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RESEARCH NOTE

CONSENSUAL PUPILLARY LIGHT REFLEX IN THE PIGMENTED RAT

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Abstract—We measured the pupillary light reflex (PLR) in 5 pigmented, Long Evans rats (under urethan sedation) in three conditions: direct stimulation, consensual stimulation, and a control condition designed to measure the effects of stray light. The average constriction (maximal amplitude) produced by a Ganzfeld stimulus delivering 1.6 log quanta absorbed per rod per sec for a duration of 3 sec was measured to be 0.78 ± 0.07 mm for the direct PLR, 0.67 ± 0.06 mm for the consensual PLR, and 0.07 ± 0.029 mm for the control condition. We corrected the consensual measurement for each rat by subtracting the value of the control (stray-light induced) constriction. A comparison of the corrected consensual constriction to the direct constriction showed that, on average, the consensual constriction attained an amplitude of 78% of the direct constriction. Our findings contradict claims that the consensual pupillary light reflex is absent in rodents. Although our results are in agreement with findings showing bilateral projections of the retina to the pretectum (which subserves the pupillary light reflex) in the rat, the consensual-to-direct ratio we report is higher than might be expected from anatomical estimates of the overall proportion of uncrossed to crossed optic fibers in the rat.

Pupil Pupillary light reflex Rat

INTRODUCTION

In virtually all vertebrates the pupil of the eye constricts in response to increased illumination of the retina (Walls, 1967). In most mammals, and in some other animals, the pupil constricts in response to increased illumination of the retina not only of the same eye, but also to that of the other eye (Harris, 1904; Magoun and Ranson, 1935; Walls, 1967; Lowenstein and Loewenfeld, 1969). These pupillary responses, which are referred to as *direct* and *consensual*, respectively, comprise what is known as the pupillary light reflex (PLR).

Among vertebrates, there is a wide range in the size of the consensual PLR as compared to the direct PLR, ranging from 100% in man (ten Doesschate and Alpern, 1967), to zero in rabbits (Harris, 1904). The variation is thought to be related to the degree of binocularity and concomitantly, to the proportion of uncrossed fibers in the optic tract. Walls (1967) pointed out that this relationship is called into question

by two kinds of inconsistent observations: First, animals such as the owl exhibit a high degree of binocularity and no consensual PLR whatsoever. Second, animals such as the pigeon and certain rays exhibit little binocularity and no uncrossed optic fibers and yet exhibit a consensual PLR.

Among mammals, the extent of bilateral retinal projection appears to be directly related to the extent of binocularity and also to the magnitude of the consensual PLR. Even among mammals, however, the literature contains reports conflicting with this rule. These conflicts are most obvious in rodents and lagomorphs, for which some authors have claimed absence of the consensual PLR (Harris, 1904; Magoun and Ranson, 1935; Lowenstein and Loewenfeld, 1969), and others have presented evidence for its presence (Clarke and Ikeda, 1981, 1985; Inoue, 1980). Recent anatomical data show that the pretectal olivary nucleus (PO), which receives retinal signals for the PLR (Clarke and Ikeda, 1981; Trejo and Cicerone, 1984) and sends them to the nucleus of Edinger–Westphal (e.g. Itaya and van Hoesen, 1982; Campbell and

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Lieberman, 1985) receives a bilateral retinal projection in the rat (Scalia, 1972; Scalia and Arango, 1979), but not in the rabbit (Scalia, 1972; Klooster *et al.*, 1983). Based on these anatomical data, we should expect to find a consensual PLR in the rat but not in the rabbit.

In this report we show clear evidence for a consensual PLR in pigmented rats. We also measure, for the first time, the magnitude of the consensual PLR as compared to the direct PLR in this animal, under conditions wherein the influence of stray light can be carefully assessed.

METHODS

Five Long-Evans rats were used. Each rat was sedated with an i.p. injection of urethan solution (400 mg/Kg), placed in a stereotaxic stand, and fitted with a specially constructed light shield which allowed monocular light stimulation. The stimulus consisted of a circular spot of light projected for a duration of 1.5–3.0 sec onto the half-shell of a ping-pong ball that covered the visual field of the right eye. Intensity was controlled by a variable neutral density wedge.

The principle of operation of our pupilometer is similar to that described by Green and Maaseidvaag (1967). Pupil diameter was measured 60 times per sec during the period surrounding the presentation of each stimulus. A thin glass plate was placed at a 45° angle to the optic axis of the eye. An infrared light source and a lens, placed at a right angle to the optic axis of the eye and in optical alignment with this glass plate, were used to focus a pencil of infrared light in the plane of the pupil. An infrared-sensitive video camera (Panasonic WV-1350A with Newvicon tube) was placed directly in line with the optic axis of the eye and on the other side of the glass plate. Thus the pupil of the eye, filled with infrared light reflected from the retina, was viewed by the camera as a bright luminous image set against a dark background. The diameter of the pupil was linearly related to the number of video scan lines exceeding a threshold voltage in the following way. A circuit was constructed to produce one pulse for each video scan line that exceeded a threshold voltage. These pulses were integrated, low-pass filtered, and passed to a chart recorder. Calibration was performed by measuring the output for circular targets of known sizes. The camera signal was also

displayed on a video monitor to provide a visual check on the pupilometer.

The response of the pupil to increasing intensities of light stimulation was measured under three conditions. The first was a control series to check for possible effects of scattered light. The right eye, which received the light stimuli, was covered with an opaque contact lens, and the diameter of the left eye was recorded. The second series was made without the contact lens. The right eye was stimulated while the diameter of the left eye was recorded, providing a measure of the consensual PLR. In the third series the camera recorded the diameter of the right eye (through a small hole cut in the ping-pong ball) as it was stimulated, providing a measure of the direct PLR. Based on a method that we have previously described (Trejo and Cicerone, 1982), we estimated that the most intense stimulus produced 1.6 log quanta absorbed per rod per second in the rat's eye.

RESULTS

Representative results obtained from one animal in the three conditions described above are shown in Fig. 1. The control condition shows little or no constriction of the left pupil in response to the light stimulus presented to the occluded right eye. This shows that the amount of light scattered to the left eye while stimulating the right eye was insignificant. The results in the other two conditions show clearly that the consensual PLR is present and that its time course is nearly identical to that of the direct PLR.

To estimate the magnitude of the consensual PLR, as compared to the direct PLR, we measured the maximum constriction (diameter at stimulus onset minus diameter at maximal constriction) of the pupil produced by a light delivering 1.6 log quanta per rod per second for a duration of 3 sec. Table 1 shows the amplitude of the control, consensual, and direct conditions for the five rats we examined.

Each of the rats showed a consensual PLR in the consensual test condition and little or no constriction of the pupil in the control condition. The average direct constriction was 0.78 ± 0.07 (SEM) mm and the average consensual constriction was 0.67 ± 0.06 (SEM) mm to this stimulus. Assuming that the constriction measured in the left eye for the control condition reflects the influence of a small amount of stray light, we corrected our consensual

Fig. 1. Shown here are responses of the pupil of one rat in control (top), consensual (middle), and direct (bottom) conditions. The lowest trace shows light onset and offset. In this example the stimulus duration was 3 sec. Stimulus intensity was increased successively in 0.2 log unit steps, with the brightest stimulus producing about 1.6 log quanta absorbed per rod per sec.

measurements by subtracting the control constriction, then calculated the ratio of (corrected) consensual to direct constriction. The average ratio of 0.78 ± 0.06 (SEM) was significantly greater than zero ($t_4 = 13.91$, $P < 0.001$).

Taking into account the average maximum constriction, and the intensity (1.6 log quanta per rod per sec) and duration (3 sec) of the stimulus, we estimate the gain of the direct and consensual PLRs as 0.0065 mm per quantum absorbed and 0.0056 mm per quantum absorbed, respectively, for our stimulus conditions. [Stark (1968) has shown that the gain of the PLR may vary with stimulus parameters.]

DISCUSSION

The results of this study show that the rat has a strong consensual PLR. These findings contradict earlier generalizations about the absence of the consensual PLR in rodents (Harris, 1904; Magoun and Ranson, 1935; Lowenstein and Loewenfeld, 1969). The source of these early

generalizations is difficult to identify. Our search of the literature disclosed no quantitative measures of the consensual PLR in rats before 1981 (Clarke and Ikeda, 1981).

One possible reason for the discrepancy between our results and earlier reports on the consensual PLR in rodents could be the predominant use of albino rats in early studies. As compared to pigmented rats, albino rats have comparable numbers of optic fibers (Sugimoto *et al.*, 1984) but have fewer ipsilateral retinal projections (Lund, 1965; Scalia and Arango, 1979; Campbell and Lieberman, 1985). This could lead to a weaker consensual PLR in albino rats as compared to pigmented rats. Another possible source of confusion about the consensual PLR in rodents may have been based on the incorrect categorization of rats as animals lacking an uncrossed retinopretectal projection (Harris, 1904; Magoun and Ranson, 1935; Lowenstein and Loewenfeld, 1969).

Our results have some bearing on the idea that the consensual PLR depends on the relative

Table 1. Magnitude of the consensual pupillary light reflex in pigmented rats

Animal Number	Control	Maximum constriction (mm) Consensual	Direct	Ratio of corrected consensual PLR to direct PLR
1	0.14	0.70	0.97	0.58
2	0.14	0.64	0.65	0.77
3	0.07	0.68	0.70	0.87
4	0.02	0.86	0.94	0.89
5	0.00	0.48	0.62	0.77
Mean	0.07	0.67	0.78	0.78
SEM	0.03	0.06	0.07	0.06

proportion of uncrossed to crossed fibers in the optic tract. Anatomists have estimated that the uncrossed to crossed fiber ratio in the rat is between 0.10 and 0.20 (Hayhow *et al.*, 1962; Walls, 1967), giving a ratio of uncrossed to crossed fibers of at most one-fourth and perhaps as little as one-ninth. Although it is possible that the published uncrossed to crossed fiber ratios are unduly low because of the predominant use of albino rats in early studies, our average value of 0.78 for the consensual to direct PLR ratio in the pigmented rat is over three times higher than one might expect solely from these anatomical ratios. (For comparison, in man, both the uncrossed to crossed fiber ratio and the consensual to direct PLR ratio are 1.0.)

If we had attained a limiting ceiling on the direct PLR, then the consensual response could appear proportionately large merely as an artifact. Since the amplitude of the direct PLR we measure is less than half the maximal amplitude which can be obtained in the rat (Trejo and Cicerone, 1982), this concern can be discounted.

There are at least three ways to reconcile our consensual to direct PLR ratio with the low uncrossed to crossed fiber ratio in the rat. The first possibility is that the smaller uncrossed projection controls a large share of the neurons in either the pretectum or in the Edinger-Westphal nucleus, each of which is involved in the PLR. This could occur, for example, if the projection from the pretectum to the contralateral Edinger-Westphal nucleus is smaller than the ipsilateral projection. Just the opposite appears to be true, however, in that the ipsilateral projection from the pretectal olivary nucleus to the nucleus of Edinger-Westphal has been difficult to identify, whereas the contralateral projection is clear (Itaya and van Hoesen, 1982; Campbell and Lieberman, 1985). The second possibility is that the uncrossed to crossed ratio of *pupilloconstrictor* fibers is greater than that for all the fibers in the optic tract. This idea appears to have some merit since both the ipsilateral and contralateral projections to the pretectal olivary nucleus are distinct in the rat (Scalia, 1972; Scalia and Arango, 1979; Campbell and Lieberman, 1985). The third possibility is that neural signals for the PLR are transmitted between the hemispheres at the level of the pretectum. Although the advantage of such a pathway is unclear, it remains as a possibility, since connections between the right and left pretectal areas have been shown, for example, in the cat (Berman, 1977).

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