with Rayleigh's z test and clustering about the home direction was tested with the V test [test statistic = u]. In Table 1, Watson's $U^2_{n,m}$ nonparametric two-sample test has been used to compare estimates made under different conditions of cloud cover, distance, and familiarity.

In Fig. 2, the Manchester data are grouped to show results for releases in four compass quadrants relative to the home site. The results of the Barnard Castle experiment are shown in Fig. 3; humans have an ability to recognize homeward direction even in the absence of visual cues.

The subjects themselves could give no convincing description of the mechanism they used during the experiment. A few claimed to have followed the outward route for a short distance (approximately 2 to 5 km) on a mental map of the area, but then to have become lost. On sunny days, some claimed also to have used the sun as a reference point by detecting the heat of the sun on the face. Most, however, were surprised when their guess was so near the correct direction.

Evidence can be presented that neither the use of solar cues nor map following was the primary method of orientation in these experiments. The dogleg technique prevents subjects from extrapolating from the direction of the first part of the route with which they may be familiar. Moreover, there was no indication of decreased accuracy of orientation with distance over the range tested (Table 1). Finally, individuals that were familiar with the release site (that is, upon removal of the blindfold claimed to have visited the area before and could name the location to within 2 km) were not more accurate when blindfolded than individuals unfamiliar with the release site (Table 1). As far as the use of the heat of the sun on the face during the outward journey is concerned, homeward orientation occurred both when displacement was under total overcast throughout and when it occurred under more or less continuous sunshine (Table 1).

The second Barnard Castle experiment examined in a preliminary way the possibility that goal orientation in humans may be influenced by perturbations in the magnetic field through the head. Under totally overcast conditions, 31 subjects were taken through a second dogleg displacement of 16 km to release points 5 km southwest (238°) and 5 km southeast (125°) of the home site. Subjects were not allowed to remove their blindfolds after making their estimates at the first site and were given no indication of the correct position. The roundabout maneuver was excluded from this journey, but the first 2 km were extremely tortuous, involving many twists and turns through the town center.

Before the experiment began, 15 experimental subjects placed at the backs of their heads bar magnets held in position by the elastic of their blindfolds. Each of the remaining 16 controls placed brass bars of dimensions 7.5 by 1.5 by 0.5 cm (similar to the real magnets) in the same position. All subjects thought they were wearing real magnets.

The results of this experiment are presented in Fig. 4. At both sites, the estimates made by the control subjects wearing brass bars were significantly clustered about the home direction (as evaluated by V tests). At neither site, however, was this true for the experimental subjects wearing magnets. This result suggests some influence of the bar magnets on orientation. Full evaluation is impossible, however, as (i) the bar magnets were not of uniform strength, having pole strengths that varied from about 140 to 300 G; (ii) the position and orientation of the magnets on the head could not be standardized, for, although positioned initially with the north pole up, they tended to twist around and slip from the elastic as the journey progressed; and (iii) seating could not be arranged to prevent control subjects from being influenced by the magnets worn by experimental subjects and at the same time to prevent interaction between the fields generated by adjacent experimental subjects. Despite these shortcomings in experimental design, the results were sufficient to encourage the design of an experimental series using Helmholtz coils to test the possible influence of the magnetic field on the goal orientation of blindfold humans (*3*).

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4. I thank all those students who cooperated as subjects in these experiments and Yorkshire Television and D. Bellamy for organizing and financing the Barnard Castle experiments. Comments by the late Professor William T. Keeton and by C. Walcott on an early draft of this work, as well as by anonymous reviewers, improved this report considerably.

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Medial Nucleus of the Amygdala Mediates Chemosensory Control of Male Hamster Sexual Behavior

Abstract. *Bilateral lesions restricted to the medial nucleus of the amygdala eliminate mating behavior in the male hamster and severely diminish the male's sniffing and licking investigation of the female hamster's anogenital region. The results suggest that olfactory and vomeronasal sensory information critical to male mating behavior is processed in the medial nucleus, which is an androgen-binding brain area. Thus the medial nucleus may act as a relay through which chemosensory information influences activity in the medial preoptic-anterior hypothalamic junction and the bed nucleus of the stria terminalis, areas important in the mediation of male sexual behavior.*

The amygdala has long been viewed as a modulator of affective behavior and neuroendocrine function (*1*). It has been suggested, for example, that the amygdala provides an appropriate "affective bias" in response to those conspecific and environmental stimuli, and endogenous hormonal cues, which govern normal social interactions (*2*). This hypothesis is based in part on well-established observations that extensive amygdaloid lesions dramatically alter male sexual behavior in human and other vertebrates (*3*). Neuroanatomical studies, however, have emphasized major differences in the afferent and efferent connections of individual nuclei in the amygdala (*4, 5, 5a*), and consequently suggest the need for a more detailed analysis of amygdaloid function. We now present evidence, from the male Syrian hamster, that the integrity of one particular nucleus of the amygdala, the medial nucleus, is necessary for normal male mating behavior to occur. On the basis of our results and evidence from neuroanatomical and hormone uptake studies, we suggest that the medial nucleus in this species may act as an androgen-sensitive site of integration of chemosensory information, which influences preoptic area activity and the display of male mating behavior.

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Normal mating behavior in male hamsters depends on odor cues provided by a receptive female (*6*). Attraction to the female's odor cues, particularly the female hamster's vaginal secretion, is mediated by both olfactory receptor input to the main olfactory bulb and vomeronasal organ input to the accessory olfactory bulb (*7*). Olfactory and vomeronasal inputs seem to have complementary control of male mating behavior (*8*), even though these two systems are anatomically segregated from the levels of their peripheral receptors to the termination of their second-order neurons within the central nervous system (*9, 10*). However, both main and accessory olfactory bulbs project via separate fiber bundles within the lateral olfactory tract to the corticomedial amygdala (CMA), where they terminate in separate but adjacent nuclei (*10*). The contiguity of these olfactory and vomeronasal terminal fields led us to hypothesize that the CMA may process chemosensory information critical to male hamster mating behavior. This hypothesis is consistent with observations that the mating behavior of male hamsters is abolished by bilateral transections of the caudal part of the lateral olfactory tract, which spare olfactory input to the rostral piriform cortex and olfactory tubercle but sever fibers to the CMA and other caudal structures (*11*). Furthermore, lesions of the CMA produce deficits in the mating behavior of male rats (*12*).

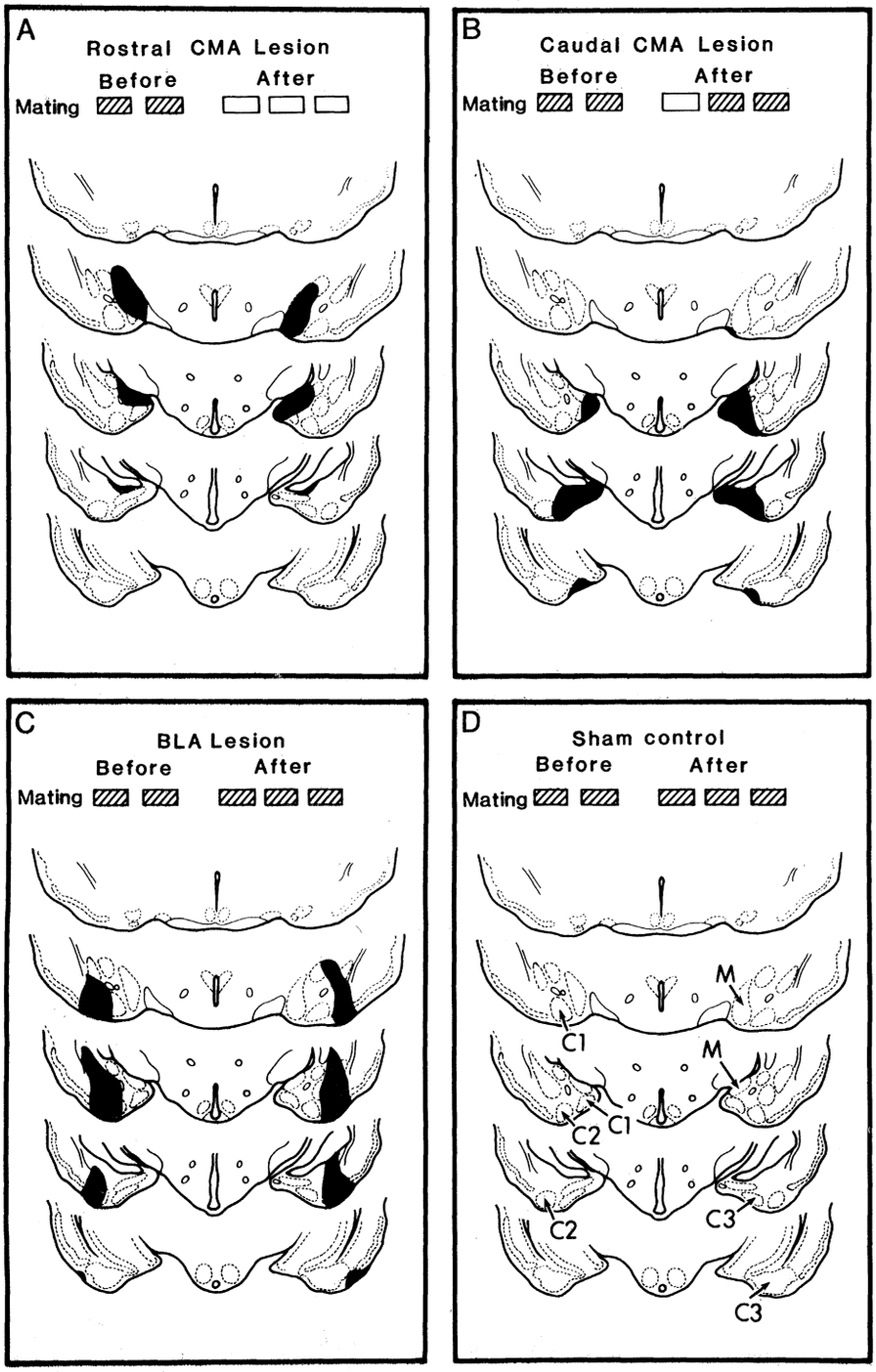

Fig. 1. Histological and behavioral records (before and after surgery) of male hamsters with rostral or caudal CMA, BLA, and sham lesions. The size and location of each lesion is shown in black on coronal sections through the amygdala from rostral (top) to caudal (bottom). Hatching: normal mating behavior; no hatching: no mounts, intromissions, or ejaculations. Abbreviations: *M*, medial nucleus; *C1*, anterior cortical nucleus; *C2*, posterolateral cortical nucleus; and *C3*, posteromedial cortical nucleus.

To test our hypothesis, we observed the mating behavior of male hamsters before and after small bilateral lesions were placed in the CMA or the basolateral amygdala (BLA) or before and after sham operations (*13*). Mating behavior was observed after introducing a behaviorally receptive female into a clean Plexiglas cage containing the experimental male hamster (*14*). The latency and frequency of all mounts, intromissions, and ejaculations displayed by the male hamster were recorded, as well as the duration of the male's sniffing and licking of the female's head, flanks, and anogenital region. Observations continued for 10 minutes, or until the male had ejaculated twice. Experimental males were screened for normal mating behavior, tested twice over a period of 1 week before surgery and then three times over a period of 3 weeks afterward.

Male hamsters with CMA lesions (N = 16) displayed obvious impairments in copulatory behavior. Six displayed no copulatory behavior, that is, severe deficits, during any postoperative test; eight males showed moderate deficits, in which mating was absent or impaired in at least one of three postoperative tests; and two males showed no behavioral changes. Four of the males with severe mating deficits were tested for 3 months after surgery and never resumed any copulatory behavior. In contrast, male hamsters with bilateral BLA lesions (N = 6) and control males with sham lesions (N = 8) mated normally during all postoperative tests.

Histological analysis of coronal sections (50 μm thick, stained with cresyl violet) revealed considerable variability in the rostral-caudal placement of the CMA lesions. Quantification of the placement and extent of these lesions through the use of a computerized image analysis system (*15*) demonstrated that

the severity of the mating deficit was closely correlated with damage to the rostrally located medial nucleus of the amygdala (Spearman rank correlation, $\rho = .61, P < .01$, one-tailed test) (Fig. 1) (*16*), which receives vomeronasal input from the accessory olfactory bulb. The rostrally situated anterior cortical nucleus, which receives olfactory input from the main olfactory bulb, was also damaged in some males, but this damage was not significantly correlated with the severity of the mating behavior deficit. Male hamsters with caudally placed CMA lesions that damaged the posterolateral and posteromedial cortical nuclei showed little or no mating behavior deficits postoperatively. The BLA lesions, like CMA lesions, varied with respect to the rostral-caudal extent of the area damaged, but all males with these lesions continued to mate normally regardless of the placement of the lesion.

Male hamsters with bilateral CMA lesions also showed a significant decrease in their rate of investigation of the female's anogenital region during postoperative mating tests [Wilcoxon matched-pairs signed-ranks test, $T(16) = 1, P < .01$), although their rate of investigation of the female's head or flank regions did not change from preoperative rates (*17*). These deficits in anogenital investigation were also closely correlated with the amount of damage to the medial nucleus of the amygdala ($\rho = .76, P < .01$) (*18*). Male hamsters with rostral CMA lesions, which destroyed more than 60 percent of the medial nucleus bilaterally ($N = 8$), showed a postoperative decrease of 85 percent in their rate of anogenital investigation [$T(8) = 0, P < .01$] (Fig. 2). After caudal CMA lesions that damaged less than 32 percent of the medial nucleus bilaterally ($N = 8$), males showed a lesser but still significant decrease of 45 percent in their rate of anogenital investigation [$T(8) = 1, P < .02$], even though some of these males continued to mate normally during postoperative tests. In contrast, males with sham operations ($N = 8$) and males with BLA lesions ($N = 6$) showed no change in their rate of anogenital investigation.

These results suggest that the medial nucleus is an important site for processing olfactory and vomeronasal sensory stimuli controlling the male's investigatory and copulatory behaviors (*19*). An alternate explanation, however, is that lesions which destroyed the rostral part of the medial nucleus in the amygdala also interrupted olfactory or vomeronasal input to more caudally placed nuclei in the amygdala and that the effective disruption of chemosensory input to the entire CMA produced the observed mating behavior deficits. To investigate this possibility, we injected [^{3}H]proline or [^{3}H]leucine bilaterally into the main and accessory olfactory bulbs of six male hamsters in which bilateral lesions had previously been placed in the medial nucleus (*20*). Autoradiographic analyses of these brains showed that if the lesion of the medial nucleus did not extend to the ventral surface of the brain, vomeronasal input to the posteromedial cortical nucleus and olfactory inputs to the anterior and posterolateral cortical nuclei were spared. If the lesion did extend to the ventral surface, vomeronasal input to the posteromedial cortical nucleus was interrupted. Because we have observed several male hamsters with severe mating deficits in which the medial nucleus lesion did not extend to the ventral surface of the brain (for example, see the left lesion Fig. 1A), we conclude that the severe mating deficits seen after rostral CMA lesions are due primarily to destruction of the medial nucleus.

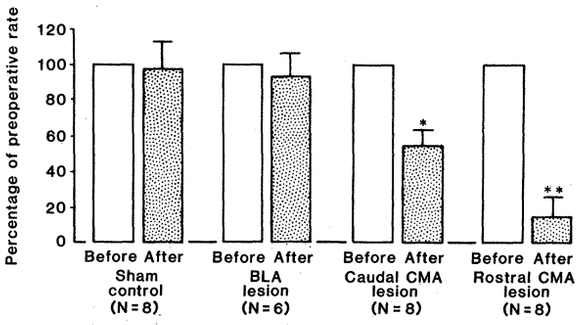

Fig. 2. Postoperative deficits in anogenital investigation by male hamsters during mating behavior tests. Wilcoxon matched-pairs signed-ranks tests were used to compare rates of anogenital investigation before and after the operations within each lesion group. *$T(8) = 1, P < .02$; **$T(8) = 0, P < .01$.

To eliminate the possibility that the lesion effects were indirect consequences of altered gonadal function, we selected five males that had developed severe mating deficits after lesions in the medial nucleus to receive subcutaneous injections of testosterone proprionate (500 μg dissolved in 0.1 ml of sesame oil) every other day. Injections for 3 weeks failed to restore normal mating behavior in these males, but the same hormonal treatment restored normal mating behavior to castrated male hamsters (*21*). Therefore the effects of medial nucleus lesions cannot be attributed to a chronic decrease in the level of plasma testosterone.

We conclude that the medial nucleus is a specific site for neural control of male copulatory behavior. This conclusion is supported by observations in the hamster that efferent fibers from the CMA to the medial preoptic-anterior hypothalamic (MPOAH) junction originate primarily in the medial nucleus (*4*) and that lesions in the MPOAH eliminate mating behavior in almost all male vertebrates (*22*). The medial nucleus is also a major source of efferents to the bed nucleus of the stria terminalis, an area in which lesions produce deficits in the mating behavior of male rats (*23*). Cells in the medial nucleus, MPOAH, and the bed nucleus of the stria terminalis concentrate testosterone (*24*), and this hormone can influence the electrophysiological properties of neurons in the CMA projecting to MPOAH (*25*). The presence of testosterone is also essential for both the maintenance of normal copulatory behavior (*21*) and the male hamster's responsiveness to the female's odor cues, including that of vaginal secretions (*26*). Thus, the medial nucleus might act as an androgen-sensitive area in which chemosensory information critical to male mating behavior is processed, and as a relay by which that information influences activity in the bed nucleus of the stria terminalis and the MPOAH.

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13. Male Syrian hamsters weighing 120 g (Engle Laboratory Animals, Famersburg, Ind.) housed individually with food and water freely available were exposed to a 14:10 light:dark illumination cycle. Electrolytic lesions were produced in anesthesized hamsters (Nembutal, 75 mg per kilogram of body weight) by sterotaxically lowering an epoxylite-insulated insect pin electrode (exposed tip, 0.5 mm long; diameter, 0.37 mm), and delivering anodal d-c current of 1.5 mA for 10 seconds. Sham operations were performed by lowering the electrode to 1 mm above CMA or BLA coordinates without the delivery of current.
14. Adult ovariectomized female hamsters were made sexually receptive by sequential subcutaneous injections of estradiol benzoate (10 μg) and progesterone (200 μg) dissolved in 0.1 ml of sesame oil and administered 42 and 6 hours, respectively, before behavior testing. The female's receptivity was confirmed prior to mating behavior tests by exposure to a stud male.
15. Through the use of a microprojector, sections through each damaged CMA were traced onto a set of standard coronal sections through the amygdala (100-μm intervals). The proportion of damage to each nucleus of the amygdala on each side of the brain was calculated by an image analysis system (Quantimet 720) interfaced with a computer (PDP-11) to compare the summated area of the lesion with the entire area of that nucleus as represented on the standard sections.
16. Male hamsters with CMA lesions were ranked according to a score reflecting the severity of their mating deficit, that is, a score summated from the number of postoperative tests during which these animals displayed mounts and intromissions, but not ejaculations (+1); mounts, but not intromissions or ejaculations (+2); or a total absence of any copulatory behavior (+3). Rank order correlations were calculated between this ranking of mating deficit severity and a ranking of males with CMA lesions with respect to the proportion of bilateral damage to each nucleus in the amygdala.
17. Since the duration of mating tests varied between animals and between pre- and postoperative tests, we measured investigatory behavior as the time spent sniffing and licking each body region per minute of test. In animals with CMA lesions a decrease between pre- and postoperative investigation rates also reflected a significant decrease in the absolute amount of investigatory behavior [$T(16 = 22, P < .02$].
18. We calculated the percentage change from pre- to postoperative investigation rate of head, flanks, and anogenital area for each male. Rank order correlations were calculated between the decrease in anogenital investigation rate for each male with CMA lesions and the proportion of bilateral damage to each nucleus in the amygdala.
19. While vomeronasal input from the accessory olfactory bulb reaches the medial nucleus directly, olfactory input may reach the medial nucleus indirectly, by way of intra-amygdaloid afferents from olfactory projection areas of the amygdala [J. E. Krettek and J. L. Price, *J. Comp. Neurol.* **178**, 255 (1978)] or by way of afferents from other olfactory-related areas of the ventral forebrain (*5*).
20. Between 10 and 20 μCi of [^{3}H]proline or [^{3}H]leucine (specific activity, 40 to 60 Ci/mmole New England Nuclear) in 0.10 to 0.20 μl of physiological saline was injected bilaterally into the main and accessory olfactory bulbs through a 5-μl Hamilton syringe with a 26S-gauge needle. After a 48-hour survival period, the animals were perfused, and the brains were removed and cut 25 μm thick on a freezing microtome. Coronal sections at 200-μm intervals were mounted, coated with emulsion (Kodak NTB-2), and exposed for 2 to 3 weeks in the cold (2°C). The slides were developed (Kodak D-19) and counterstained with cresyl violet.
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Ecology of Colors of Firefly Bioluminescence

Abstract. *Dark-active North American fireflies emit green bioluminescence and dusk-active species emit yellow, in general. Yellow light and yellow visual spectral sensitivity may be adaptations to increase the signal-to-noise (that is, foliage-reflected ambient light) ratio for sexual signaling during twilight. The peaks of the electroretinogram visual spectral sensitivities of four species tested, two dark- and two dusk-active, correspond with the peak of their bioluminescent emissions.*

Firefly sexual signaling involves species-specific male flash patterns and coded time delays in female flash responses (*1*). Provided that there is sufficient light flux received in the region of the firefly visual spectral sensitivity, the precise color of the bioluminescent flash is not a factor in identification between males and females (*2*). Until now there has been no explanation proposed for the range of species-specific colors of bioluminescence from green through orange (λ_{max} = 546 to 594 nm), as determined by spectrophotometric measurements of the light organs of live fireflies (*3*). Since the use of bioluminescence as a signaling adaptation arose of necessity subsequent to the evolution of vision (*4*), it would be expected that the peaks of the bioluminescence emission spectra (*5*) would correspond with the peaks of visual spectral sensitivities for various species.

Bioluminescence cannot compete with ambient sunlight intensities, and therefore its evolution as a communicative mode in diverse species is associated with dimly lit environments and circumstances (such as nocturnal, subterranean, deep-sea) (*6*). In Fig. 1 are plotted histograms of the peak wavelengths of spectrophotometrically measured in vivo bioluminescence emission spectra for 55 species of North American (temperate zone) fireflies for which the time of onsets of flashing activity are known from direct field observations. The data form two broad groups: "early-starting" species, that is, those beginning flashing activity in advance of 30 minutes after sunset, and "late-starting" species, beginning after this. The determination of "early" or "late" was made from field records and the observer had no knowledge of the peak wavelengths of bioluminescence emission. There is a high degree of statistical significance of this correlation of peak wavelength of bioluminescence with time of beginning of flashing activity. Of 32 dark-active species, 23 emit green light ($\lambda_{max} \leq 558$ nm) and 21 of 23 dusk-active species emit yellow light ($\lambda_{max} \geq 560$ nm). Closely related (sibling) species might be expected to have similar or identical bioluminescent colors. However, the early flashers exhibit the yellow color, while late flashers emit green: for example, *Photinus ignitus* (556 nm) late, *Photinus consanguineus* (562 nm) early and *Photinus macdermotti* (565 nm) early, *Photinus tanytoxus* (555 nm) late, *Photinus collustrans* (560 nm) early.

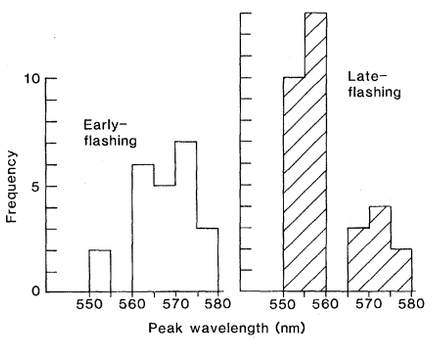

Fig. 1. Histograms of the peak wavelengths of the in vivo bioluminescence emission spectra from 55 species of North American fireflies. The wavelength intervals are arbitrarily 5 nm wide. The crosshatched area is representative of dark-active (*Late-flashing*) fireflies. The open area is representative of dusk-active (*Early-flashing*) fireflies. For each species the number of individuals measured ranged from 4 to 12.

Absorption bands of visual pigments are broad and have a significant degree of overlap with one another. Most visual pigments can be described by the Dartnall nomogram or by Ebrey and Honig nomograms (*7*). The electroretinogram (ERG) spectral sensitivites of the compound eyes (*8*) of two dark-active and two dusk-active firefly species were de-

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