 明 赵信珍 孙复川	73
14. Eye movements in reading chine language: paragraph, single character and pinyin Fuchuan Sun	

15. 动态瞳孔控制系统双眼之间的耦合及计算机模型	
孙复川 赵信珍 林家瑞 L. Stark	92
16. 无限动条件下中文阅读的研究	
孔 勇 孙复川	102
17. 不同运动图象同时刺激左右眼时的交替视动震颤(OKN)现象	
韦 敏 孙复川	108

## 蜜蜂模式识别及平行加工机理研究

18. Motion cues provide the bee's visual world with a third dimension	
M. Lehrer, M. V. Srinivasan, S. W. Zhang and G. A. Horridge	118
19. 家蝇复眼性特化光感受器的进一步研究	
吴卫国 徐智敏 石淑珍 吴盛立	120
20. 雄蝇追逐飞行的加速度分析	
张少吾 王 翔	123
21. 飞蝗复眼生理和结构上的节律变化	
吴卫国 G. A. Horridge	131
22. 计算机三维重建华虹复眼性特异小网膜细胞结构	
吴盛立 陆惠民 吴卫国 徐智敏 石淑珍	137
23. 用生理数据和光学方法模拟视觉系统的空间滤波特性	
陈宜君 田丽娟 张少吾	142
24. 神经重叠复眼感杆光导的模式与性特化光感受器	
吴卫国 徐智敏 石淑珍 吴盛立 吴梅英	146
25. On the fine structure of the retina and lamina of the horsefly <i>Tabanus manassarius</i>	
Xu Zhi-min(徐智敏), Shi Shu-zhen(石淑珍), Wu Sheng-li(吴盛立) and Wu Wei-guo(吴卫国)	152
26. Further studies of the sex-specific photoreceptor of the compound eye of the housefly	
Wu Wei-guo(吴卫国), Xu Zhi-min(徐智敏), Shi Shu-zhen(石淑珍) and Wu Sheng-li(吴盛立)	159
27. How honeybees measure their distance from objects of unknown size	
M. V. Srinivasan, M. Lehrer, S. W. Zhang, and G. A. Horridge	163
28. Physiological changes of photoreceptor of bush cricket compound eyes as a function of time and adaptation state	
吴卫国等	172
29. Quantitative investigation on structural changes of photoreceptor in the bushcricket <i>Gampsocleis gratiosa</i>	
Xu Zhi-min(徐智敏), Shi Shu-zhen(石淑珍), Wu Wei-guo(吴卫国), Wu Mei-ying (吴梅英) and Chen Chuan-juan(陈传涓)	175

30. Colour inputs to motion and object vision in an insect	
G. A. Horridge, X. Wang and S. W. Zhang	181
31. Visual edge detection in the honeybee and its chromatic properties	
M. Lehrer, M. V. Srinivasan and S. W. Zhang	188
32. Visual tracking of moving targets by freely flying honeybees	
S. W. Zhang, Wang Xiang, Liu ZiLi, and M. V. Srinivasan	198
33. 昆虫复眼瞳孔调节的一种新机制	
吴卫国 吴梅英 E. J. Warrant 徐智敏 石淑珍 王翔 高奔 张少吾	206
34. 自由飞行蜜蜂跟踪运动目标的研究	
张少吾 王翔 刘子立	211
35. 蜻蜓运动检测神经元的光谱反应	
张少吾 王翔	220
36. 蜜蜂光感受器结构变化的定量研究	
徐智敏 石淑珍 吴卫国 吴梅英 陈传渭	227
437. 华蚊复眼光感受器的昼夜变化	
徐智敏 石淑珍 吴盛立 吴卫国	231
38. 一种模拟昆虫视觉系统并行信息处理功能的光学实现	
田丽娟 陈宜君 张少吾	236
39. 用红外方法对蝇翅视动行为的探索	
张宏 张少吾 王翔	241
40. 复眼透镜光学信息保密编码及译码的研究: I	
吴梅英 马重光 彭连惠 田丽娟 杜连芳 张少吾	247
41. 复眼透镜光学信息保密编码及译码的研究: II	
吴梅英 马重光 彭连惠 田丽娟 杜连芳 张少吾	253
42. 不同质地背景对自由飞行蜜蜂跟踪运动目标的影响	
王翔 任小军 高奔 张少吾	259
43. 蜜蜂复眼光感受器的生理变化	
吴卫国 吴梅英 E. J. Warrant 石淑珍 徐智敏	265
44. 利用共聚焦显微镜系统进行视觉显微结构的三维重建	
陆惠民 刘守忠 颜坤 吴卫国 王荫亭	271
45. 用DOG函数进行边缘检测的硬件网络模型	
刘子立 王翔 张少吾	276

## 视觉信息处理中基本神经网络的算法理论描述

46. 时空分离Gabor函数模型和感受野的时间特性	
汪云九 齐翔林 于德山	282

47. 用数量场描述方向敏感感受野	
汪云九 齐翔林	288
48. 感受野和拓扑图对的识别	
于德山 汪云九	294
49. Extended gabor function model and simulation of some Characteristic curves of receptive field	
Wang Yunjiu (汪云九), Qi Xianglin (齐翔林), Xing Jing (邢 静) and Yu Deshan (于德山)	297
50. 广义Gabor函数模型和感受野某些特性曲线的模拟	
汪云九 齐翔林 邢 静 于德山	307
51. 人类视觉系统超视锐度现象的神经网络数学模型研究	
汪云九 程子习 姚国正 吴新年	315
52. 运动视觉的奇次倍频现象	
吴新年 姚国正 高 千 汪云九	321
53. 一个模拟视觉交变现象的神经网络	
潘 峰 汪云九 姚国正 齐翔林	327
54. 线画图形质地辨认的一个神经网络模型	
姚国正 李锋 汪云九 吴新年 齐翔林	332
55. 人眼的阈上调制传递函数	
吴新年 姚国正 汪云九 杜连芳	338
56. 人眼的阈上调制传递函数	
吴新年 姚国正 汪云九 杜连芳	346
57. 时空联合不确定性关系和广义Gabor函数	
齐翔林 汪云九 王 孟 姚国正	353
58. 不同运动速度下人眼的阈上调制特性	
吴新年 姚国正 汪云九	366
59. 窗口形状对视觉局域运动知觉的影响	
吴新年 汪云九 姚国正	361
60. 神经形态发生的一种细胞自动机(CA)模型	
姚国正 王 孟 汪云九 成小平	366
61. 双眼立体视觉可塑性的实验研究	
姚国正	370
62. 一种以准DOG分布为基元的体视匹配算法	
姚国正 刘 磊 郑竺英	376
63. The joint spatio-temporal uncertainty principle and extended gabor function	
Qi Xianglin (齐翔林), Wang Yunjiu (汪云九), Wang Meng (王孟) and Yao Guozheng (姚国正)	383
64. 初级视觉的神经波表象	
汪云九 齐翔林 姚国正 王 孟	387

# 视觉图象识别中眼动对图象特征提取 作用的研究



## Human Pupillary Response to Ramp Changes in Light Intensity

GEORGE K. HUNG\* AND FUCHUAN SUN†<sup>1</sup>

\*Rutgers University, College of Engineering, Piscataway, New Jersey 08855-0909; and

†Shanghai Institute of Physiology, 320 Yo Yang Road, Shanghai, China

Received May 22, 1987; revision received September 15, 1987

The dynamic behavior of the pupillary system was explored using different velocity ramp changes in light intensity. Ramp stimuli ranged in velocity from 0.02 to 8.00 log units/s and the responses were recorded from three subjects. For ramp velocity below 0.066 log units/s, the responses were mainly ramps. Above 1.0 log units/s ramp velocity, the responses were mostly steps. In the stimulus velocity range of 0.066 to 1.0 log units/s, the primary responses were step-ramps. The amplitudes of the initial step movement in step-ramp responses were found to be proportional to stimulus ramp velocity. Thus the pupillary system appears either to convert the total energy in a time interval or the rate of change of intensity of the ramp stimulus into a step signal for driving the pupillary plant output. © 1988 Academic Press, Inc.

### INTRODUCTION

The pupillary response to light stimulus has been used extensively in the clinic to assess central nervous system function and in the laboratory to examine the fundamental behavior of the pupillary system. Static and dynamic anomalies of pupillary responses, such as those seen in Argyll Robertson's pupil, Adie's pupil, and Horner's syndrome, have been used to differentially diagnose central nervous system diseases (14, 16). Normal pupillary light responses parallel many functions found in visual psychophysics. For exam-

<sup>1</sup> The experiments were conducted at the Shanghai Institute of Physiology, China. The research reported here was partially supported by the National Science Foundation of China. Professor Hung would like to thank the Shanghai Institute of Physiology of the Chinese Academy of Sciences for their invitation to do cooperative research with Professor Sun. The authors thank W. Weng for his assistance in the experiments, H. Zhu and F. Yuen for helping with programming, and M. Zhang and X. Zhou for laboratory assistance.

ple, incremental thresholds were found to be proportional to background illumination (Weber's law); responses were proportional to the product of stimulus flash intensity and duration for durations less than 100 ms. (Bloch's law); and responses were equal to the time average of the intermittent stimuli above the flicker fusion frequency (Talbot's law) (18). A variety of stimuli have been used to probe the pupillary system in the study of its control properties. Different amplitude step inputs showed responses that were faster for on-step than off-step of light (8), and also revealed the pupillary escape (7) and capture (15) phenomena. Pulse inputs of opposite directions showed the dominance of the faster on-response relative to the off-response (3). Pulse stimuli at different pupil sizes showed a range nonlinearity with the highest responsiveness at midrange (9, 12, 13). Small-amplitude sinusoidal stimulation showed responses corresponding to a system with a third-order lag element with a cutoff frequency of 1 Hz. Other investigators used double-pulse (2) and band-limited noise (17, 6) to examine the nonlinear properties of the pupillary system. We describe here an investigation using different velocity ramp changes in light intensity. The majority of pupillary responses found were step-ramps, with the initial step amplitude proportional to the stimulus ramp velocity. The implication of the control process converting the ramp velocity to step output is discussed.

## METHODS

*Instrumentation.* Pupil area was measured dynamically using an infrared camera pupillometer system (PUP1). An infrared source was directed at the subject's eye to provide infrared reflected light to an infrared camera. The infrared television camera was mounted on a movable stage, which allowed forward and sideways horizontal movement. A screw ring allowed vertical camera adjustment. The degree of focus of the eye was monitored on a (625 lines) television monitor. The video signal was then processed by a pupillometer electronic module. This specially designed pupillometer circuit allowed the experimenter to control the size and location of a circular window surrounding the television image of the pupil. Thus, most of the lid, eyelash, and scleral reflection artifacts could be eliminated in this way. A trigger level adjustment was used to select the pupil as the dark central circular area for signal processing. The pupillometer output was a voltage signal proportional to pupil diameter.

The light stimulus system used continuous gradient neutral density wedges in which the density of the wedges changed logarithmically with linear change in wedge position. One wedge (Barr and Stroud, Ltd., WGN2) was mounted on the pen drive of an X-Y servo-controlled plotter. The weight of the wedge was counterbalanced by a dead weight via a pulley system. An-

other wedge, with oppositely directed density gradient complementing the first wedge, was fixed on the plotter itself. Thus at any particular relative displacement of the two wedges, the density throughout the intersected region was the same. The X-Y plotter was mounted on its side, so that actual movement of the first wedge was in the vertical direction. Thus, if one views a light stimulus through the fixed wedge, movement of the first wedge yielded a uniform change in luminance. The light source was a tungsten bulb driven by a constant current source circuit. A diffuser was placed in front of the light bulb to provide a uniform luminance light source at a fixed focal distance. A 10 diopter lens was positioned in front of the diffuser to give a collimated light output. A 2-cm<sup>2</sup> aperture stop gave a sharp delineation of the source boundary. This entire light source system was enclosed in a black case so that only the output light could be seen by the subject.

As the initial stimulus light level for all patterns of stimuli was 0.33 lux (7900 Trol), this level was used as the reference for calculation of values of log light intensity. A photometer (United Detector Technology, Inc., Model 11A Photometer/Radiometer) was used to calibrate both the static and dynamic light signal outputs.

A PDP 11/23 Plus computer was used to drive the light source and record the pupil responses. The computer A/D board limited the recorded response resolution to 0.03 mm<sup>2</sup>. A stimulus program allowed the experimenter to configure a variety of stimulus intensity time courses such as different velocity ramps or different amplitude steps. The computer was also used for editing the data, calculating velocity curves from amplitude records, and averaging the responses. The computer terminal could also be used as a graphics screen. Figures on the screen could be selected for plotting on an HP 7470A plotter.

*Subjects.* Subjects included two graduate students from the Shanghai Institute of Physiology and one of the authors (G.H.). They all gave prior consent to serve as subjects in the experiments. The subjects have normal oculomotor function and 20/20 vision based on standard optometric tests (except one, but whose refractive error was corrected in the stimulated eye).

*Experimental protocol.* The stimulating light source was presented to the subject's left eye as a collimated light source 2 cm in diameter. Thus the experiments were conducted under closed-loop conditions to approximate normal pupil operating conditions. Note, however, that because the pupillary system feedback loop has low gain, the responses would be nearly the same whether the system is open or closed-loop (Webster). The consensual pupil response in the right eye was monitored by the infrared TV camera. A partition was placed at the subject's midline so as to prevent vergence stimulation. The subject was instructed to view the diffusing source with well-marked contours and maintain constant clarity, thus keeping accom-

modation constant. After the right eye's image was focused on the TV screen and the pupillometer window and trigger level were adjusted to give a sharp image of the pupil, the experimental room light was turned off. The subject then adapted to the stimulus background light for at least 2 min. Initial pupil diameter was about 6.2 mm for all responses. Before each stimulus presentation, the computer sent three "beep" sounds to warn the subject. Two seconds later, the light stimulus was presented to the subject; the stimuli were presented in random order. Ramp stimulus velocity ranged from 0.02 to 8.0 log units/s. The maximum amplitude was 2 log units. Step stimuli ranged in amplitude from 0.4 to 2.0 log units. After the stimulus presentation, the computer emitted another "beep" sound to signal the end of the stimulus presentation record. The interstimulus interval varied from 5 to 20 s, depending on the light level reached in the previous presentation. This allowed the subject to adapt to the background light level and prepare for the next stimulation presentation. Record lengths were 10 s for steps and ramps above 0.25 log units/s, and 20 s for slower ramp stimuli. After about 20 presentations, the subject was allowed to rest 5 min outside the experimental room. Then the setup process was repeated, but generally this was much faster than the first setup.

*Data analysis.* The numerous data record curves were visually inspected on the computer graphics terminal to determine which of the four types of response patterns each response belonged to. For example, a step response could be seen in the amplitude trace as a fast downward movement followed by a flattening of the response. The corresponding velocity trace has the shape of a pulse. A ramp response was characterized by a constant slope movement in the amplitude trace and a flat velocity trace. Combination responses such as step-ramp and multiple-step were similarly analyzed. In this manner, responses were categorized as ramp, step-ramp, multiple-step, or step. Due to inherent noise in the pupillary system (11, 15), the responses to a particular velocity ramp (or step) stimulus and belonging to a particular type of response were averaged. In the response selection process, the beginning of the response was marked by a movable cursor on the computer graphics terminal and the delay was recorded but removed before averaging was performed. If the beginning was slightly ambiguous, a small range of the plot could be expanded both in time and amplitude to help mark the beginning of the response. Flattening or distinct change in curvature of the corresponding velocity curve also helped to define the beginning of the response movement. The average time delay for a particular set of responses was first adjusted for mechanical delay of the stimulus source, which was empirically determined to be 100 ms. The net delay was then added to the average of that set of responses. Individual and averaged curves and the corresponding velocity curves were plotted on the HP-7470A plotter.

TABLE I  
Frequency Distribution of Response Types in Percentage\*

Ramp velocity	R	SR	MS	S	N
8.0		39		61	38
4.0		36		64	22
1.0		58	5	37	19
0.66		78	9	13	23
0.50		74	11	15	38
0.33		72	23	5	44
0.25	14	60	12	14	35
0.20	5	95			38
0.13	26	70	4		51
0.066	17	83			42
0.020	77	23			22

\* Pupillary responses are categorized as ramp (R), step-ramp (SR), multiple-step (MS), and step (S). Stimulus ramp velocities (in log units/s) are shown in the left column. The total number of responses at each stimulus ramp velocity is listed in the right column. Values are the percentage of occurrence of each type of response for a particular stimulus ramp velocity.

## RESULTS

*Percentage of different types of responses.* Responses to various stimuli for the three subjects were similar. For clarity of presentation, data for only one subject (G.H.) are presented. Individual responses to a particular ramp velocity light stimulus are categorized as ramp, step-ramp, multiple-step, or step. The percentage of occurrence of different types of responses at each ramp velocity are tabulated in Table I. The total number of responses to each ramp velocity stimulus are tabulated in the right column. The center of the distribution of responses shifted from ramp to step-ramp, then to mainly steps as stimulus ramp velocity increased. This provided a general overview of the control strategy used by the pupillary system in response to ramps at different velocities. For ramp velocity below 0.066 log units/s, the responses are mainly ramps. In the stimulus ramp velocity range of 0.066 to 1.0 log units/s, the primary responses were step-ramps. Above 1.0 log units/s ramp velocity, the responses consisted mostly of steps.

*Representative curves: initial step amplitude vs stimulus velocity.* Using an arbitrary criterion of greater than 50% occurrence of a response type as representative of the response to a particular ramp velocity stimulus, the averaged curve for that response type was selected for display. The representative average curves at each stimulus ramp velocity are plotted as a composite plot in Fig. 1A; the corresponding velocity curves are plotted in Fig. 1B. The

# PUPILLARY RESPONSE TO LIGHT INTENSITY

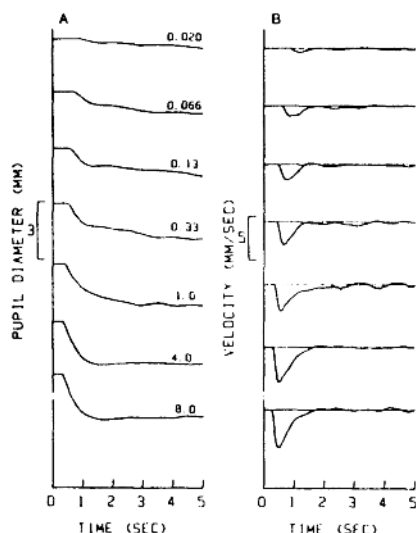


FIG. 1. A (left)—averaged representative curves for ramp stimuli ranging from 0.2 to 8.0 log units/s. Criterion for choice as representative curve was based on  $>50\%$  occurrence of a response type for a particular ramp velocity stimulus (see Table 1). Stimulus velocity (in log units/s) is shown next to the representative curve. Subject, G.H. B (right)—velocity curves corresponding to averaged curves of A.

progression of increased initial step amplitude in the responses to increasing stimulus ramp velocity can be seen in the curves in Fig. 1A. This is more explicitly plotted in Fig. 2.

*Step responses: comparison of amplitude-velocity characteristics.* In order to be certain that the initial step in step-ramp responses as well as secondary steps in multiple-step responses seen for ramp stimuli are the same as actual step responses, we conducted a series of step stimuli experiments at different stimulus amplitudes. Averaged step responses are shown in Fig. 3A; the corresponding velocity traces are shown in Fig. 3B. The amplitude-velocity relationship over a range of amplitudes and velocities represented the characteristic dynamic behavior of the pupillary system. The relationships for step movement in response to ramp stimuli and for actual step responses are shown in Fig. 4. As the data for initial step, multiple-step, and step responses to ramp stimuli were very close to those for actual step stimuli, all the step movements most likely came from the same control process. The amplitude-velocity relationship for saccades has been called the "main sequence"

HUNG AND SUN

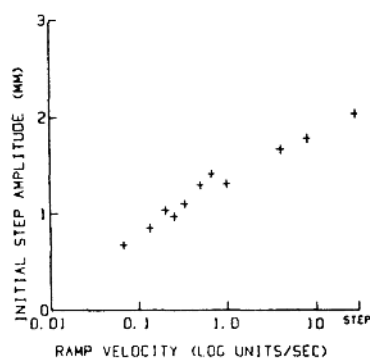


FIG. 2. Semilog plot of initial step amplitude vs ramp stimulus velocity derived from the averaged curves of Fig. 1A. Subject, G.H.

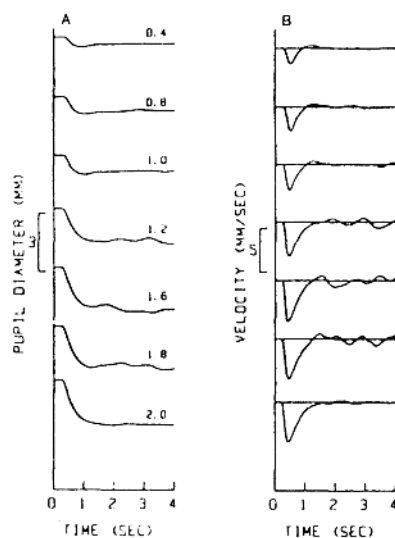


FIG. 3. A (left)—averaged responses to pure step stimuli ranging in amplitude from 0.4 to 2.0 log units. The stimulus step amplitude values are shown next to each curve. B (right)—velocity curves corresponding to the averaged response curves of A. Subject G.H.

# PUPILLARY RESPONSE TO LIGHT INTENSITY

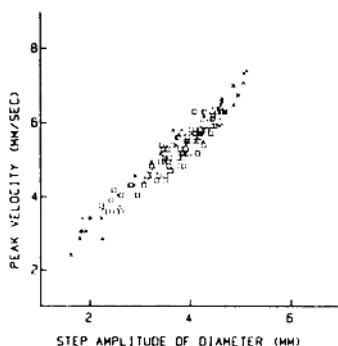


FIG. 4. Peak velocity vs initial step amplitude obtained from individual responses. This relationship may be called the "main sequence" for pupillary responses. It can be seen that this relationship is similar for responses to actual step stimuli (X), initial steps in step-ramp and multiple-step responses to ramp stimuli (□), step responses to ramp stimuli (Δ), and step following the initial step in multiple-step responses to ramp stimuli (○). Subject G.H.

for saccades (1) as it describes the dynamic relationship over a wide range of amplitudes and velocities. Thus, Fig. 4 may be called the "main sequence" for pupil light response.

## DISCUSSION

Pupillary responses to different light stimuli reveal the basic control properties of the pupillary system. The initial movement to ramp stimuli shows amplitude vs velocity characteristics which occur on the main sequence for actual pupillary step responses. This indicates that the initial part of the ramp response has the same dynamic characteristics as step responses and this may be called a step movement. The fact that the amplitude of the initial step movement is proportional to the stimulus ramp velocity suggests that either the rate of change of light intensity or the total amount of light accumulated during a time interval is converted to an effective neural step command signal. Perhaps part of this signal is due to a manifestation of Block's law, which states that responses are proportional to the stimulus energy within a 100-ms interval. Thus the faster the stimulus ramp velocity the greater the amount of energy that is accumulated in the 100-ms interval. However, this does not explain how the pupillary system would respond to the continued increase in stimulus light intensity of a ramp stimulus. Perhaps a rate-sensitive mechanism in the pupillary system converts the rate of change of light to an effective step signal which drives the pupillary plant. Evidence for a rate-sensitive



mechanism is found in the unidirectional rate sensitivity of the pupillary system proposed by Clynes (3), in which positive rate of change of light intensity produces a faster response than that for negative velocity stimulus.

The use of ramp stimuli adds to the repertoire of stimuli available to vision research scientists and clinicians for probing the pupillary system. The basic control properties of the pupil are revealed in the responses to ramp stimuli as discussed above. Additional experiments, for example, using different velocity ramp intensity inputs to the two eyes, may be used to determine whether the site for synthesis of the ramp information is before or after the motor controller. Clinically, pupillary responses to ramp stimuli may be a more sensitive indicator of pupillary system function than other stimuli which involve large changes in velocity, such as pulses and steps. Pupillary pathway abnormalities that involve gradual degradation of pupillary responsiveness may be more easily seen in ramp responses than in pulse or step responses, as the latter two tend to overwhelm the system and obscure the response deficit.

Ramp stimuli have also been used in other oculomotor systems and have revealed important control properties of those systems. Ramp changes in stimulus disparity resulted in vergence eye movement that show step-ramp and multiple-step responses (10, 5). The accuracy of the vergence step movements in matching the stimulus led Hung *et al.* (5) to suggest a preprogramming mechanism in the vergence eye movement system. Similar results were found for the accommodation system (4). Although the mechanism for generating step-ramp responses to ramp stimuli in these systems may be quite different from that in the pupillary system, it is interesting to note the parallel in response patterns to ramp stimuli for all three systems.

## REFERENCES

1. BAHILL, T., M. CLARK, AND L. STARK. 1975. The main sequence, a tool for studying human eye movements. *Math. Biosci.* 24: 191-204.
2. BAKER, F. 1963. Pupillary response to double-pulse stimuli: A study of nonlinearity in the human pupillary system. *J. Opt. Soc. Am.* 53: 1430-1436.
3. CLYNES, M. 1964. Unidirectional rate sensitivity as a biological function. *Ann. N.Y. Acad. Sci.* 92: 946-969, 98: 806-845, 112: 468-508.
4. HUNG, G., AND K. J. CIUFFREDA. Dual-mode behavior in the human accommodation system. Submitted for publication.
5. HUNG, G. K., J. L. SEMMLOW, AND K. J. CIUFFREDA. 1986. A dual-mode dynamic model of the vergence eye movement system. *IEEE Trans. Biomed. Eng.* 33: 1021-1028.
6. HUNG, G., AND L. STARK. 1979. Interpretation of kernels. III. Positive off-diagonal kernels as correlates of the dynamic process of pupillary escape. *Math. Biosci.* 46: 189-203.
7. LEVATIN, P. 1959. Pupillary escape in disease of the retina or optic nerve. *Arch. Ophthalmol.* 62: 768-779.
8. LOWENSTEIN, P., AND I. E. LOEWENFELD. 1969. Effect of various light stimuli. Page 274 in H. DAYSON, Ed., *The Eye*, Vol. 3. Academic Press, New York.