tions of dopamine in the contact zone of the ventral region of the median eminence, not directly associated with GnRH terminals, suggests that dopamine is available for direct release into portal blood to influence the anterior pituitary gland. A recent report (*10*) has shown high concentrations of dopamine in portal blood during different stages of the estrous cycle, which may support the idea that dopamine influences the release of prolactin from the anterior pituitary gland (*11*). It is also possible that dopamine in these regions of the median eminence may be involved directly in the regulation of other hypothalamic releasing hormones.

Thus, the correlative fluorescence-immunocytochemical technique provides for the simultaneous demonstration of monoamines and GnRH within the same tissue block and potentially offers a means for examining transmitter-hormone interactions microscopically at a given point in time. These data support the concept that dopamine may affect the release of both hypothalamic GnRH and anterior pituitary hormones. This technique may help to elucidate the role of neurotransmitters and neuropeptides in brain function by allowing the examination of simultaneous alterations in neuronal peptides and transmitters during different functional stages.

THOMAS H. MCNEILL
JOHN R. SLADEK, JR.
Department of Anatomy,
School of Medicine and Dentistry,
University of Rochester,
Rochester, New York 14642

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12. We thank T. M. Nett for the antiserum 38; S. Sorrentino for antiserum F; L. Sternberger for the rabbit antiserum to horseradish peroxidase; E. A. Zimmerman and A. G. Robinson for the estrogen-stimulated neurophysin that was used to produce the section shown on the cover; and B. Putnam Buell for technical assistance in the preparation of this manuscript. The work was supported by PHS grant NS 11642.

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Behavior and Phylogeny: Constriction in Ancient and Modern Snakes

Abstract. *Comparative analyses of behavior have an underappreciated potential for revealing the role of ethoecological factors in the origins of higher taxa. Twenty-seven species (13 genera) in the advanced family Colubridae exhibited 19 patterns of coil application; one or two patterns were usually consistent within a genus. Forty-eight species (26 genera) in the primitive families Acrochordidae, Aniliidae, Boidae, and Xenopeltidae usually used a single pattern, despite differences in age, size, shape, habitat, and diet. This implies the shared retention of an action pattern used by their common ancestor no later than the early Paleocene. Constriction must have been used as a prey-killing tactic very early in the history of snakes and might have been a behavioral "key innovation" in the evolution of their unusual jaw mechanism.*

Three methods have been used to study the evolutionary history of behavior: structural correlates in extinct taxa, such as the head ornaments of some dinosaurs and the surface relief of cranial endocasts (*1*); fossil trackways and other artifacts (*2*); and comparative analyses of extant forms (*3*). Rigorous studies of the third type are infrequent, perhaps because of recent skepticism regarding behavioral homologies and because it is difficult to obtain large enough samples of taxa to be informative (*4*). However, comparisons across taxa can have important consequences for evolutionary biology. Given a fossil record of separate lineages in a group, an estimate of the minimum age of the behavior can be obtained. The behavior can then be correlated with morphology and paleoecology to suggest selective factors in the adaptive radiation of the group. We now report the modal action patterns used for constricting prey by 75 species of snakes in five families (*6–8*). We also specify an operational rationale for evaluating the origins of similar behavior in different species. Our results contribute to an understanding of ethoecological aspects of the origin of a highly unusual and widespread group of vertebrates and thus illustrate an underappreciated potential for comparative studies of animal behavior.

Constriction is a behavior pattern in which prey is immobilized by pressure exerted from two or more points on a snake's body (*9, 10*). Each portion of the

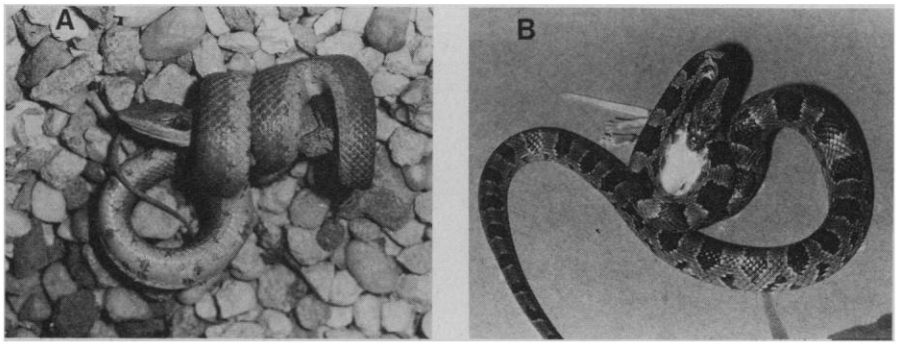

Fig. 1. Constricting coils in snakes. (A) Bahaman dwarf boa, *Tropidophis canus* (Boidae), showing an anterior, horizontal coil with an initial twist in the first loop. Length of the snake, ~ 22 cm. The prey is a lizard (*Anolis carolinensis*). (B) North American corn snake, *Elaphe guttata* (Colubridae), showing an anterior, vertical coil without an initial twist. Length, ~ 40 cm. The prey is a laboratory mouse.

Table 1. Constricting behavior in snakes.

Number	Acro-chordidae	Anili-idae	Boidae	Colu-bridae	Xeno-peltidae
Genera					
In family	1	3	24	300	1
Known to constrict	1	1	23	48	1
Observed	1	1	23	13	1
Species					
In family	3	~ 10	79	~ 1400	1
Known not to constrict	0	?	0	Many	0
Known to constrict	1	2	51	76	1
Observed	1	1	45	27	1
Individuals	1	2	116	60	1
Observations	1	3	346	227	2

body that encircles a prey item once is termed a loop, and all of the loops applied at one time form a coil. Alternative states of four characters were used to describe coil application patterns (*11*).

1) Application movement: (i) in winding, the prey was seized and turned about its long axis by the snake, so that loops were applied like rope on a windlass (*12*); (ii) in wrapping, prey was seized in the jaws, pinned to the substrate, and one to several loops were placed over, under, and around it; and (iii) both winding and wrapping were sometimes used during a single coil application.

2) Initial twist: (i) if a twist was present in the snake's body as the first loop was wrapped or wound, the snake's belly faced its head or against the prey (Fig. 1A); (ii) if a twist was not present, the snake's belly faced away from its head (Fig. 1B); and (iii) occasionally both states occurred in different loops of a single coil.

3) Coil composition: (i) the anterior, (ii) the posterior, or (iii) both parts of the snake were used.

4) The long axis of the coil was usually approximately either (i) horizontal, (ii) vertical, or (iii) at an angle with respect to the substrate; combinations of these states sometimes occurred during a single coil application. This character proved to be more variable than the others and was not used for initially defining the patterns.

Twenty-seven species of colubrids exhibited intergeneric, interspecific, and in some cases individual variability in coil application movements (Table 1). Each character state was observed in more than one species. Nineteen of 27 possible state combinations for the first three characters were seen, and one or two such patterns were usually consistent within a genus (*13, 14*). In contrast, 45 species of boids wound anterior, usually horizontal coils with an initial twist (Table 1) (*15*). This was confirmed for 40 of these species on flat or irregular substrates, seven species striking from elevated beams, and five species striking in water. The prey were usually rodents, but we also observed certain boids constrict birds, lizards, and frogs (*16*). A photograph of a *Boa constrictor* constricting a coati (*Nasua narica*) in Costa Rica demonstrates these states in a free-living snake (*17*). One *Acrochordus javanicus* (Acrochordidae), one *Xenopeltis unicolor* (Xenopeltidae), and two *Cylindrophis rufus* (Aniliidae) also immobilized prey by winding anterior, horizontal coils with an initial twist.

There are four possible origins of similar phenotypes in different taxa: (i) chance; (ii) similar experiential factors in the lives of individual animals; (iii) convergence, in which similar traits are evolved independently in response to similar ecological or morphological constraints; and (iv) phylogenetic continuity and the presence of the trait in a common ancestor. It is difficult to directly test for the last possibility without a continuous fossil record, but the first three can be falsified (*18*). Chance becomes rapidly less likely as more species are involved; similar behaviors in unrelated species with similar selective constraints can be attributed to convergence; the effects of experience can be evaluated within and between individuals; and similar behaviors in related species that vary in ecology, individual experience, and morphology can be attributed to common ancestry.

The diversity of prey types and substrates we used and the presence of the adult pattern in newborn snakes (*19*) refute individual experience as an exclusive explanation of similar coil application behavior in boids. Convergence is also unlikely because our sample included 23 of the 24 genera of boids and encompassed the substantial ecological and morphological variation in this family (*16*). For example, we observed *Exiliboa placata*, a 30-cm terrestrial cloud-forest boa that eats amphibians; *Eryx johnii*, a 75-cm fossorial desert boa that eats lizards and rodents; *Corallus caninus*, a 1.5-m tree boa that eats birds; and *Eunectes murinus*, the semiaquatic anaconda, which reaches a length greater than 8 m and feeds on a variety of large vertebrates. Although most boids are relatively stout-bodied, our sample included the extremely slender Hispaniolan vine boa, *Epicrates gracilis*. It is also noteworthy that we observed the Madagascan (*Acrantophis*, *Sanzinia*) and South Pacific island (*Candoia*) boas, perhaps relicts of an early Gondwanaland radiation (*20*). Since chance, individual experience, and convergence are highly unlikely explanations for the coil application behavior of extant boids, we concluded that the similarity probably reflects the shared retention of an action pattern used by their common ancestor.

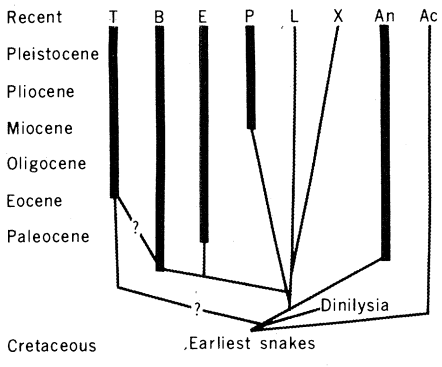

Fig. 2. Evolutionary history of primitive constricting snakes (*30*). Dark bars indicate known age of separate lineages, on the basis of the fossil record; wavy lines indicate presumed relationships. Taxa: *T*, Tropidophiinae; *B*, Boinae; *E*, Erycinae; *P*, Pythoninae; *L*, Loxoceminae; *X*, Xenopeltinae; *An*, Aniliidae; and *Ac*, Acrochordidae. *Dinilysia* is the oldest well-known fossil snake genus.

Fossils of the boid subfamilies Boinae, Erycinae, Pythoninae, and Tropidophiinae indicate some divergence in the family at least as early as the Paleocene, and probably in the Cretaceous [figure 2 of (*8*)]. Our sample included these subfamilies (as well as the even more primitive Loxoceminae, which lacks a fossil record), so ancestral boids probably constricted prey in the Paleocene and perhaps much earlier. *Cylindrophis* and *Xenopeltis* are generally considered survivors of proboid stock (*8*), and *Acrochordus* is probably the most primitive living snake genus (*21*). If our observations accurately indicate the behavior of these genera, this method of coil application might date back to the earliest snakes (*21, 22*).

Functional innovations are often thought to provide a new selective advantage for subsequent structural changes during the origins of adaptive radiations (*23*), but there is rarely evidence for the presence or timing of such shifts. As ancestral snakes evolved increased gape, tactics for overpowering prey too strong to have been eaten while it struggled would have become advantageous (*24*). It follows that constriction might have been a behavioral protoadaptation that both permitted and favored evolutionary loss of the mandibular symphysis and development of a highly movable (streptostylic) quadrate bone, the key modifications for ingesting large prey items (*24*). However, Frazzetta (*25*) suggested that the earliest well-known snake, *Dinilysia patagonica* of the Upper Cretaceous, was not a constrictor. *Dinilysia* is usually placed with acrochordids, aniliids, boids, bolyerids, uropeltids, and xenopeltids in the superfamily Booidea (*26*). Like aniliids (its closest living relatives), the stout jaws of *D. patagonica* seem well suited for crushing prey, and the aniliids that Frazzetta observed (species not stated) did not constrict. Furthermore, birds and mammals, thought to be especially vulnerable to constriction because of high metabolic rates, were not yet widespread in the Cretaceous. We know of nothing in the morphology of *D. patagonica* that would preclude constriction (*27*), and Frazzetta's arguments are weakened by the fact that many Recent snakes (including some boids and aniliids) use constriction to subdue ectotherms (*28*). Our study provides evidence for the great antiquity of constriction in boids and probably the entire superfamily Booidea. We therefore suggest that *D. patagonica* probably did constrict prey and that this behavior was an ethological "key innovation" (*29*) in the early evolution of snakes.

A recent review concluded that there are no known behavioral homologies above the family level in vertebrates (*5*). We have demonstrated that a modal action pattern is probably homologous among at least four families of snakes. Broader issues are indicated. What kinds of movements are stable over long periods of evolutionary time? What kinds change rapidly, and why? How are the rates and directions of change constrained by other factors? Rigorous comparative studies might provide answers to these and other questions regarding the evolution of behavior and the role of behavior in evolution.

HARRY W. GREENE*
Department of Zoology,
University of Tennessee,
Knoxville 37916
GORDON M. BURGHARDT
Department of Psychology,
University of Tennessee

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4. For a thought-provoking critique of the concept of behavioral homology, see J. W. Atz (*5*). We regard Atz's criticisms as applicable to comparative studies of any aspect of the phenotype. For a discussion of the definition of homology, with special reference to behavior, see J. P. Hailman [in *Evolution, Brain, and Behavior: Persistent Problems*, R. B. Masterton, W. Hodos, H. Jerison, Eds. (Erlbaum, Hillsdale, N.J., 1976)].
5. J. W. Atz, in *Development and Evolution of Behavior: Essays in Memory of T. C. Schneirla*, L. R. Aronson, E. Tobach, D. S. Lehrman, J. S. Rosenblatt, Eds. (Freeman, San Francisco, 1970).
6. The classification of primitive snakes is controversial; we followed A. d'A. Bellairs [*The Life of Reptiles* (Weidenfield and Nicholson, London, 1969)] with minor modifications. The changes suggested by S. B. McDowell (*7*) and G. Underwood (*8*) may prove appropriate but do not affect our conclusions. We examined the following subfamilies and genera of boids: Boinae (*Acrantophis, Boa, Candoia, Charina, Corallus, Epicrates, Eunectes, Lichanura, Sanzinia*), Calabariinae (*Calabaria*), Erycinae (*Eryx, Gongylophis*), Loxoceminae (*Loxocemus*), Pythoninae (*Aspidites, Bothrocheilus, Chondropython, Liasis, Morelia, Python*), and Tropidophiinae (*Exiliboa, Trachyboa, Tropidophis, Ungaliophis*).
7. S. B. McDowell, *J. Herpetol.* **9**, 1 (1975).
8. G. Underwood, in *Morphology and Biology of Reptiles*, A. d'A. Bellairs and C. B. Cox, Eds. (Academic Press, London, 1976).
9. Literature accounts of constriction have usually not described the movements involved in coil application. T. H. Frazzetta [*J. Morphol.* **118**, 217 (1966)] accurately described and figured the method used by *Python*. Shrewsbury (*10*) dealt with five species of colubrids. D. E. Willard [*Copeia* **1977-I**, 379 (1977)] observed 22 species of boids and 19 species of colubrids; he recognized only three methods of constriction, none of which adequately characterizes any pattern. O. E. Greenwald (*Copeia*, in press) studied the coil application movements of *Pituophis* with high-speed cinematography; her observations confirm our characterization of the behavior of this genus. A detailed critique of these studies and an extensive account of the behavior and ecology of constricting snakes are presented elsewhere [H. W. Greene, thesis, University of Tennessee (1977); _____, in preparation].
10. K. Shrewsbury, *Proc. Okla. Acad. Sci.* **48**, 274 (1969).
11. We recorded topographic variables with checksheets, videotapes, and 8-mm cine film of snakes in our laboratory and in zoos. Our information on *Acrochordus* is based on a photographic sequence provided by R. Honegger of the Zurich Zoo.
12. This metaphor was suggested by Shrewsbury (*10*).
13. For example, horizontal or vertical coils were wound without an initial twist (*Boaedon, Elaphe, Pituophis, Trimorphodon*), wound with a twist (*Arizona*), or wrapped with a twist (*Spalerosophis*). Individual *Lampropeltis* and *Spilotes* used several of these patterns as well as posterior coils that were wrapped with or without a twist. Most measures of behavioral stereotypy are not appropriate for nominal variables. We assessed stereotypy across the four characters as $S = 2w/(O + E)$, where w is the minimum sum of the frequencies of states in common between the expected and each observation (that is, the sum of the expected frequencies for each state observed in a particular coil application event), E is the average frequency of each state for all observations, and O is the sum of the frequencies of all states for each observation (S. E. Riechert, *Behav. Ecol. Sociobiol.*, in press). For nine genera with three or more observations, S ranged from 0.17 to 0.92. We measured variability in patterns (based on combinations of the first three characters) as the percentage of nonmodal patterns (V) for each taxon and the weighted average percentage of nonmodal patterns (A_w) across taxa (expressed as decimal fractions) [H. K. Voris, *Syst. Zool.* **20**, 442 (1971)]. For the 13 colubrid genera, V ranged from 0 to 0.75 and $A_w = 0.46$.
14. Among colubrids, some coils of *Arizona* and *Lampropeltis* resembled those of boids; two of three *Arizona* coils were horizontal, as in primitive snakes. Of 82 *Lampropeltis* coils, 19 were horizontal, 39 were vertical, and 24 were angled or some combination of these states. A published drawing of *Regina alleni* (Colubridae) suggests that this species might also at least sometimes use the boid pattern [R. Franz, *Herpetologica* **33**, 91 (1977)]. Constriction perhaps evolved independently and repeatedly in the Colubridae, but observations of additional genera and species will be necessary for a thorough phylogenetic and ontogenetic assessment of this perplexing and now highly successful family [R. Estes, *Forma Functio* **3**, 139 (1970); G. B. Rabb and H. Marx, *Evolution* **27**, 69 (1973)].
15. Of 327 coil applications by boids for which the first three characters were observed, 299 (91.4 percent) were wound, anterior, and with a twist. This pattern was modal (or exclusive) for each species of boid studied. Of 26 other possible patterns, 8 were observed a total of 28 times (8.6 percent). For 26 genera of booid snakes (332 observations that included the first three characters), pattern variability was low ($A_w = 0.08$) (*9*). Stereotypy across characters in boids was high; mean S values for 13 genera with three or more observations were 0.81 to 0.96. For 29 observations of a single *Epicrates cenchria*, S ranged from 0.75 to 0.89 ($\bar{X} = 0.83$). Of 340 applications for which coil orientation was recorded, 281 (82.6 percent) were horizontal, 28 (8.2 percent were vertical, and 31 (9.2 percent) were other states.
16. The diversity of boids in our sample was as follows (number of species, followed by genera in parentheses). Natural habitat: aquatic, 4 (2); terrestrial, 35 (18); arboreal, 7 (5). Prey accepted by captives: frogs, 3 (3); lizards, 8 (4); birds, 8 (6); mammals, 38 (21). Average adult size: ≤ 0.5 m, 4 (3); 0.6 to 0.9 m, 15 (10); 1.0 to 1.9 m, 15 (10); 2.0 to 2.9 m, 6 (5); ≥ 3.0 m, 6 (4).
17. D. H. Janzen, *J. Mammal.* **51**, 387 (1970).
18. H. P. Zeigler, *Ann. N.Y. Acad. Sci.* **223**, 126 (1973); J. P. Hailman and R. G. Jaeger, *Anim. Behav.* **22**, 757 (1974).
19. Thirteen newborn *Epicrates cenchria* (from two litters), three newborn *Corallus enydris* (from two litters), and one newly hatched *Python molurus* constricted their first prey with coils applied like those of adult boids; one newborn *E. cenchria* wound an anterior coil without a twist.
20. J. Cracraft, *Ann. Rev. Ecol. Syst.* **5**, 215 (1974).
21. S. B. McDowell, *J. Herpetol.*, in press.
22. Our sample included *Loxocemus bicolor*, usually considered the most primitive living boid. McDowell (*7*) argued that it should be treated as a separate family, more closely related to aniliids, uropeltids (in which he placed *Cylindrophis*), and xenopeltids than to boids. If this view is correct and if the boid pattern occurred in the common ancestor of these snakes, constriction is surely older than the Paleocene. Observations on the behavior of anguimorph lizards (probably the closest living relatives of snakes) also suggest that the boid pattern is a shared primitive trait (H. W. Greene and D. Gove, in preparation).
23. C. Gans, *Biomechanics: An Approach to Vertebrate Biology* (Lippincott, Philadelphia, 1974).
24. _____, *Am. Zool.* **1**, 217 (1961).
25. T. H. Frazzetta, *Forma Functio* **3**, 205 (1970).
26. R. Estes, T. H. Frazzetta, E. E. Williams, *Bull. Mus. Comp. Zool.* **140**, 25 (1970).
27. J. A. Ruben [*Herpetologica* **33**, 1 (1977)] suggested that perhaps only stout-bodied snakes can constrict. Examples of slender constrictors include *Epicrates gracilis* (Boidae) and *Stilosoma extenuatum* (Colubridae). In any case, the partial postcranial skeleton suggests that *Dinilysia patagonica* was relatively stout-bodied (R. Estes, personal communication).
28. Theoretical considerations suggest that constriction should be associated with proportionately heavy prey, not endothermic prey [C. Gans (*24*); H. W. Greene, in preparation]. Among primitive snakes, we have observed constriction of ectotherms by *Cylindrophis, Candoia, Corallus, Epicrates, Exiliboa, Loxocemus, Trachyboa, Tropidophis*, and *Ungaliophis*.
29. G. von Wahlert, *Syst. Zool.* **14**, 288 (1965); K. F. Liem, *ibid.* **22**, 425 (1973).
30. Based on S. B. McDowell (*7, 21*) and G. Under-

wood (8), who discuss the controversial position of tropidophine boas relative to other primitive snakes.

31. The breadth of this study was made possible by the personnel and collections of zoological parks in Atlanta, Georgia; Columbus, Ohio; Dallas, Fort Worth, and Houston, Texas; and Knoxville, Tennessee. We especially thank J. A. Campbell for the exceedingly rare *Exiliboa*, L. Porras for the *Cylindrophis*, and R. Honegger for photographs of *Acrochordus*. G. W. Barlow, H. Drummond, B. A. Dugan, R. Estes, C. Gans, G. A. Middendorf, III, G. B. Rabb, P. Sutherland, and P. Weldon commented on drafts of the manuscript. Supported by a University of Tennessee honors fellowship to H.W.G.; grants from Sigma Xi, the National Science Foundation, the American Museum of Natural History (Theodore Roosevelt Memorial Fund), and the Field Museum of Natural History (Karl P. Schmidt Fund) to H.W.G.; and grants from the National Institute of Mental Health and the National Science Foundation to G.M.B.

* Present address: Laboratories of Anatomy, School of Veterinary Medicine, University of Pennsylvania, Philadelphia 19104.

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Development of Sensitivity to Pictorial Depth

Abstract. *Sensitivity to static pictorial information for depth develops between 22 and 26 weeks of age. When conflicting binocular and surface-texture information was minimized, 26- to 30-week-old infants directed their reaching to the apparently closer side of a photograph of a window rotated in depth. Younger infants, from 20 to 22 weeks of age, did not direct their reaching to the pictorially nearer side of the display but did reach with a high degree of directionality when presented with a real window rotated in depth.*

In the 15th century, Leonardo da Vinci described a set of techniques for representing the third dimension on a flat canvas. He pointed out that light, shadow, and linear, detail, and aerial perspective could specify distance in a painting, but that other depth information, such as movement and binocular parallax, could not be used on a flat surface. More recently, psychologists have described additional monocular cues for depth, including relative size, interposition, and texture gradients (*1*). Olson and Boswell have demonstrated that 2-year-old children will respond to pictorial depth as specified by interposition and relative height in the picture plane but not to the depth information provided by relative size (*2*). Although earlier research has suggested that young infants are sensitive to binocular and kinetic information for depth, there are reports that infants younger than 16 weeks of age are insensitive to pictorial depth (*3*). Our study provides evidence that when conflicting binocular and surface information is minimized, infants from 26 to 30 weeks of age are sensitive to pictorial depth; younger infants from 20 to 22 weeks of age do not show such sensitivity.

The pictorial display used in these experiments was a fronto-parallel Ames trapezoidal window (*4*), which creates an effective illusion under monocular viewing of a rectangular window oriented at 45° to the viewer, such that one side appears closer than the other. We hypothesized that if an infant were sensitive to the pictorial information for depth specified in the trapezoidal window, we would expect his or her reaching to be directed to the apparently nearer side.

Other researchers have reported that an infant will reach more frequently to a near rather than a far object (*5*). In a preliminary experiment, we determined that infants would direct their reaches with enough accuracy to exhibit sensitivity to the differential distances of the two sides of a slanted surface. Thirteen 26- to 30-week-old infants were presented with a real rectangular window rotated 45° about a vertical axis, with either the left or the right side of the window brought nearer to the infant. Presentations were randomized as to which side was closer. Direction of reaching was scored from a videotape recording. The infants' reaches were directed toward the closer side of the window on 75 percent of the trials, and toward the farther side on only 6 percent of the trials. The remaining reaches were directed either to the middle or simultaneously to both sides of the display.

For experiment 1, the trapezoidal window was created by photographing from 21 cm a real rectangular window rotated 45° about the vertical axis (Fig. 1A). The resulting black-and-white matte photograph was enlarged during printing to produce a retinal image that was the same size as that projected by the real window when viewed from 21 cm. The photograph was glued to a metal sheet cut to match the shape of the pictured object, allowing the infant to see through the internal spaces of the display and thereby minimizing the pictorial surface texture. The larger and apparently nearer side was actually 25.5 cm in height, and the smaller side, 14 cm in height. The width of the display was 20.3 cm.

A control display, lacking a pictorial surface, was created to test for the possibility that reaching might be determined by the unequal size of the sides of the trapezoidal display (Fig. 1B). This display was produced by photographing the real rectangular window in the fronto-parallel plane. Two prints were made, one matching the vertical dimensions of the small side of the trapezoidal print, and one matching the larger side. The two prints were combined, and the shape was cut from metal. Again, the internal spaces were removed. The surface was painted gray to match approximately the overall reflectance of the trapezoidal display. The control display therefore appeared to be a single object, with one side smaller than the other side, but with no information that the sides were at different distances.

Fifty infants from 26 to 30 weeks of age served as subjects; half were presented with the trapezoidal display, and half with the control display. To eliminate binocular information, each infant wore an eye patch over the left eye or a small pair of eyeglass frames with the left eye occluded. The infant sat upright in a

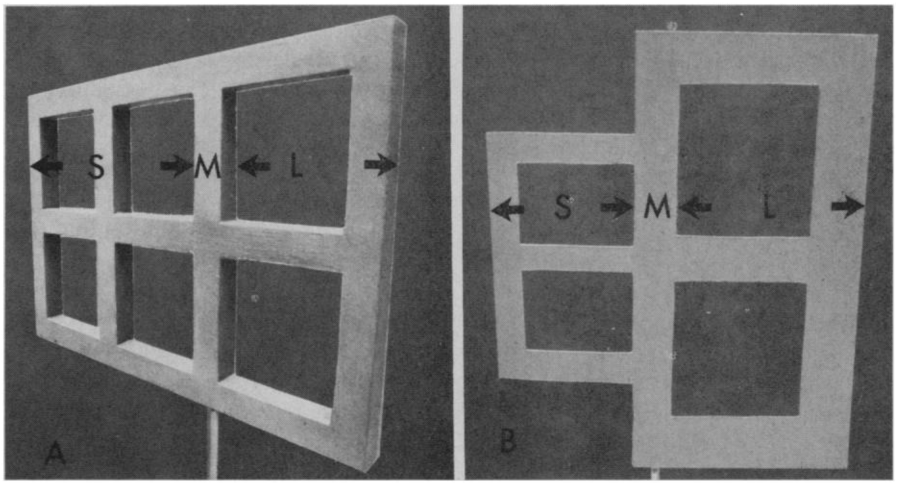

Fig. 1. Display windows, mounted on rods 3 feet (0.914 m) in front of dark blue cloth background. (A) Fronto-parallel Ames trapezoidal window. (B) Control display. Abbreviations: *L*, large side; *M*, middle area; and *S*, small side.