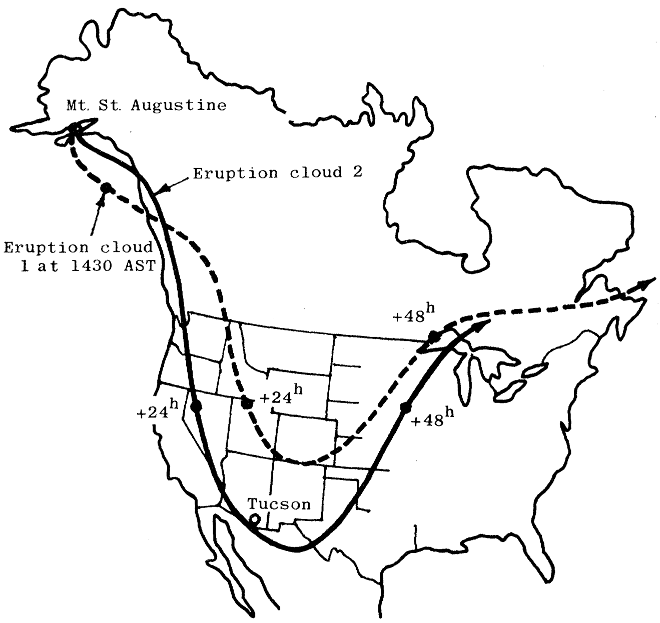

Fig. 2. Trajectory of the two ash clouds from the St. Augustine eruption, deduced from the 300-mbar level meteorological data.

The lack of enhancement of the 20-km aerosol layer led us to conclude that either the eruption of St. Augustine was small compared to that at Agung, Irazu, or Fuego, or that the total amount of reactive gases which lead to the enhancement of the 20-km layer through photochemical reactions was smaller. We do not think that the ballistic strength of these four eruptions is important in causing high altitude "ash stratum" effects, as discussed by Meinel and Meinel (*3*). Instead, we believe these effects are influenced by the integral of the SO_2 emission during the lifetime of the activity of each volcano.

Shaw has provided the trajectory of the two principal eruption clouds of St. Augustine, as shown in Fig. 2. This trajectory is based on velocities and directions of the 300-mbar weather maps for the dates involved, and indicates that the second cloud did pass over Tucson. This trajectory would predict passage of the cloud beginning at 0230 M.S.T. on 25 January, whereas it was observed at 1630 M.S.T. The time difference could be explained because the cloud may have been at a different pressure altitude than 300 mbar (9.2 km) and thus traveling at a lower velocity of approximately 94 km/hour.

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References

1. J. Kienle, private communication with G.E.S.
2. M. P. Meinel and A. B. Meinel, *Science* **142**, 582 (1963); A. B. Meinel and M. P. Meinel, *ibid.* **188**, 477 (1975).
3. A. B. Meinel and M. P. Meinel, *ibid.* **155**, 189 (1967).

4 May 1976

Suckling in Newborn Rats: Eliminated by Nipple Lavage, Reinstated by Pup Saliva

Abstract. *Chemical lavage of the nipples of anesthetized maternal rats virtually eliminated suckling by their 4- to 5-day-old pups. Normal suckling was immediately reinstated, however, by painting a vacuum distillate of the wash or of pup saliva onto the nipples. Thus, a substance necessary to direct and release suckling, possibly rat pup saliva, appears to coat the nipple surface.*

Suckling is the defining behavioral characteristic of Mammalia. Yet, despite its preeminence, little is known about either the factors that control newborn suckling or the means by which these controls recede during the course of ontogeny. To identify these factors we studied suckling in rats. Unlike newborns of other species, which are led to or placed on the nipple (*1*), newborn rats locate and suckle the teat without maternal assistance, even from the first. Also, in contrast with others, infant rats do not suckle objects other than the teat. Thus, suckling in the blind and deaf newborn rat is controlled by a narrow spectrum of stimuli—olfactory, thermal, and tactile—that define the mother and, more particularly, her mammary area.

In seeking the stimuli that release suckling we were guided by the work of Kovach and Kling (*2*) and Tobach and coworkers (*3*) who, by making very young kittens and rats anosmic through bulbectomy, eliminated suckling. Centrally produced olfactory deficits are difficult to interpret, however (*4*), the more so in infant rats whose nervous systems are rapidly maturing and differentiating. Accordingly, in a more direct approach, we determined if removing olfactory cues from the mother's nipples disrupted suckling in normal newborn rats and, in the counter experiment, if cue replacement reinstated suckling. We report that removal of such cues by chemical lavage prevents previsual and preaudial 4- to 5-day-old rats from either finding or attaching to nipples, even when held directly in contact with them. Returning the scent reinstates suckling, as does pup saliva, presumably a source of this vital olfactory cue.

Sprague-Dawley rats were mated and bred in our colony. A litter of 10 to 12 pups and their natural mother were used in each test. At the start of each test session, half the pups from a litter were removed and placed in a warm and moist incubator; this is the deprived group. Four hours later the mother was anesthetized with Equi-thesin (2 ml per kilogram of body weight), a barbiturate-based agent that blocks milk letdown under these test conditions (*5*), and laid supine in a clear Plexiglas trough. The method of Hall *et al.* (*6*) was used to assess suckling behavior. Deprived and nondeprived pups were placed in successive groups of three next to the anesthetized mother. Thus, the full complement of maternal cues were presented to the pup, but in the absence of maternal participation. Number of pups attaching, latency to attach, and general activity were determined during the 5-minute test. After all pups were tested once with this procedure, the mother was removed from the trough and placed on a table. Then, following a protocol similar to that of Drewett *et al.* (*7*), each pup was assigned a different nipple, and gently held and positioned by the experimenter so that its snout was in direct contact with the assigned teat. Latencies to attach were recorded; a 1-minute ceiling was employed. While both methods appear to be sensitive indices of suckling, the method of Hall *et al.* (*6*) (pups on mother) demands that the pups locate the nipples, while that of Drewett *et al.* (7) (pups on nipples) does not. After testing, the deprived pups were returned to the incubator, and nondeprived pups were given to a lactating mother whose own pups (of the same age) had been removed.

The anesthetized mother was then moved to a different room where her nipples were subjected to chemical lavage. Specifically, a Teflon tube, slightly larger in diameter (5 mm) than the nipple base, was lowered over the teat and gentle suction (less than 100 mm-Hg below atmospheric pressure) was applied. A 3:2 solution of methylene chloride and 95 percent ethanol was pipetted around the bottom of the tube and percolated around the nipple surface until the tube was removed; the increased air circulation delivered the solution to a collecting tube. Each nipple was repeatedly extracted, the entire process taking 2 hours (8).

The wash solution was vacuum distilled (Buchi-Rotovapor R) at 30°C to remove the organic solvents. After all the solvent used for the lavage had evaporated off the mother's nipples (9), the pups were tested on the extracted mother. Then the residue from the extraction was painted onto the mother's nipples and the pups were tested a third time. A total of 44 pups from four litters were tested under these conditions in a within-subject design.

Nipple lavage virtually eliminated suckling. Restoring the distillate essentially reinstated suckling to prewash levels. Thus, it appeared that a substance, attractive to the pups, was found on the nipple surface. Conceivably, this substance was a maternal secretion; alternatively, the pups themselves were depositing this substance on the nipple. We studied the latter alternative because we (10) and others (2) observed that the probability of attachment to a recently suckled nipple is very high. Accordingly, the entire series was replicated in an additional 34 pups (three litters), only now, instead of a distillate of the nipple wash, a saliva extract obtained from deprived pups (11) was painted onto the nipples.

There was a highly significant overall treatment effect for all tests. The effect of deprivation was not significant, but the deprivation-treatment interaction was statistically significant in two cases (12). For clarity of presentation, subjects at different deprivation levels were pooled. Nipple lavage drastically reduced the percentage of pups attaching to the nipples: from 83 to 7 percent for pups placed on mother (Fig. 1, upper right, open versus filled columns) and from 86 to 11 percent for those placed on nipple (Fig. 1, lower right). Latencies to attach were also profoundly affected by nipple lavage (Fig. 1, left). They increased to virtually ceiling values under both test conditions. Pups when placed on the washed mother otherwise behaved in much the same way as they did on the mother before wash. In both cases activity rose and exploration ensued, although nearly all pups failed to locate the nipples of the washed mother. Aversive reactions to the washed nipples were not observed, and pups were occasionally seen sleeping with their noses directly contacting a nipple. Thus, removing an essence from the nipple prevents 4- to 5-day-old rats from either locating or apprehending the teat. The scent does not just aid in nipple location, but appears necessary to release suckling, even after nipple contact has been ensured. The absence of mouth movements and probing responses that usually precede attachment and the efficacy of pup saliva in releasing suckling lead us to believe that the chemical cue is olfactory.

Restoring either the removed extract or that obtained from pup saliva dramatically reversed the disruption. For pups placed on mother, mean latency to attach plummeted from that on the washed mother [extract: $P < .001$; saliva: $P < .001$; Scheffé test (13)], and did not differ statistically from latency to attach to mother before washing (extract: $P > .05$; saliva: $P > .05$; Scheffé test). The same holds for percentage of pups attaching [extract versus wash: $Z = 5.55$, $P < .001$; saliva versus wash: $Z = 5.78$, $P < .001$; extract versus fresh: $Z = 1.90$, $P > .05$; saliva versus fresh: $Z = 0.60$, $P > .20$; two-proportion test (14)].

The behavior of pups when placed on the nipple was likewise affected. Both extract and saliva replacements dramatically improved latencies to attach and percentage of pups attaching. All comparisons between washed and replacement tests were highly significant statistically (15). The percentage of pups attaching to saliva-treated nipples did not differ from that on the fresh mother. On the other hand, differences in latency to attach between the fresh and treated conditions, although small, were reliable (extract: latency 13 seconds longer than for fresh, $P < .001$; saliva: latency 8 seconds longer than for fresh, $P < .005$; Scheffé test), as was the percentage comparison between the fresh mother and extract return condition. We are inclined to minimize the importance of these small differences, mainly because at the time of the extract test some pups had been deprived for about 11 hours and the mother anesthetized for 7 hours. Either hyperactivity or slight nipple involution could account for these small differences. In any event, scent replacement sharply reversed the suckling deficit: the behavior of pups placed on the "reconstituted" mother did not differ from placement on the fresh mother; and the behavior of pups placed on the nipples closely approximated normal. Taken together,

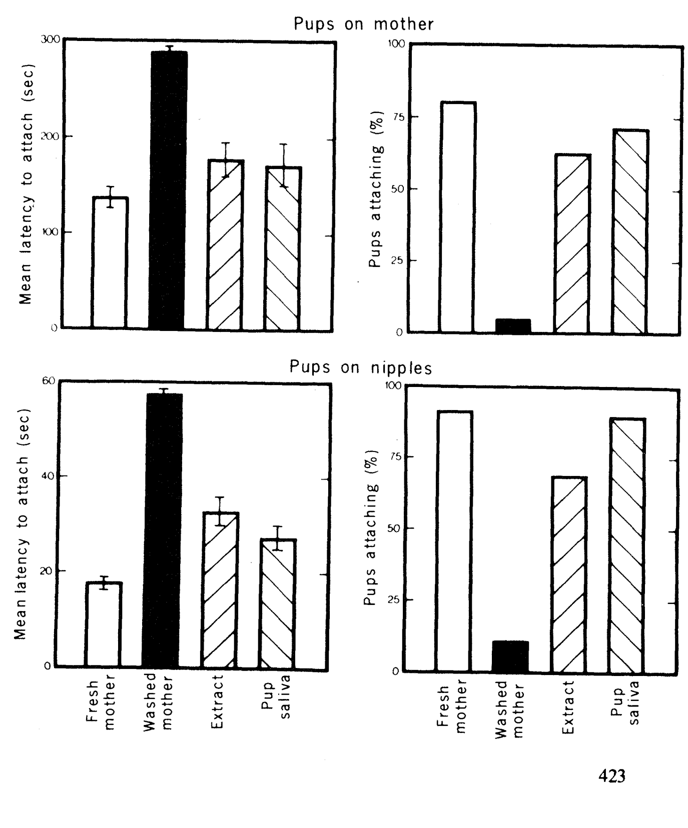

Fig. 1. Mean latencies (± standard error of mean) for nipple attachment and percentages of pups attaching for pups placed on the mother or placed on the nipple following the manipulations described in the text.

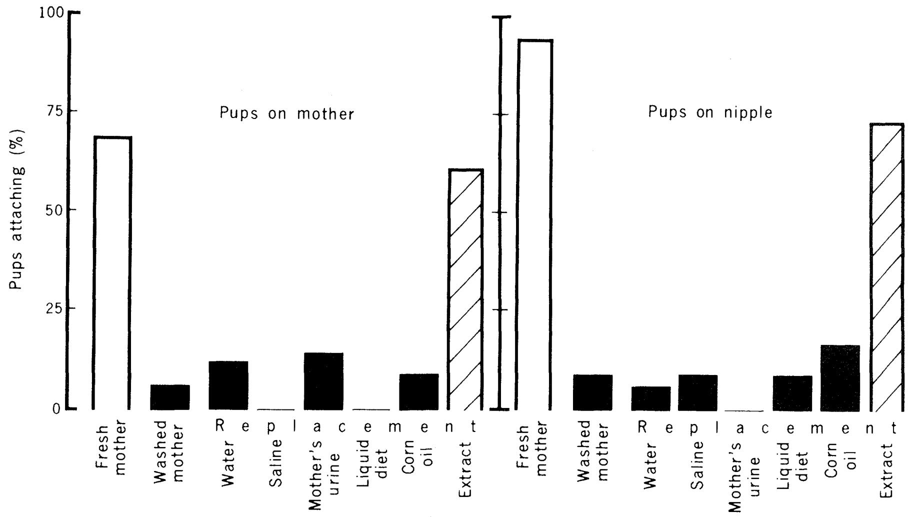

Fig. 2. Percentage of pups attaching to the unwashed mother, to washed mother, and to washed mother following replacement with water, isotonic saline, maternal urine, a milk-based liquid diet, corn oil, or nipple wash extract.

these experiments demonstrate that an olfactory cue is a necessary stimulus for the release of suckling in rats of this age. Also, pup saliva is a sufficient, although not necessarily the exclusive, source of this olfactory cue. Analysis of both the nipple wash extract and pup saliva residue by thin-layer chromatography indicates that they contain similar components.

Several controls have established the specificity of the effect. First, reinstatement of suckling is not due to a possible resecretion or synthesis of the scent by the mother during the delay between tests. Twenty-three pups (two litters) were twice tested on their washed mother, with a 2-hour delay between tests. Both percentage of pups attaching and the latencies to attach were unaffected by this delay, a result indicating the insufficiency of a time lag alone to reinstate attachment. Painting with extract, however, immediately returned suckling to prewash levels.

Next, we considered whether replacement worked simply because it was wet, oily, contained milk sugar, smelled like the mother, or simply camouflaged an aversive odor. Thirty-three pups (three litters) were tested on their own mother, first after she was anesthetized, then washed, and finally after each of the following substances were applied to the nipples: water, isotonic saline, mother's urine, corn oil, and liquid diet. None of these ingredients reinstated suckling above the washed baseline (Fig. 2) (all $P > .16$). As before, the extract returned suckling to prewash levels.

Finally, the direct application of the methylene chloride–ethanol solution to the nipples and ventrum without vacuum aspiration failed to disrupt suckling after drying in 14 pups. Thus, the disruption in suckling produced by the wash procedure is not simply due to depositing an aversive chemical odor. Rather, it appears that a specific chemical substrate, necessary to direct and release suckling, coats the nipple surface. Removal of this cue by chemical lavage virtually eliminates suckling. Normal suckling behavior could not be reinstated by a variety of nonspecific substances, but was reinstated by painting the nipple with either a vacuum distilled residue of the wash or of pup saliva.

The importance of this olfactory cue for normal suckling behavior in 4- to 5-day-old rats has been established, as well as the possibility that the pup, through its saliva, refurbishes the cue during this part of the suckling period. Yet, these results cannot account for the very first attachment. We see four major alternatives: (i) a pheromone is secreted by the nipple itself; (ii) the mother's saliva, at least during parturition, contains the cue; (iii) the birth fluids contain the cue and are spread appropriately by the mother; and (iv) the first attachment is not under olfactory control. Of particular interest here is the fact that pregnant female rats undergo a dramatic increase in the amount of time spent grooming and licking their nipples in the few days before birth (*16*).

The generality of these findings remains to be established both for rats during the course of ontogeny and for other species. In regard to the former, initial data obtained from seven additional litters of rats tested 2 to 9 days after birth confirm the results reported here. Whether they apply to older rats whose visual and auditory systems have developed remains to be determined. Likewise, phylogenetic generalizations must be made with caution. However, mothers of several species appear, by licking, to direct their young to the nipples for the initial suckling bouts (*1*, *17*).

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References and Notes

1. G. Alexander and D. Williams, *Science* **146**, 665 (1964); D. B. Stephens and J. L. Linzel, *Anim. Behav.* **22**, 628 (1974); J. S. Rosenblatt, in *The Biopsychology of Development*, E. Tobach, L. R. Aronson, E. Shaw, Eds. (Academic Press, New York, 1971), pp. 345–410.
2. J. K. Kovach and A. King, *Anim. Behav.* **15**, 91 (1967).
3. E. Tobach, Y. Rouger, T. C. Schneirla, *Am. Zool.* **7**, 792 (1967); P. J. Singh and E. Tobach, *Dev. Psychobiol.* **8**, 151 (1975).
4. B. M. Wenzel, in *Limbic and Autonomic Nervous System Research*, L. V. Dicara, Ed. (Plenum, New York, 1974), pp. 1- J. R. Alberts, *Physiol Behav.* **12**, 657 (1974); T. P. S. Powell, W. M. Cowan, G. Raisman, *J. Anat.* **99**, 791 (1965).
5. D. W. Lincoln, A. Hill, J. B. Wakerley, *J. Endocrinol.* **57**, 459 (1973).
6. W. G. Hall, C. P. Cramer, E. M. Blass, *Nature (London)* **258**, 318 (1975).
7. R. F. Drewett, C. Statham, J. B. Wakerley, *Anim. Behav.* **22**, 907 (1974).
8. Pilot data have indicated that this is a useful end point. Additional washes appear devoid of constituents when examined by thin-layer chromatography.
9. Twenty to 30 minutes are allowed for evaporation. Methylene chloride has a low boiling point (39.9°C), which allows for rapid evaporation from the 36°C nipples. Its residue is insignificant (0.0003 percent). We generally screen the washed nipples with the unused pups from the surrogate mother. Marked aversive reactions are seen to the nipples before drying, but never after dryness. Application of the agents to the nipples without vacuum aspiration fails to disrupt suckling after evaporation.
10. W. G. Hall, C. P. Cramer, E. M. Blass, in preparation.
11. The saliva was obtained for each test from approximately four pups removed from the surrogate mother and housed in the incubator during the preceding day. They were anesthetized by freezing and their mouths were gently aspirated. Water was added to the oral cavity dropwise and aspirated as well. The lines were purged with the mixture of methylene choloride and ethanol; this was also collected. The entire mixture was vacuum distilled to near dryness at 35°C.
12. Overall analysis of variance indicates a high treatment effect with extract replacement ($F = 40.30$; $F = 56.52$; d.f. = 2, 84; $P < .001$) and saliva replacement ($F = 33.03$; $F = 88.46$; d.f. = 2, 64; $P < .001$) under both test protocols. The deprivation effect was not significant ($F = 2.34$, $F = 0.07$, $F = 0.02$, $F = 2.88$, all $P > .1$) with both replacements under either test protocol. Likewise, the interaction between deprivation and treatment was nonsignificant for the saliva replacement tests ($F = 0.36$, $F = 0.86$, $P > .2$) but was significant for the extract return conditions ($F = 3.28$, $F = 3.47$, $P < .05$). In this later instance the pups in the deprived groups showed a slightly greater reinstatement of suckling.
13. G. Keppel, *Design and Analysis: A Researcher's Handbook* (Prentice-Hall, Englewood Cliffs, N.J., 1973), pp. 133–163.
14. J. L. Bruning and B. L. Kintz, *Computational Handbook of Statistics* (Scott, Foresman, Glenview, Ill., 1968), pp. 199–201.
15. The comparison between wash and extract replacement was highly significant ($P < .001$) under both test protocols as was the difference between wash and saliva replacement ($P < .001$, Scheffé test). Comparisons by two-proportion test (*13*) were similar ($Z = 5.55$, $Z = 5.45$, $Z = 5.78$, $Z = 6.55$, all $P < .0001$).
16. J. S. Rosenblatt and D. S. Lehrman, in *Maternal*

Behavior in Mammals, H. L. Rheingold, Ed. (Wiley, New York, 1963).
17. E. S. E. Hafez, M. W. Schein, R. Ewebank, in *The Behavior of Domestic Animals*, E. S. E. Hafez, Ed. (Baillière, Tindal & Cassell, London, 1969), pp. 253–257; E. S. E. Hafez, R. B. Cairns, C. V. Hulet, J. P. Scott, in *ibid.*, pp. 310–313; I. E. Selman, A. D. McEwen, E. W. Fisher, *Anim. Behav.* **18**, 284 (1970).
18. Supported by NSF grant BMS75-01460 and NIH grant AM18560 to E.M.B. We thank B. A. Teicher for invaluable technical advice.

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Sex and the Single Hemisphere: Specialization of the Right Hemisphere for Spatial Processing

Abstract. *Specialization of the right hemisphere for spatial processing was studied in 200 normal boys and girls between 6 and 13 years of age. Boys performed in a manner consistent with right hemisphere specialization as early as the age of 6. Girls showed evidence of bilateral representation until the age of 13. The results suggest a sexual dimorphism in the neural organization underlying cognition during a major period of childhood. The results, which have implications for reading instruction, are discussed in terms of a possible sex difference in neural plasticity during development and the clinical consequences of such a difference.*

The right hemisphere plays the major role in adults in nonlinguistic, spatial, and holistic cognitive processing, which includes two (possibly related) sets of skills: (i) visual- and tactile-spatial processing and (ii) nonlinguistic and nonsequential auditory processing (*1*). Study of hemisphere specialization during development has focused on the left hemisphere (*2–6*) and relatively ignored the right (*7–9*), particularly its role in spatial processing. Unlike language, spatial perception is prominent in the behavior of both human infants and nonhuman species. Consequently, hemisphere specialization for spatial processing may be critical in human ontogenetic and possibly in phylogenetic development of lateralization of function in general, and it is an important aspect of the neural substrate of cognition.

I now report some initial information concerning the early course of specialization of the right hemisphere for spatial processing, with regard to both age and sex. In the course of experiments with children, it was discovered that, in boys, the right hemisphere has the dominant role in processing nonlinguistic spatial information by at least age 6 years; in contrast, in girls the right hemisphere is not dominant even by age 13 years, but rather, there is bilateral representation. These results suggest (i) that boys have greater hemisphere specialization and (ii) that there is a sexual dimorphism in the neural organization related to cognition for an extended period of development.

Suitable methods for studying specialization of the right hemisphere in children have been lacking (*10*). I used a new behavioral test procedure involving tactual perception, which was devised specifically to assess the relative participation of the two hemispheres in spatial processing in neurologically intact children (*11*). In essence, the test requires that the subject palpate simultaneously, out of view, two different meaningless shapes for 10 seconds, each one with the index and middle fingers of one hand. He then tries to choose these two shapes from a visual display containing six such shapes. After many practice trials, ten test trials are given; the scores are the number of left- and right-hand objects correctly chosen. The test has two crucial features. (i) It requires tactile shape discrimination, which, in adults, depends mainly on the right hemisphere (*12*). Furthermore, to make the test as dependent on the right hemisphere as possible, the stimuli were designed to be meaningless shapes, not readily labeled; the simultaneous palpation of different stimuli tends to hinder linguistic encoding; and the incorrect items in the recognition display were designed to have details similar to those of the test stimuli, so that a correct response depends on a gestalt perception of the whole stimulus. (ii) Different stimuli are presented simultaneously, here termed "dichhaptic" stimulation: "dich," from dichotomy, to refer to the simultaneous and different stimulation; and "haptic," referring to active touch. It was hoped that this procedure would produce competition in the neural system (*13, 14*) such that any superiority of the right hemisphere for the required cognitive processing would be reflected in superior perception of the contralateral (left) hand stimuli (*15*). Such was the empirical result in an earlier study of a small group of boys (*11*), but the present study indicates it to be so only for boys.

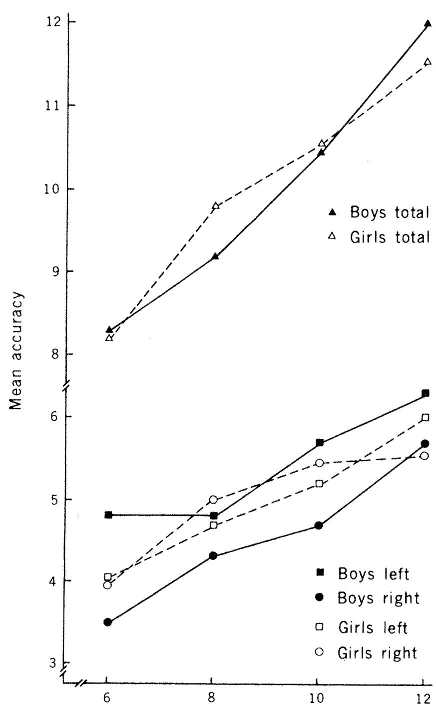

Fig. 1. Mean accuracy scores for recognition of nonsense shapes presented to the left and right hands on a dichhaptic stimulation test. Maximum possible score per hand is 10.

I studied 200 right-handed children, as defined by consistent preference for the right hand for writing and on at least eight of ten unimanual tasks. There were 25 subjects of each sex within each 2-year interval from 6 to 13 years, all with at least normal tested intelligence, age-appropriate academic achievement, and normal medical and behavioral status. Each child was given the dichhaptic stimulation test. The boys, but not the girls, obtained greater left- than right-hand scores (Fig. 1). A mixed design analysis of variance was done with sex and age as the between-subject variables and hand as the within-subject variable. There was no difference in overall accuracy between boys and girls ($F < 1.0$); overall performance improved with age in a linear fashion [$F\ (3{,}192) = 24.2$, $P < .0001$]; hand was a significant factor [$F\ (1{,}192) = 7.1$, $P < .01$]. In addition, there was a significant interaction between hand and sex [$F\ (1{,}192) = 6.8$, $P < .01$]. No other interactions were significant ($F < 1$ in all cases). The left-hand score of the boys (5.4) was significantly better than their right-hand score (4.6). There was no difference between hands (5.0 and 5.0) for the girls. The difference between the sexes for each hand was not significant ($.05 < P < .10$, in both cases). The Duncan Multiple Range Test (*16*) was used for all comparisons. Significantly more boys than girls had