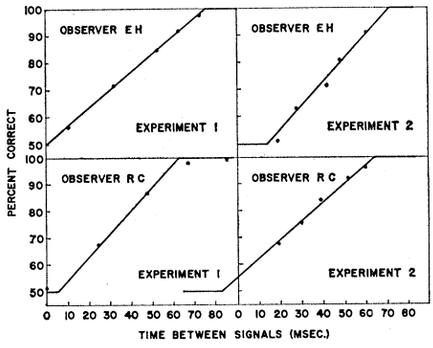

Fig. 1. Percentage of trials on which the variable pair, rather than the standard pair, was designated "more successive" plotted against the time interval between the terminations of the light and of the sound that comprise the variable pair.

function relating the probability of indicating the variable as the successive pair to T should be linear, intersecting the chance level (.50) at $T = x$ and rising to 1.00 at $T = x + M$.

In the experiments reported here, values of x and M were first estimated by means of a method of limits. The value of T for the standard pair in the forced-choice procedure was determined from these estimates. The forced-choice data were then obtained in daily sessions of 120 trials each, 24 for each of five values of the variable.

A neon lamp provided the visual signal, and a pure tone, delivered over a speaker, was the auditory signal. The observer was instructed to indicate the pair in which the likelihood was greatest that the light terminated before the sound. Termination rather than onset was used in order to define the relevant channels as unequivocally as possible for the observer. The stimuli came on together and remained on for about 2 seconds before termination of the first one.

The data obtained are presented in Fig. 1. Two experiments, each consisting of 12 sessions, were completed for each of two observers. The number of responses determining each point in the graphs is 288.

Experiment 1 for observer R.C. provided only two data points within the range of primary interest. Least-square lines were fitted to each of the other three sets of data; omitted from the analysis was one point which did not exceed chance expectancy for observer E.H. in experiment 2.

These data are clearly consistent with the hypothesis in that they are described adequately as linear functions. The mean absolute deviation of the points from the lines in the vertical direction is 0.74 percentage unit. Testing goodness of fit by chi-square yields values of chi-square having associated probabilities of .55 to .90.

The inferred difference in conduction time x for auditory and visual stimuli averages 6.9 msec for observer E.H. and −1.1 msec for observer R.C. Positive values of x imply more rapid conduction in the auditory channel.

The mean period of attention, M, calculated for observer E.H. is 66.4 msec; for observer R.C. it is 63.8 msec. There is no indication of a directional change in M from experiment 1 to experiment 2 in these limited data. For E.H. the values are 74.5 and 58.3, respectively; for R.C. they are 56.5 and 72.2. The difference in M for the two experiments is fairly large for both observers, but the differences are of opposite sign.

Psychophysical data are almost invariably described by cumulative normal distribution functions. The data presented here do not appear to require any hypothesis more complex than the linear hypothesis. However, it is extremely difficult to choose between these types of function (see, for example, *1*), and the data obtained so far are not adequate for that purpose.

The theory discussed has much in common with theories proposed by several other workers in recent years (*2*). It has frequently been suggested, by us and by others, that a physiological correlate of periodic attention may be the alpha rhythm of the electroencephalogram. If this is so, M would be expected to fall within a range of 77 to 110 msec. Results for the two observers in this study do not satisfy that expectation, but experiments are being conducted with additional observers to establish this point more convincingly (*3*).

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References and Notes

1. H. R. Blackwell, *Am. J. Psychol.* **66**, 397 (1953).
2. W. Pitts and W. S. McCulloch, *Bull. Math. Biophys.* **9**, 127 (1947); W. G. Walter, *The Living Brain* (Norton, New York, 1953); J. Stroud, in *Information Theory in Psychology*, H. Quastler, Ed. (Free Press, Glencoe, Ill., 1956), pp. 174–205; P. McReynolds, *Psychol. Rev.* **60**, 319 (1953).
3. This report summarizes part of a doctoral dissertation to be submitted to the Graduate School of the University of Cincinnati by one of us (M.W.S.). We thank the Graduate School for its support of parts of this research.

22 October 1962

Natural Triploidy in Salamanders Related to Ambystoma jeffersonianum

Abstract. *Female salamanders with large erythrocytes and erythrocyte nuclei produced triploid larvae; females with small erythrocytes and erythrocyte nuclei produced diploid larvae. Larval chromosome counts, dimorphism in cell size, and sex inheritance indicate distinct, persisting populations of triploid females in parts of the range of the* Ambystoma jeffersonianum *complex.*

During an investigation of the biology of salamanders of the *Ambystoma jeffersonianum* complex, 13 experimental matings, involving individuals from Massachusetts, Michigan, and Ohio, were made. The salamanders were confined in wire baskets placed in natural ponds. After courtship and egg deposition, the parents were removed. When the larvae hatched, they were brought into the laboratory and reared. The chromosomes were counted in epidermal nuclei from tail fins that were fixed, stained, and squashed in orcein and acetic acid. Regenerating tissue was found to be more satisfactory for this purpose than the original tail fin because of the increased number of mitotic figures and the decreased amounts of melanin in the regenerating tissue.

Chromosome counts for larvae of five matings (Table 1) indicate that two matings produced diploid larvae ($2n = 28$), while three matings produced triploids ($3n = 42$). Photomicrographs and camera-lucida drawings of diploid and triploid mitotic figures are shown in Fig. 1. In many of the preparations, not all the chromosomes could be disentangled, hence enumeration of all those present was not possible. In the offspring of matings that produced triploid larvae, many of these incomplete counts were above the diploid number but none was above the triploid number. In offspring of matings that produced diploid larvae, incomplete counts were consistently less than the diploid number.

The parents of the larvae from which chromosome counts were made were collected in Delaware and Lorain counties, Ohio, and in Washtenaw County, Michigan. Females of the *Ambystoma jeffersonianum* complex in Lorain and Washtenaw counties are dimorphic with respect to size of erythrocytes and erythrocyte nuclei; females in Delaware County are uniformly small-celled. The males at all three localities are consistently small-celled. The females that

produced triploid larvae (females from Washtenaw and Lorain counties) were large-celled; the females that produced diploid larvae (females from Lorain and Delaware counties) were small-celled. Thus, whether the larvae are diploid or triploid is evidently determined by the female parent.

Table 1. Chromosome counts of larvae from small-celled and large-celled females.

County	Number of larvae		Mitotic phase; strands; number of cells (in parentheses)	Number of chromosomes; number of counts (in parentheses)
	Produced	Represented by complete counts		
		Small-celled females		
Delaware	91	3	Metaphase, double (1)	28 (1)
			Anaphase, single (3)	28 (4)
Lorain	33	3	Metaphase, double (2)	28 (2)
			Anaphase, single (2)	28 (3)
		Large-celled females		
Lorain	107	2	Metaphase, double (3)	42 (3)
Washtenaw	94	2	Metaphase, double (1)	42 (1)
			Anaphase, single (1)	84*
Washtenaw	96	1	Anaphase, single (2)	42 (3)

* Both halves; 1 count.

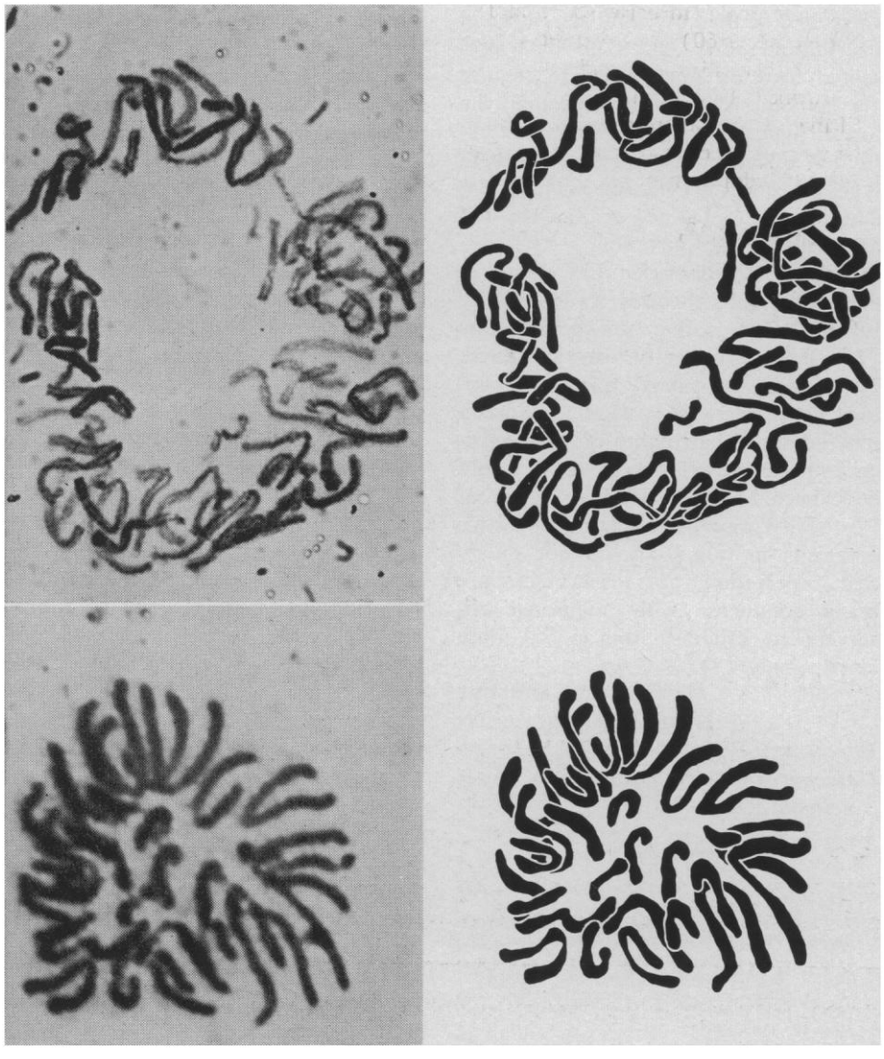

Fig. 1. Mitotic figures in epidermal cells of larvae related to *Ambystoma jeffersonianum*. The triploid set (top row) from a larva of a large-celled female from Lorain County, Ohio, has 42 double strands. The diploid set (bottom row) from a larva of a small-celled female from Lorain County, has 28 single strands.

Fankhauser (*1*) found small percentages of triploids among larvae obtained from field-impregnated females of *Notophthalmus viridescens* and *Eurycea bislineata* that subsequently spawned in captivity. Although chromosome counts were not obtained for all the individuals in any of the sets of *Ambystoma* larvae, the consistency of complete counts within sets and the correlation of triploid counts with the large-celled female parents suggest that triploidy is normal for larvae of these females, rather than a spontaneous aberration such as Fankhauser observed.

Henley and Costello (*2*) removed and examined the original and the regenerating tail fin of *Ambystoma maculatum* larvae obtained from eggs laid under natural conditions. Although they found polyploid cells in a small percentage of these larvae, especially in regenerating tissue, none of the larvae were completely polyploid. In contrast, all of the complete counts obtained from larvae of the large-celled females related to *A. jeffersonianum* were triploid. It seems very unlikely that these larvae were diploid-triploid mosaics.

Humphrey (*3*) reported that six species of the genus *Ambystoma* are diploids with 28 chromosomes. One of the species listed by Humphrey is *Ambystoma jeffersonianum*. The counts for *A. jeffersonianum*, based on spermatogenic material from a male collected near Ithaca, Tompkins County, New York (*4*), are confirmed by the counts for larvae of the small-celled females from Delaware and Lorain counties, Ohio. *Ambystoma laterale*, another member of the *Ambystoma jeffersonianum* complex, is also a diploid with 28 chromosomes (*5*).

Of 377 larvae produced by six large-celled females, 212 were reared and sexed at metamorphosis; all of these were females. Of 269 larvae produced by four small-celled females, 170 were eventually sexed; 40 percent of these were males. Thus it appears that the offspring of the large-celled females are consistently female as well as triploid.

The dimorphism in cell size, the inheritance of sex, and the larval chromosome counts indicate that there are distinct, continuing populations of triploid females associated with certain populations of the two diploid species, *A. jeffersonianum* and *A. laterale*. Data supporting this interpretation are on file (*5*).

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References and Notes

1. G. Fankhauser, *Proc. Am. Phil. Soc.* **79**, 715 (1938); *J. Heredity* **30**, 379 (1939).
2. C. Henley and D. P. Costello, *J. Morphol.* **89**, 91 (1951).
3. D. G. Humphrey, *Science* **128**, 304 (1958).
4. J. Kezer, personal communication.
5. T. M. Uzzell, Jr., thesis, University of Michigan (1962).

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Paraplegic Dogs: Urinary Bladder Evacuation with Direct Electric Stimulation

Abstract. *Stimulation of the detrusor muscle by means of two implanted wire electrodes increased intravesical pressure markedly in ten trials in normal dogs and in nine trials following transection of the dog's lumbar spinal cord. The urinary bladder could be completely emptied up to 2 or 3 weeks postoperatively. Later stimulation provoked an equally copious urinary flow but a residue persisted even when progressively higher voltage was applied.*

Although the mortality rate in paraplegic patients with spinal cord injuries has been greatly reduced since World War II, more than half of the deaths in this group still are attributable to complications involving the urinary tract (*1*). These complications include persistence of large amounts of residual urine in the bladder with subsequent infection, vesico-ureteral reflux, and incontinence.

We have found only two reports of attempts to evacuate the neurogenic or cord bladder by electric stimulation in the literature. In the first (*2*), two electrodes were sutured to the parasympathetic pelvic nerves. These nerves are known to predominate in supplying the bladder (*3, 4*). In the second (*5*), an electrode attached to a catheter was placed within the lumen of the bladder.

In our experiments on dogs, one stainless steel wire electrode was implanted in the anterior wall and one in the posterior wall of the detrusor muscle, midway between the trigone and the dome. The muscle was directly stimulated by applying a train of biphasic square waves generated by a Grass stimulator (model S4B). Basic experiments on normal dogs showed that 15 to 35 cy/sec stimuli of 3 to 8 msec duration provoked a good contraction of the entire detrusor, a finding which corresponded closely with that reported by Burghele, Ichim, and Demetresco (*2*). The best response in our experiments was achieved with a 20 cy/sec stimulus of 4 msec duration.

A catheter connected to a Statham strain-gauge (model P23D) was introduced into the bladder through a small cystotomy for measurement of intravesical pressure which was registered on a Sanborn recorder. The minimum voltage required to obtain maximum pressure was determined individually on all dogs before and after spinal cord transection. The limits in the former group were 3.2 and 8 volts and in the latter 1.4 and 10 volts, with a range of 3 to 7 volts in most instances. Voltages above this level did not raise the pressure further. At least 1.5 to 2 volts was usually necessary to provoke a pressure increase to 20 or 25 cm of water, a level at which some urine was eliminated. When the voltage was increased, intravesical pressure in the 10 normal dogs rose to levels between 22 and 81 cm (average 50) and in the 9 paraplegic dogs to between 25 and 180 cm (average 60) 4 to 6 seconds after onset of the stimulus, and 50 to 80 ml of urine flowed in a good stream (Table 1). Maximum pressure determinations exceeded 40 cm in 7 of 10 group I dogs and in 7 of the 9 in group II.

Intravenous injection of neostigmine (1 mg) in addition to the electric stimulus provoked a consistent increase in pressure in all six dogs examined before transection and in two of seven dogs examined after transection.

Three types of contraction were noted with a 5-second stimulus. Maximum contraction was usually achieved within 5 seconds and was not augmented by a longer stimulus. Proof that the bladder can be completely emptied in both normal and acutely paraplegic dogs by this method supports the modern concept of micturition advanced by Lapides (*6*), Muellner (*7*), and Woodburne (*4*). These authors have disproved Elliott's old hypothesis of antagonism between the detrusor and the internal sphincter muscle (*8*) and have demonstrated that the so-called internal sphincter is merely an elongation of the detrusor's bundles and contracts simultaneously with them. According to Woodburne (*4*), micturition is initiated by relaxation of the striated external sphincter muscles, especially the levator ani, and is carried through by concomitant contraction of the detrusor, including the internal sphincter bundles.

Care of the nine paraplegic dogs was difficult. Two died early in the postoperative period. In the other seven, electric stimulation was applied one or several times and was always followed by the evacuation of 100 to 200 ml of urine. Four of the seven died within 20 days from complications related to paraplegia.

Two dogs are alive at 4 months and one at 2½ months postoperatively. These dogs were all examined cystographically with 20 ml Hypaque, administered intravenously. Each electric stimulation provoked a copious flow of urine but progressively higher voltage was required. After 2 or 3 months a stimulus of 20 to 30 volts was necessary to provoke micturition. Cystography in one animal revealed that 10- and 15-volt stimuli were sufficient to empty

Table 1. Resting to maximum intravesical pressures in dogs (in centimeters of water) before and immediately following spinal transection with stimulus alone or with stimulus plus 1.0 mg of neostigmine. A stimulus of 20 cy/sec of 4 msec duration was used.

Animal (No.)	Preoperative				Postoperative			
	Stimulus only		Stimulus plus neostigmine		Stimulus only		Stimulus plus neostigmine	
	Volts	Pressure	Volts	Pressure	Volts	Pressure	Volts	Pressure
198	7.2	5–22						
216	3.8	7–56						
222	8.0	5–41						
225	3.2	11–50						
124	5.4	5–28	5.4	15–41				
235	6.0	3–60	6.0	5–90	4.0	4–56	6.0	7–71
236	4.5	3–33	3.8	6–65	3.2	4–40	4.5	4–35
245	6.8	8–80	6.8	6–93	10.0	2–73	6.8	12–55
260	4.4	20–81	5.6	12–245	4.4	18–180		
270	6.0	7–50	6.0	3–56	6.0	4–29	6.0	4–58
333					3.0	3–45	3.0	4–48
341					6.0	18–44	6.0	14–46
342					5.2	25–44	4.0	16–40
352					1.4	10–25		
Average		7.5–50		7.5–98		10–60		
				7.0–69*		10–43*		8.5–53*

* Average not including dog No. 260.