If a pair of female CA and a 0 day ova-
ry were implanted into the males, the pattern of JH synthesis (Fig. 1) resembled that of normal females and was identical in timing to that of females with denervated CA (Fig. 3) (7). The final de-
cline in the cycle of activity of implanted CA was achieved by implanting an ova-
ry, and this occurred in concert with the completion of oocyte maturation. This inhibition of JH synthesis by the implanted ovary must occur by way of a humoral pathway. Figure 4 shows ovaries implanted into males with and without CA. Ovaries im-
planted into males in the absence of female CA showed no growth. Even after 10 days the basal oocytes remained in the previtellogenic stage as at implantation (0.65 ± 0.001 mm in length) (Fig. 2). Hence the production of JH by male CA was insufficient for oocyte development. However, in the presence of female CA the oocytes increased in length to 1.40 ± 0.06 mm by day 5 and complete chorion deposition occurred between days 7 and 8. These observations indicate that the event leading to the decline in rates of JH synthesis after day 7 is the completion of vitellogenesis as sig-
naled by chorion formation.

In D. punctata, an ovary usually con-
tains six ovarioles (13). In ovaries im-
planted into males, only a fraction pro-
duced mature oocytes (Fig. 2). To com-
pare the relative suitability of male and female environments for ovarian growth, oocyte lengths were measured in ovaries implanted into females ovariectomized and implanted on day 0 with one ovary and a pair of CA from day 0 females. On days 5 and 7 after the operation, the mean lengths of the oocytes were greater than those of ovaries grown in males; and more oocytes have developed (Fig. 2). In addition, the vitellin content was greater by a factor of 10 (9). Hence the male environment, although able to sup-
port oocyte growth in the presence of fe-
male CA, did not do so to the same ex-
tent as that which occurs in normal fe-
males.

The presence of ecysteroids in ma-
terial cockroach ovaries and hemolymph (14) suggests that ecysteroids may par-
ticipate in regulating the rates of JH syn-
thesis by the CA. To test this hypothesis, CA from day 0 females were implanted into day 0 males and males injected on days 6 and 7 with doses of ecysterone (15). CA were assayed for JH synthesis on day 8. The rates of JH synthesis as a function of the total dose (two equal in-
jections) of ecysterone are shown in Fig. 3. These data show that the inhibi-

Eveblinks and Visual Suppression

Abstract. A technique for bypassing the eyelids permits equivalent visual stimulation of the retina before, during, or after a blink. Sensitivity to these stimuli decreases during voluntary blinks. This indicates that the source of the deficit is neural rather than optical. Such a visual loss may help to explain the common experience that most blinks go unnoticed.

Under normal conditions of vision, eyeblinks occur every few seconds (1-3), each blink producing an almost total inter-
ruption of light and pattern reaching the eye. It is a surprising feature of visual perception that the interruption of vision typically goes unnoticed, and the sub-
jective visual world remains continuous and stable. The effect is even more sur-
prising when one considers the magni-
tude and duration of this interruption. Consider the voluntary blink dia-
gramed in Fig. 1A. As the upper lid drops over the pupil, it severely attenu-
ates the light reaching the eye (4) and wipes out nearly all visual information in the form of contour and contrast. The time during which the pupil is completely obscured is relatively long: 110 msec in the example shown (5, 6). Yet the blink is scarcely noticed. By contrast, in the absence of a blink, a much briefer inter-
ruption of room lights has a pronounced visual effect (3, 7).

The observation that the perceptual ef-
fect of a blink is small with respect to the

References and Notes

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6. B. Stay and S. S. Tobe, Gen. Comp. Endo-
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8. CA were inserted through an incision in the neck; ovaries were injected into the abdomen. Animals were anesthetized with cold and treated postoperatively with a few crystals of strep-
tomycin.
10. S. S. Tobe, A. Musters, B. Stay, Physiol. Ento-
11. J. H. JH is methyl (2E,6E)(10F)-10,11-epoxy-
3,7,11-trimethyl-2,6-dodecadienoate. For this in vitro radiochemical assay, individual pairs of CA were incubated for 3 hours at 28°C in media-
t (190 ml saline, with glutamine, Hapes buffer, 25 m M, pH 7.2; Glucose, plus tigocoll (20 mg/ml) to which [methyl-3H]-methionine (Amersham/Searle, final specific radioactivity 35 to 39 mCi/mmol) was added. (see (6) and S. S. Tobe and G. E. Pratt, J. Exp. Biol. 62, 611 (1973)).
15. Ecysterone from Sigma was injected in 5 
ml of medium containing 5 percent ethanol; controls were injected with ethanol medium alone.
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version of ecystene to ecysterone.
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19. Supported by USPHS grant AI 15230 and the Natural Sciences and Engineering Research Council of Canada.
October 1979
changes that it actually produces on the retina suggests that the brain generates an inhibitory signal that accompanies the blink and diminishes the effect of the blink on the visual system. Such a neural inhibition has already been shown in the case of saccadic suppression, the reduction of visual sensitivity that accompanies saccadic eye movements (8).

If a neural inhibitory mechanism operates during blinks, its properties can be assessed by measuring visual sensitivity under special experimental conditions such that closing the eyes has no effect on the amount of light reaching the retina. Accordingly, we have bypassed the normal optical path through the pupil and optic media. We placed a fiber-optic bundle against the roof of the mouth and used it to deliver light to a region directly below the right eye, stimulating the retina through the back of the eyeball. Opaque goggles eliminated all other sources of light, and the dark-adapted subject saw a diffuse cloud of light located over a large portion of the upper temporal visual field, that is, the lower nasal retina.

The stimulus event was a brief decrement of the otherwise steady, diffuse light. On a given trial, the decrement occurred at one of a number of possible times before, during, or after a voluntary blink. To detect the blink, we placed standard skin electrodes above and below the eye. A large electromyographic response wave appeared between these electrodes during the closing and opening of the lids. We call this wave the “electroblepharogram” (EBG) (Fig. 1B). The EBG was used to monitor blinks and was differentiated to activate trigger and delay circuits to present the stimulus decrement at preset times during or after a blink. To stimulate the retina just before a blink, the decrement was presented manually by the experimenter just after a signal to the subject to execute the blink. The exact time interval between the stimulus decrement and the blink onset was read from a digital clock. A sufficient number of intervals were sampled to analyze temporal changes in visual sensitivity associated with the blink.

Our experiments were conducted with two highly practiced adult male subjects, according to a constant stimulus method and a two-alternative forced-choice response paradigm; on each trial, the subject executed two voluntary blinks and judged which one was accompanied by the stimulus decrement. Across trials, the order of presentation was randomized, as were the principal stimulus variables: amplitude of decrement and time of decrement in relation to the onset of the blink. Such procedures are characterized by lack of bias.

For each time of occurrence of the decrement in relation to blink onset, the experiment yielded a curve relating the proportion of stimuli detected to the amplitude of the decrement. We corrected these proportions for chance success (50 percent), transformed them to a normal probability scale, and performed linear regression analyses to arrive at a threshold. We defined threshold as the particular size of decrement that would yield 75 percent correct detection (that is, halfway between chance and complete success).

Figure 2 shows log sensitivity (the log of the reciprocal of the threshold) for each of the designated times of occurrence of the decrement in relation to blink onset. During blinks there was a pronounced loss of visual sensitivity. For both subjects, the loss began before blink onset and reached a maximum before the lid covered the pupil. That maximum was about 0.4 log unit for subject L.A.R. and 0.5 or 0.7 for subject W.J.D., relative to the sensitivity of the steady eye (closed or open). Sensitivity did not fully recover until about 200 msec after blink onset.

The magnitude and time course of visual suppression during blinks are in close agreement with comparable measurements for voluntary saccades (8). Thus, the question arises whether saccades might be so closely associated with blinks that blink suppression can be explained by saccadic suppression. We have conducted preliminary observations of eye movements during blinks (9, 10), with results in substantial agreement with those of Lawson (6), Ginsborg and Maurice (10), and Doane (11). They show no evidence of saccades, and no evidence of Bell’s phenomenon (the upward rotation of the eyes when closed as in sleep). They support Doane’s conclusion that a small inward rotation of the globe results from a lateral motion of the lower lid, and a small downward rotation results from the pressure of the upper lid. They also show that the extent and direction of these small movements depend on the primary position of the eyes in the head as the blink occurs. Thus, these eye movements are not of the type that could account for visual suppression during blinks.

A remaining question concerns the generality of blink suppression to spontaneous, and perhaps also to reflex, blinks, in addition to voluntary ones (12-14).
Sparing of the Brain in Neonatal Undernutrition: Amino Acid Transport and Incorporation into Brain and Muscle

Abstract. Rates of tyrosine and lysine transport and incorporation into protein were measured in control and undernourished weanling rats. Undernutrition was induced by feeding lactating dams a low protein diet (12 percent casein) from birth to day 21. At weaning, body and brain weights of undernourished rats were 50 percent and 88 percent, respectively, of control values. Lysine and tyrosine transport rates into skeletal muscle were reduced by over 75 percent, more than twice the reduction seen in brain. Rates of amino acid incorporation into muscle protein were reduced by approximately 50 percent; the change in rate of incorporation into brain protein was not statistically significant. These data indicate that, in spite of marked retardation of amino acid transport into brain, the brain seems fully capable of maintaining normal rates of protein synthesis.

Nutritional deprivation during critical periods of development in early life has profound and persistent effects on the body and brain (1). The fact that the growth impairment of the brain is smaller than that of the body as a whole has led to the concept of brain “sparing” (2). We have studied the mechanisms by which the brain is spared by measuring the transport of two amino acids, tyrosine and lysine, into brain and skeletal muscle and their incorporation into tissue protein. Both activities were sharply reduced in skeletal muscle of undernourished animals. In brain, the reduction of amino acid transport was about half that seen in muscle, yet the reduction in incorporation into brain protein was not statistically significant.

Female sperm-positive rats (3) were caged individually and housed in a temperature-controlled room with a 12 hour light and 12 hour dark (0900 to 2100 hours) diurnal cycle. The animals were fed a normal protein diet containing 25 percent casein (4) throughout gestation. At birth, litter size was made uniform by randomly distributing the rat pups among the lactating females, eight per litter. During lactation, experimental mothers were fed a low protein diet containing 12 percent casein (4), whereas control mothers continued on the 25 percent casein diet. The low protein intake reduces the volume of milk without altering its composition (5). Thus, throughout lactation the experimental pups were subjected to undernutrition by receiving suboptimal amounts of a diet of normal composition; during the third week of life, we subjected the pups to a deprivation of both voluntary and involuntary eye movements.

**References and Notes**

1. Blinking is a temporary closure of both eyes that is under both voluntary and involuntary control. It has been categorized into three types: (i) voluntary blinks, which can be executed on external or internal command; (ii) spontaneous or periodic blinks, which are involuntary, centrally programmed, and which constitute most of normal blinking; and (iii) reflex blinks, which are produced involuntarily in response to peripheral stimulation, such as a foreign body approaching or touching the eye (2, 3).


4. We have assessed the light attenuation due to the eyelids by measuring absolute visual thresholds to 0.2-second flashes in fully dark-adapted eyes. Using full-field (Ganzfeld) conditions, the thresholds for eyes closed were 1.8 to 2.0 log units higher than for eyes open.

5. Investigators have correctly distinguished between blink duration, which is typically reported to be 300 to 400 msec, and blackout duration, the time during which the upper lid covers the pupil, which is reported to range from 40 to 200 msec [R. W. Lawson, *Nature (London)* 162, 531 (1948); A. T. Slater-Hammel, *Res. Q. Am. Assn. Physiol. Educ. Recreat.* 24, 363 (1953)].


7. We have confirmed this observation and have found that subjects consistently match the visual effect of a blink of a much briefer and shallower decremental pulse in the illumination of a visual field.


9. Our observations involved two techniques. First, we used a double Purkinje image eye tracker to measure the time during which the pup was actually uncovered during a blink and to indicate whether any movements occurred before the lids cut off the input to the tracker and after the lids reopened (T. N. Cornsweet and H. D. Crane, *J. Opt. Soc. Am.* 63, 921 (1973)). A second technique, modeled after that of Ginsborg and Maurice (10), involved subjective observations of a small spot of light which could be made to move either horizontally or vertically across a large field. When an observer succeeded in blinking just as the spot crossed the fovea, the trace of the spot appeared to be deflected, and the subjective deflection could be used to estimate the speed, duration, and extent of the eye movement produced it. We estimate that just before a normal blink there is an inward and downward motion of the eyes of about 0.3 deg arc.


12. In two subjects, neither the form of the blink as reflected in the EOG, nor the mean duration of pupil covering as measured on the eye tracker (9) was markedly different for voluntary and spontaneous blinks.

13. These experiments were conducted at Brown University, supported by grant EY 00744 from the National Eye Institute. We thank K. D. White, W. J. Donovan, K. Fulld, and J. Volk- man for their contributions. Preliminary re- ports of portions of this research were presented at the 1978 meeting of the Optical Society of America and at the 1979 meeting of the Association for Research in Vision and Ophthalmology.

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**Table 1. Body and brain weights of control and undernourished rats.** The data are expressed as means ± standard error (N = 30).

<table>
<thead>
<tr>
<th>Tissue</th>
<th>Control</th>
<th>Experimental</th>
<th>Percentage decrease*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td>50.6 ± 1.13</td>
<td>30.4 ± 0.93</td>
<td>49.8</td>
</tr>
<tr>
<td>Whole brain</td>
<td>1.438 ± 0.0166</td>
<td>1.267 ± 0.0117</td>
<td>11.9</td>
</tr>
<tr>
<td>Forebrain</td>
<td>1.128 ± 0.0112</td>
<td>1.009 ± 0.0105</td>
<td>10.5</td>
</tr>
<tr>
<td>Brainstem</td>
<td>0.128 ± 0.0049</td>
<td>0.115 ± 0.0030</td>
<td>10.3</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>0.181 ± 0.0053</td>
<td>0.142 ± 0.0042</td>
<td>21.5</td>
</tr>
</tbody>
</table>

*P < .001, one-tailed t-test.
Editor's Summary

Eyeblinks and visual suppression
FC Volkmann, LA Riggs and RK Moore (February 22, 1980)
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