in a quantitative descriptive theory of the variables responsible for stereopsis. Reviews and discussions of this work can be found in H. Helmholtz [*Physiological Optics* (Optical Society of America, Washington, D.C., 1925; Dover, New York, 1962)], K. N. Ogle [in *The Eye*, H. Davson, Ed. (Academic Press, New York, 1962), vol. 4, pp. 271–417], B. Julesz (*2*), and W. L. Gulick and R. B. Lawson [*Human Stereopsis: A Psychophysical Analysis* (Oxford Univ. Press, London, 1976)].

2. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).

3. The emergence of binocularity during the course of mammalian evolution has attracted considerable attention, and several hypotheses have been advanced to account for it [see, for example, G. E. Smith, *The Evolution of Man* (Oxford Univ. Press, London, 1924); G. L. Walls (*4*); S. Polyak (*5*); W. E. LeGros Clark, *Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959); M. Cartmill, in *The Functional and Evolutionary Biology of Primates*, R. H. Tuttle, Ed. (Aldine-Atherton, Chicago, 1972), pp. 97–122]. Only recently, however, has the assumption been confirmed that stereopsis is present in animals other than humans. R. Fox and R. Blake [*Nature (London)* 233, 55 (1971)], J. Packwood and B. Gordon [*J. Neurophysiol.* 38, 1485 (1975)], and R. Blake and H. V. B. Hirsch [*Science* 190, 1114 (1975)] have found behavioral evidence for stereopsis in the cat. E. W. Bough [*Nature (London)* 225, 42 (1970)], R. F. Sarmiento [*Vision Res.* 15, 493 (1975)], and A. Cowey, A. M. Parkinson, and L. Warnick [*Q. J. Exp. Psychol.* 27, 93 (1975)] have found behavioral evidence for stereopsis in the rhesus monkey. These data complement recent neurophysiological investigations that have revealed cortical neurons in cat and in monkey that respond optimally to retinally disparate stimuli [see, for example, H. B. Barlow, C. Blakemore, J. D. Pettigrew, *J. Physiol. (London)* 193, 327 (1967); P. O. Bishop, in *The Neurosciences: Second Study Program*, F. O. Schmitt, Ed. (Rockefeller Univ. Press, New York, 1970), pp. 471–485; D. H. Hubel and T. N. Wiesel, *Nature (London)* 225, 41 (1970)].

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7. Neuroanatomical investigations by Karten and colleagues [for example, H. J. Karten, W. Hodos, W. J. H. Nauta, A. M. Revzin, *J. Comp. Neurol.* 150, 253 (1973)] have revealed many structures and pathways in the avian visual system that seem to be analogous to those in the mammalian visual system. In the bird telencephalon a region known as the visual Wulst receives extensive input from both eyes and appears to be an analog of the visual cortex in mammals. Pettigrew and Konishi (*8*) have recorded from single neurons located within the Wulst of the owl and found neurons optimally responsive to disparate binocular stimuli.

8. J. D. Pettigrew and M. Konishi, *Science* 193, 675 (1976).

9. Behavioral tests of kestrel acuity revealed that it exceeds human acuity by a factor of 2.6 (*10*), a result consistent with estimates of falcon and hawk acuity derived from optical characteristics of the eye [R. Shlaer, *Science* 176, 922 (1972)] and from the anatomy of the retina [K. V. Fite and S. Rosenfield-Wessels, *Brain Behav. Evol.* 12, 97 (1975)]. The retinas of falcons and hawks have a well-developed temporal fovea in addition to a central fovea; the lateral position of the temporal fovea provides binocular overlap [Walls (*4*), Polyak (*5*), Fite and Rosenfield-Wessels (above)].

10. R. Fox, S. W. Lehmkuhle, D. H. Westendorf, *Science* 192, 263 (1976).

11. The two-choice discrimination task we used is very similar to the one described in our prior investigation of kestrel acuity (*10*). The bird learns to fly from the starting perch to a perch located below each stimulus display. The distance between the starting perch and the stimulus perch is 168 cm. The weight of the bird landing on the correct perch triggers the reward delivery system, which exposes a small cup containing a morsel of beef heart that can be seized by the bird's beak. If the bird lands on the incorrect perch the cup is not exposed and the stimulus

display and other illumination in the alley is turned off briefly. Training to perform in the test apparatus is accomplished by gradually shaping behavior, following the tenets of operant conditioning, with food as the reward. The bird, weighed daily before and after testing sessions, was maintained in excellent health at an average weight of 100 g. All the bird's daily food ration was earned in two daily training-testing sessions of 20 to 25 trials, one session in the morning and one in the afternoon. Since beef heart does not satisfy all the bird's digestive and nutritive requirements, it was fed a mouse once a week.

12. Random element stereograms [developed and systematically investigated by B. Julesz; see, for example, *Bell Syst. Tech. J.* 39, 1125 (1960) and (*2*)] produce compelling stereoscopic depth percepts in the absence of monocularly discernible contours.

13. The technique of dichoptic stimulation through color separation, the anaglyph method, is well known [see, for example, Y. LeGrand, *Form and Space Vision* (Indiana Univ. Press, Bloomington, 1967); R. S. Woodworth, *Experimental Psychology* (Holt, New York, 1938)]. We have found that Wratten filters 29 (red) and 58 (green) provide acceptable color separation for the red and green colors produced by most modern color or television receivers. The system we used for generating stereograms consisted of an electronic device that controlled the sweep and on-time of the red and green electron guns of a color television receiver. A large number of red dots and green dots, produced by a random generator, appeared to be continuously present on the screen (physically, a new dot pattern was generated every 16 msec, the time required for one scan of the cathode-ray tube). Disparity was introduced by delaying the on-time of one of the guns at predetermined points during the scan. Variations in disparity magnitude and configuration of the stereoscopic form could be introduced. The device controlled two identical television receivers (Hitachi model 100-C), one for each alley of the testing apparatus; from the starting perch the display portion of each receiver was 4.4° by 6.2°. The stereoscopic form could be generated on either one of the receivers at the option of the experimenter.

14. The abscissa of Fig. 2 indicates the eight disparities that could be generated by the display system. The disparities are derived, with appropriate correction for bird interpupillary distance, from the formula used for calculating disparity induced by discrete, monocularly visible contours [C. H. Graham, in *Handbook of Experimental Psychology*, S. S. Stevens, Ed. (Wiley, New York, 1951), pp. 868–920]. While it was not possible to compare human performance with falcon performance under comparable conditions, we did ask humans to report on the magnitude of perceived depth induced by the eight disparities. With their heads located adjacent to the starting perch they estimated, in arbitrary units, how far in front of the background the vertical rectangle appeared. For the first six disparities perceived depth increased. For the two largest disparities it became difficult to maintain the depth percept. Some observers reported that the rectangle no longer appeared in depth but lay in the same plane as the background. This difficulty with the larger disparities parallels the decrement in performance exhibited by the falcon for the same disparities. These observations suggest to us that there are no dramatic differences in the range of disparities to which falcon and human are sensitive.

15. Stereopsis by discrete contours has been called local stereopsis, while stereopsis by random element stereograms has been called global stereopsis. See Julesz (*2*) and P. O. Bishop and G. H. Henry [*Annu. Rev. Psychol.* 22, 119 (1971)] for a discussion of the distinction between local and global stereopsis.

16. Since many nonmammalians are oviparous, sophisticated techniques derived from embryological research might be used to investigate the development of the binocular visual system. In this regard, Pettigrew and Konishi (*8*) report that early experience influences the development of binocular vision in owls.

17. We thank the Tennessee Wildlife Resources Agency and the U.S. Fish and Wildlife Service for the excellent cooperation extended to us. The work was authorized by state scientific collectors permit No. 516 and federal scientific collectors permit PRT-7-01-C-Z-NV. Support was provided by NIH grant EY00931.

14 January 1977; revised 22 March 1977

Homosexual Rape and Sexual Selection in Acanthocephalan Worms

Abstract. *Acanthocephalan males have cement glands associated with the vas deferens, secretions from which seal the female vagina with a cap after copulation and so prevent subsequent insemination. Homosexual rape results in the male victim having the genital region sealed off with cement and effectively removed from the reproductive population. Sperm and cement are transferred to females during copulation, but apparently only cement is transferred to males during homosexual rape. Acanthocephalans conform to a parental investment model, and we interpret the evolution of the cement gland and sexual behavior as the result of sexual selection.*

Rape occurs in a variety of circumstances, but in nonhumans it usually is related to male reproductive success. In some species of *Drosophila*, males are able to rape females that have already copulated (*1*). The sperm of the rapist, since it is the last insemination, is then packed into the seminal receptacle on top and is used first by the female fertilizing a majority of the eggs (*2*). In the rhabdocoel turbellarian *Stenostomum oesophagium*, behavior has been reported (*3*) that we interpret as rape. Individuals are nonselfing hermaphrodites, and cross-fertilization occurs; but individuals will approach quiescent individuals and rapidly evert the penis, hypodermically impregnating the quiescent individual without allowing cross-fertilization. There are other reports (*4*) of this sort of behavior among turbellarians, suggesting that individuals will promiscuously inseminate but selectively allow themselves to be inseminated. After homosexual rape in the anthocorid bug *Xylocaris maculipennis*, the sperm of the rapist enters the vas deferens of the victim and is used by the victim during copulation. An individual may be raped even while he is copulating with a female (*5*). We report here homosexual rape in the acanthocephalan worm *Moniliformis dubius* and interpret this behavior and other aspects of the biology of acanthocephalans in the context of parental investment and sexual selection.

Acanthocephalans are dioecious parasitic worms that undergo larval development in arthropods and occur as adults in the alimentary tract of various vertebrates (6). In experimental infections of *M. dubius* in laboratory rats the sex ratio of immature adults is approximately 1 : 1 (7). The juveniles segregate spatially in the intestine with females in the carbohydrate-rich anterior region (15 to 35 cm posterior to the stomach) and males posterior to the females (8). At maturity males apparently migrate anteriorly to the females. Thus, from a single infection all females reach maturity at about the same time in the same place, about a 20-cm portion of the intestine. Copulation begins when the worms are 16 days old, and under experimental conditions in which a single male has access to many females he can fertilize as many as 17 females ($\overline{X} = 7.88 \mp 4.79$, range 2 to 17) (9).

Males have cement glands posterior to the level of the testes, which eventually empty into the vas deferens, which then enters the cirrus; the cirrus terminates in a muscular eversible cup, the bursa (6). During copulation the everted bursa of the male wraps around the posterior end of the female, the cirrus enters the female gonopore or vagina, and spermatozoa are transferred (6). The female vagina and genital region is packed and then "capped" by secretions from the cement gland, which block the vaginal region. The external cap is lost after a few days (10). The length of time that the cement remains in the genital tract is unknown, but it must be dissipated when egg release, via a remarkable and unique "egg sorter" (11), begins on or about day 38 (9, 12). A single insemination is apparently sufficient for the fertilization of a single batch of eggs. This is due, in part, to the fact that the sperm are long-lived and that females will continue to release fertilized eggs for up to 105 days in the absence of males (9) and to the possibility that females may store sperm (13). However, a prolonged egg-producing period seems to depend on continued male-female contact (9). Males have a higher mortality rate than females and may live for as long as 154 days, whereas females on the average live longer (7).

The above data on the biology of *M. dubius* can be interpreted in the context of sexual selection and parental investment (14). Acanthocephalans conform to the model where one sex (female) invests considerably more than the other; males should therefore compete among themselves to mate with females. We examine the biology of males to determine wheth-

er competition possibly exists and, if so, which form it takes.

Acanthocephalan sperm are long-lived, and the potential exists for multiple inseminations resulting in progeny of mixed parentage, conditions under which sperm competition can occur. This results in evolutionary forces favoring males that either (i) displace stored sperm from a previous insemination or (ii) reduce the probability of subsequent inseminations (2). Since there is no physical structure, such as a spermatheca, for sperm storage in acanthocephalans, the evolution in males of mechanisms that reduce the probability of subsequent inseminations may be predicted. While we do not reject previous hypotheses that the cement gland and capping behavior have a function in preventing the escape of sperm (4, 6, 15) or that cement holds the couple together during copulation since the act requires precise positioning (16), we emphasize the possibility that cement glands and capping behavior evolved in response to sexual selection and function in preventing subsequent inseminations.

The distribution in time and space of reproductive females also affects sexual selection among males (14). In *M. dubius* and other acanthocephalans females are contagiously distributed in the intestine, and all mature from a single infection at about the same time. Thus the availability and location of reproductive females is highly predictable; consequently competitive interactions may be severe. Selection may favor male adaptations that lead to high reproductive success at the cost of increased mortality. There is differential male mortality in *M. dubius* (7) and in other acanthocephalans (6). We suggest that it occurs by "washout" during the migration to females (against peristalsis and the spiraling action of the intestine) and by additional male-male interactions that may cause dislodgement from the intestinal wall. In support of our hypothesis it is important to note that differential male mortality does not occur until well after the time of sexual maturity (7).

Homosexual rape, by removing competitors from the reproductive population, may be another manifestation of the intense interactions for the resource of reproductive females. We observed an instantaneous frequency of homosexual rape of 2.5 percent in *M. dubius* (17). From 0 to 1 percent of males of *Acanthocephalas parksidei* were capped, whereas capped males were noted only occasionally in *Echinorhynchus truttae* and *Polymorphus minutus* (18–20). The estimates are probably conservative

since it is difficult to detect males that had been raped and subsequently lost the exterior portion of the cap. In addition, the 0 to 2.5 percent figures represent instantaneous rates. If the external portion of the cap remains only 2 or 3 days, then, over the course of a single infection, as many as 50 percent of the males may be capped (21). We observed at least three additional males that appeared to have lost the external portion of the cap because the bursa was partially inverted, and portions of what appeared to be cement were present. Loss of the external portion of the cap would not necessarily allow the male to copulate since cement in the bursa area may prevent the full extension of the bursa cup required for copulation. We examined sections of capped and uncapped males of *M. dubius* to determine whether sperm were present in the bursal portion of the genital area of the capped male. We also examined whole mounts of the bursal region of two additional capped males. Sperm in the bursal region beneath the cap would likely belong to the rapist since sperm of the victim would be in the sperm duct of the cirrus. We were able to identify sperm in the duct of the uncapped males but were unable to locate any evidence that sperm was transferred with the cement during the rape. This supports our hypothesis that males differentiate between males and females, although we caution that sperm in the bursal region is probably in a foreign environment and could rapidly disintegrate. We do not reject the hypotheses that homosexual rape may be due to poor sex recognition (19) or indiscriminate copulation (18, 19). (However, two instances of homosexual rape occurred in the absence of females, suggesting that the males were not stimulated by any possible pheromone.) We postulate, however, that sperm competition may have led to the evolution of the cement gland and capping behavior and that this may represent a preadaptation that under sexual selection may have assumed the additional function of removing male competitors from the reproductive population. Caps found away from the genital region (20) on both males and females would then not be the result of poor sex recognition or indiscriminate copulation, but the result of activities of individual males and females attempting to avoid being capped. Males should avoid being capped since it prevents them from reproducing and females because it prevents them from releasing eggs (22).

Moniliformis dubius conforms to a parental investment model, and we interpret the evolution of the cement gland

and sexual behavior to be the result of sexual selection, generated by (i) small male parental investment, (ii) long-lived sperm, (iii) males being capable of multiple inseminations, and (iv) females being contagiously located at a predictable site and time in the host's intestines. Since the reproductive morphology of males and at least some of the population characteristics of *M. dubius* are characteristics of the entire phylum Acanthocephala, we suggest that our interpretation is a general situation in the phylum.

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8. We found no overlap in the distribution of males and females prior to the 16th day of infection when males overlapped with females. P. L. Burlingame and A. C. Chandler [*Am. J. Hyg.* 33, 1 (1941)] report maximum densities of adult females and males to be 18 and 38 cm posterior to the stomach, respectively; J. C. Holmes, *J. Parasitol.* 47, 209 (1961).
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10. This is based on our observation that mature females with fertilized eggs can be found without caps 2 to 5 days after copulation. Cement may remain in the vaginal region.
11. P. J. Whitfield, *Parasitology* 61, 111 (1970).
12. D. W. T. Crompton, S. Arnold, D. Barnard, *Int. J. Parasitol.* 2, 319 (1972).
13. K. H. Atkinson, thesis, Florida State University (1973).
14. R. L. Trivers, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 136.
15. This is the most widely cited explanation. G. H. Ball [*Univ. Calif. Berkeley, Publ. Zool.* 33, 301 (1930)] suggested that the caps prevent sperm from entering immature females but this was based on the misconception that the females themselves secrete the caps.
16. H. J. Van Cleave, *J. Morphol.* 84, 427 (1949).
17. For *M. dubius*, rape occurred under male to female ratios of 3:0, 2:0, and 12:18. We found no obvious relation between sex ratio or density and rape. This is due in part to the small sample size for capped males. We ran experimental ratios (male to female) of 1:1, 1.5:1, 2:1, 3:1, 0.8:1, 0.5:1, and 0.3:1. All were run with infections of 10, 20, and 30 cystacanths to test for density. We again emphasize that all estimates are conservative since many authors probably do not report capped males, and lost external caps are difficult to detect. For example, *M. dubius* is a widely used experimental animal, yet we could find no reference, other than our own, to capped males.
18. For references to capped males for *A. parksidei*, see O. M. Amin, *J. Parasitol.* 61, 318 (1975).
19. For references to capped males for *E. truttae*, see J. B. E. Awachie, *J. Helminthol.* 40, 11 (1966).
20. For references to capped males for *P. minutus*, see W. L. Nicholas and H. B. N. Hynes, *Ann. Trop. Med. Parasitol.* 52, 36 (1958).
21. This is based on males reaching sexual maturity at about 16 days and living for 125 to 150 days. If we assume an average figure of 1.4 percent for homosexual capping and estimate that the external portion of the cap remains 3 days, then (125 − 16) divided by 3, times 1.4 percent is equal to 50.8 percent.
22. It benefits a female to avoid copulation at the time she begins releasing eggs. If the sperm becomes depleted following the release of eggs, it would be advantageous to copulate again at such a time so as to maximize egg production. The report of O. M. Amin (*18*) of capped females with mature embryos suggests that more than one copulation can occur. In fact it should occur, for, if the cap was 100 percent effective, selection would eventually not favor the male capacity for multiple inseminations.
23. We thank E. Connor, J. Farr, K. Heck, W. Lindberg, E. McCoy, R. Short, D. Simberloff, D. Strong, R. Trivers, W. Tschinkel, and N. Williams for comments; J. Byram for the initial stock of *M. dubius*; N. Contos and W. Heard for technical assistance; and M. Greenberg for enthusiasm.

23 February 1977, revised 18 April 1977

Morphine and Enkephalin: Analgesic and Epileptic Properties

Abstract. *Systemic and intracerebroventricular administration of analgesic doses of morphine resulted in large increments of spontaneous multiple unit activity in the periaqueductal gray matter of the awake rat. Intracerebroventricular injection of methionine enkephalin gave analgesia in only 8 of 19 rats, but in all 8, and in no others, increased periaqueductal multiple unit firing was also seen. These findings support the view that the periaqueductal gray matter is actively involved in endogenous mechanisms of analgesia. A striking observation was that enkephalin caused electrographic and behavioral epileptic phenomena in most animals. This observation together with other recent findings suggests that endogenous enkephalin may play some role in epileptogenesis.*

Considerable attention has been paid to disclosing the site and mechanism of action of narcotic analgesic drugs. Stereospecific opiate binding sites have been discovered and mapped in the mammalian brain (*1–3*). A substance (enkephalin) has been identified in brain tissue that appears to be an endogenous ligand for the opiate receptor, and its peptidic structure has been described (*4*). The midbrain periaqueductal gray matter (PAG) seems to be a major site of opiate analgesic action. Significant opiate binding as well as enkephalin-containing fibers and fiber terminals are found here (*2, 3, 5*). Microinjections of morphine into PAG and electrical stimulation of this structure cause particularly potent analgesia (*6, 7*), and microinjections of enkephalin and other, more recently discovered, opioid peptides into the ventricular system or into the PAG likewise yield analgesic effects (*8*). We have reported that analgesic doses of either systemically administered morphine or PAG electrical stimulation augment spontaneous multiple unit firing in the PAG (*9*). These and other findings suggest, as we have previously concluded (*9, 10*), that activation of the PAG might normally be associated with pain inhibition.

In our study we sought to examine further the effects of systemically injected morphine on PAG multiple unit firing and to determine whether intracerebroventricular (ICV) administration of analgesic doses of morphine and enkephalin would also influence neural activity in this brain region. We found that analgesic doses of morphine, whether administered via the systemic or ICV route, reliably augmented PAG multiple unit activity. The ICV injections of enkephalin provided comparable analgesia in only some animals, but only those showing analgesia exhibited a significant increase in PAG multiple unit firing. An unexpected but striking observation was that enkephalin caused potent and long-lasting electrographic seizures in most animals.

Male Sprague-Dawley rats (300 to 400 g) were prepared with permanently implanted cannula guides, multiple unit recording electrodes, and skull electroencephalogram (EEG) leads according to standard procedures. Guides were made of 23-gauge stainless steel tubing and aimed for the lateral ventricle on one side. Multiple unit electrodes consisted of bundles of three to five 70-μm Nichrome wires cemented together and insulated except at their cross-sectioned tips. Each rat received one such bundle of electrodes aimed at caudal PAG; several rats were implanted with a second bundle in locus coeruleus. Stainless steel screws were threaded into the skull over frontal and occipital cortex for EEG recording. The ICV injections were administered via 27-gauge cannulas inserted into the guides. Testing began more than 1 week after surgery.

A modification of the tail-flick method (*7, 11*) was used for analgesia testing. Animals were restrained in plexiglass tubes from which their tails extended. An opening in the top of the tube gave access to the animal's electrode connector for simultaneous electrophysiological recording. Baseline latencies to tail-flick withdrawal from the radiant heat source were averages of the first four (before treatment) trials in any test session and ranged between 3.0 and 3.5