Homology and the Development of Infant Handedness

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Intentions

I will use my research on the development of handedness in humans to illustrate some of the problems associated with the establishment of behavioral homologies both developmentally and comparatively.

I will argue that behavioral homologies require precise definitions of the behaviors examined and systematic investigation of the presence and development of the presumed homologous behaviors among phylogenetically related organisms.

I will suggest that we are far from meeting the needs either for precise definitions or systematic comparative developmental research.

Intentions

I will address two questions prompted by Michael Anderson:

1. Does homology across species matter in the study of handedness? Or what is unique about humans?
2. Does homology across development matter in the study of handedness? Or does it really develop and if so, what develops.

I will answer “yes” to both questions but with qualifications.

What is Homologous in Handedness?

Clearly, symbolic speech and the complex manual skills enabling sophisticated tool-use are unique behavioral characteristics of humans.

They associated in the human adult brain with functional and anatomical hemispheric asymmetries in the networks for speech perception/production and for sensorimotor processing.

Although cerebral dominance for language and handedness vary among different members of the population, they are linked in their distributions.

Handedness and Cerebral Assymetries

The evolution of human upright posture and locomotion have freed the hands to develop the complex manual skills that we employ in tool-use and construction and in gestural communication.

This display of manual skills has made handedness an obvious behavioral trait in humans which is remarkably consistent across cultures.

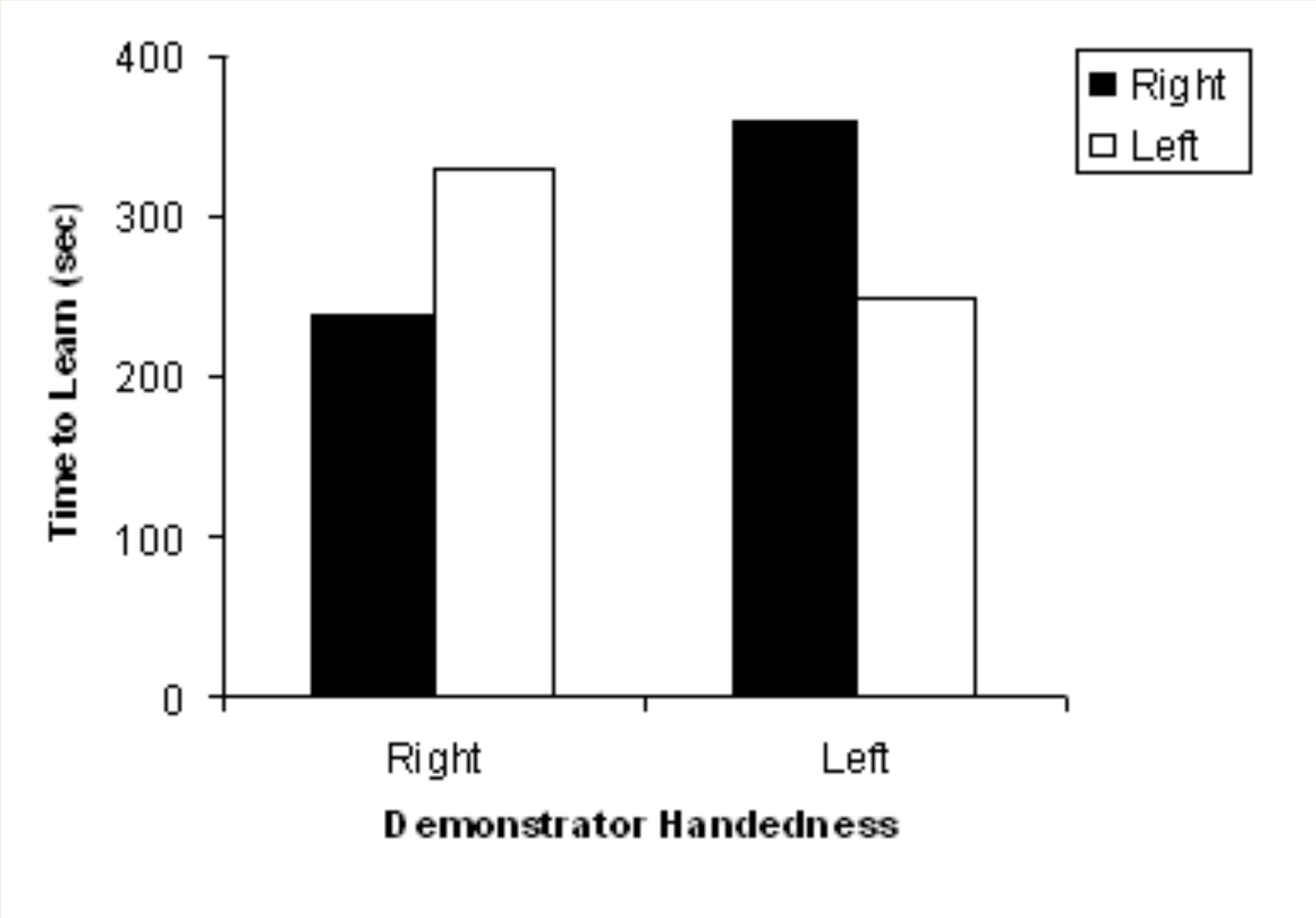
Since handedness is associated with cerebral dominance for language and other functions, handedness becomes the most transparent representation of cerebral asymmetries of function.

The Polyethism of Handedness

Two aspects of handedness are immediately apparent: There is a right-handed predominance in the population (upwards of 90%) and a persistently stable left-handed minority (upwards of 14%) across both prehistoric and historic periods.

This persistent "polymorphism" provokes theories about balanced genetic mechanisms with special advantages to the heterozygous individual (as in sickle-cell anemia and malaria) or special advantages for the minority trait only if it remains a minority (as in hawk-dove scenarios).

Consequence of the Population Bias in Handedness



What is Homologous in Handedness?

There is little doubt that both cerebral and manual lateralization exist at the species level in many nonhuman species, including fish, frogs, birds, and mammals – especially primates.

However, It is often suggested that handedness and cerebral asymmetry resulted from some genetic mutation at some point after the split of the hominids from the other great apes

Nevertheless, several researchers (Hopkins & Rogers) have proposed homology in the traits of handedness and cerebral asymmetries of structure and function.

What is Homologous in Handedness?

Vallortigara & Rogers (2005) state that "the overall similarities across species strongly support the hypothesis of a common origin of lateralization in vertebrates" (p. 578)

Nevertheless, they suggest that the evolutionary pressures for lateralization are indifferent as to whether it is the product of homology or convergent evolution.

However, the issue becomes critical to the question of whether the cerebral and manual asymmetries in humans somehow set our species apart in a fundamental way from all other species.

Handedness in Humans and Chimps

One activity common to tests on both chimpanzees and humans is throwing; the proportion of chimpanzees throwing with the right hand is 58%, 25% left-handed, and 17% ambigious.

However, more than half of the sample of nearly 200 chimpanzees did not throw at all.

Compare these data to a sample of over a million humans in the USA - the self-reported incidence of right-handed throwing was 89.9% for men and 92.4% for women (Gilbert & Wysocki 1992).

Handedness in Humans and Chimps

Handedness in primates is most often identified in the acquisition of food.

In 2005, we analyzed data from 118 studies of primate handedness from 1987 to 2004.

We were able to obtain individual data only from 62 studies and concluded that there was little persuasive evidence for a predominance in handedness for any ape group but left-handedness seems to predominate in prosimians and old-world monkeys.

We concluded that something other than primate handedness may have been the evolutionary precursor of the right bias in hand-use distribution among hominids

Proportion of Preferred Left-Hand Use

Test and parameter	Estimate	*SE*	*p*	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
Complete handedness						
Fixed effects						
Prosimian	**0.39**	**.16**	**.01**	**.60**	.48	.40
New World monkey	−0.17	.09	.07	.46	.35	.46
Old World monkey	**0.43**	**.11**	**< .0001**	**.61**	.44	.23
Lesser ape	−0.02	.34	.96	.50	.44	.44
Greater ape	−0.12	.07	.06	.47	.28	.37
Random effect						
Subject variability	**1.72**	**.04**	**< .0001**			
Reach handedness						
Fixed effects						
Prosimian	**0.43**	**.16**	**.01**	**.61**	.50	.42
New World monkey	−0.12	.10	.22	.47	.36	.44
Old World monkey	**0.66**	**.14**	**< .0001**	**.66**	.52	.17
Lesser ape	−0.02	.33	.96	.50	.44	.44
Greater ape	−0.12	.09	.16	.47	.28	.40
Random effect						
Subject variability	**1.70**	**.05**	**< .0001**			
Nonreaching						
Fixed effects						
Prosimian	−0.08	.55	.89	.48	.50	.42
New World monkey	−0.37	.22	.09	.41	.32	.54
Old World monkey	0.08	.18	.65	.52	.32	.32
Greater ape	−0.13	.10	.19	.47	.27	.33
Random effect						
Subject variability	**1.76**	**.07**	**< .0001**			

Note. Boldface indicates that results are significant at $p < .05$.

Genes and Handedness

The consistency in the direction of asymmetry on both language representation and handedness suggests selection of a gene or genes determining the asymmetry in at least the majority of humans.

Contemporary genetic models of handedness (Annett, 2002; Klar, 1999; McManus, 1999) postulate two alleles on a putative laterality gene, one allele coding for left-cerebral dominance for language and handedness, and the other leaving these asymmetries to chance.

The balance between these alleles might be held through a heterozygotic advantage, ensuring that both remain in the population (Annett, 2002).

What is Handedness?

Annett - continuous not categorical

Differences between left and right hands in skill, frequency of use, or pattern of use varies from individual to individual in a continuous manner.

McManus, Klar – categorical not continuous

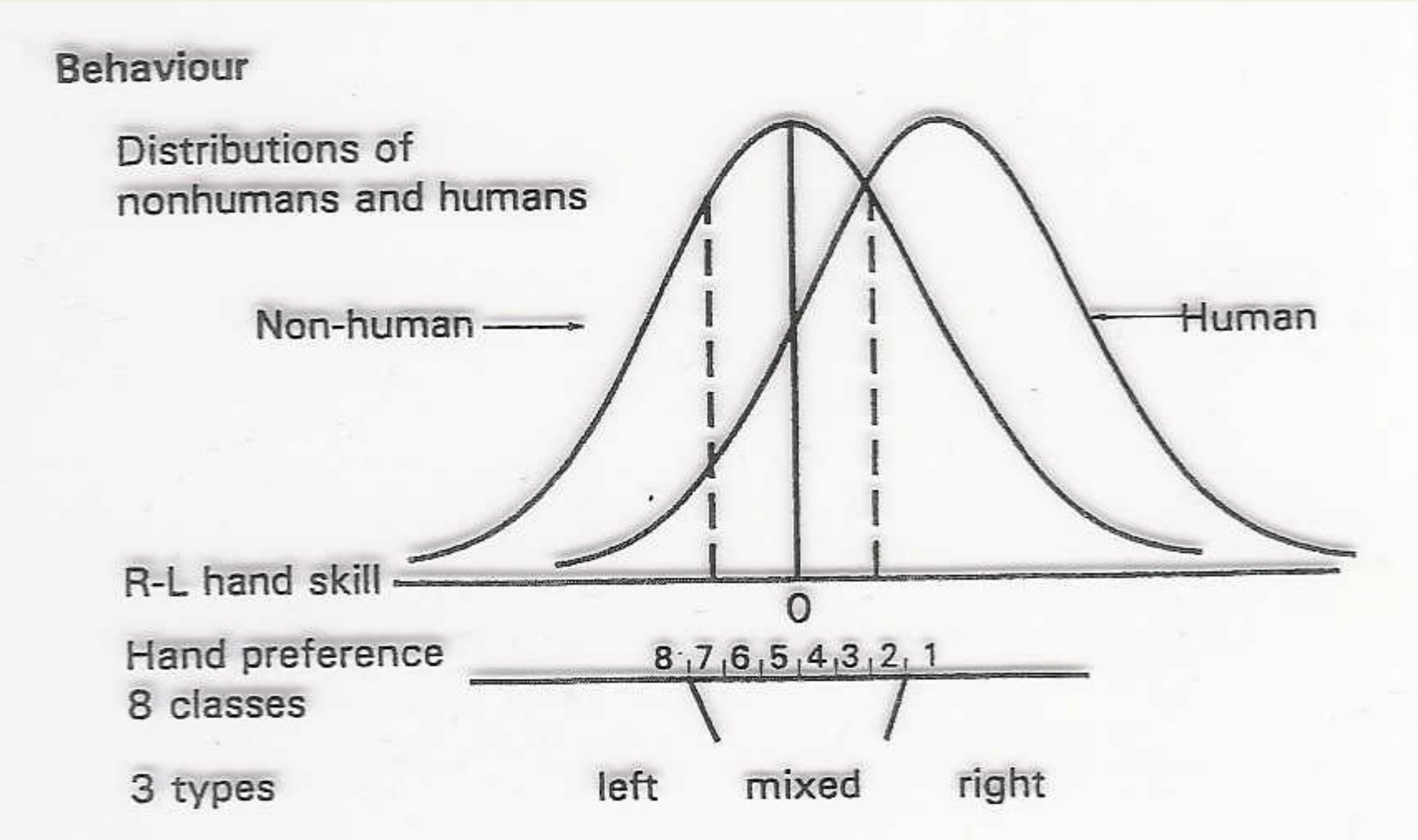
Many studies arbitrarily classify individuals into "right-handed" and "not right-handed".

How is Handedness Defined?

1. Self-assessment (tends to be categorical: “right”, “left”, “ambi”)
2. Questionnaire assessment (can use pantomime but requires knowledge of language or filling-out by others)
3. Skill assessment (requires following instructions)
4. Preference in use (valuable for early development)

Although significantly associated, there is much variability among these assessment techniques with self-assessment being the most reliable but least useful because of questionable validity.

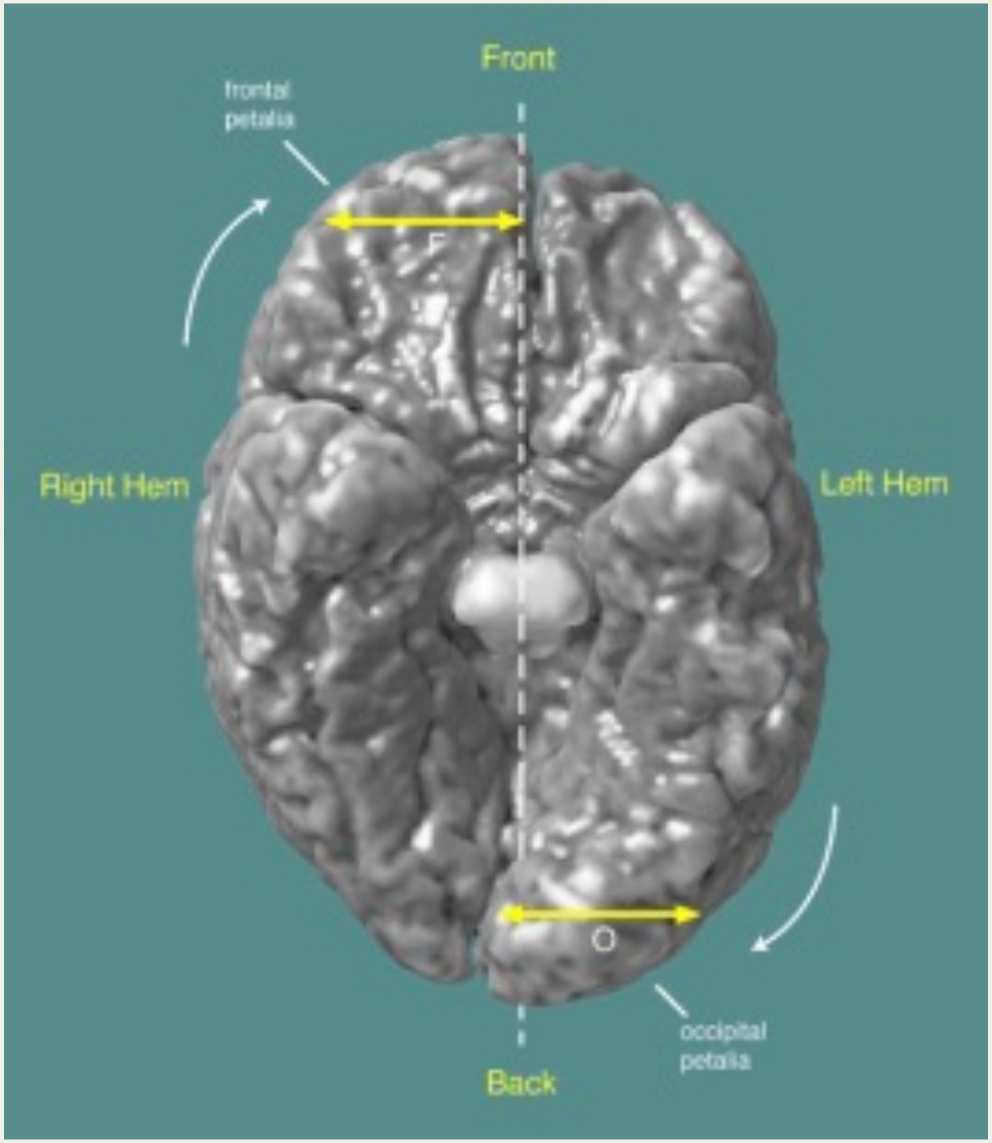
Is Human Handedness Species-Typical?



Extreme Right Bias in Human Handedness is <u>Species-Typical</u>

- Is handedness heritable?
  - Yes but may be facultative (Laland, et al. 1995)
- Are there mechanisms for its inheritance?
  - Polygenic inheritance is as predictive as single gene models (Risch & Pringle, 1985)
  - Candidate genes include ProtocadherinX and ProtocadherinY (Crow), LMO4 (Sun, Et al.), RHD (Hatfield)
- Is handedness a consequence of brain asymmetry?

Gross Anatomical Asymmetries of the Brain



Annett's Genetic Model

Dominance: rs+/+ and rs+/- produce the same effect on handedness and hence we should identify two underlying groups – one group representing rs+/+ and rs+/- and the other group representing rs-/-. Percentages should be roughly 81 vs. 19.

Additive: rs+/+ and rs+/- produce different effect on handedness and hence should be three underlying groups with percentages of 32, 49, and 18 respectively.

Annett's Theory Implies a High Percentage of <u>Infants with Mixed Handedness</u>

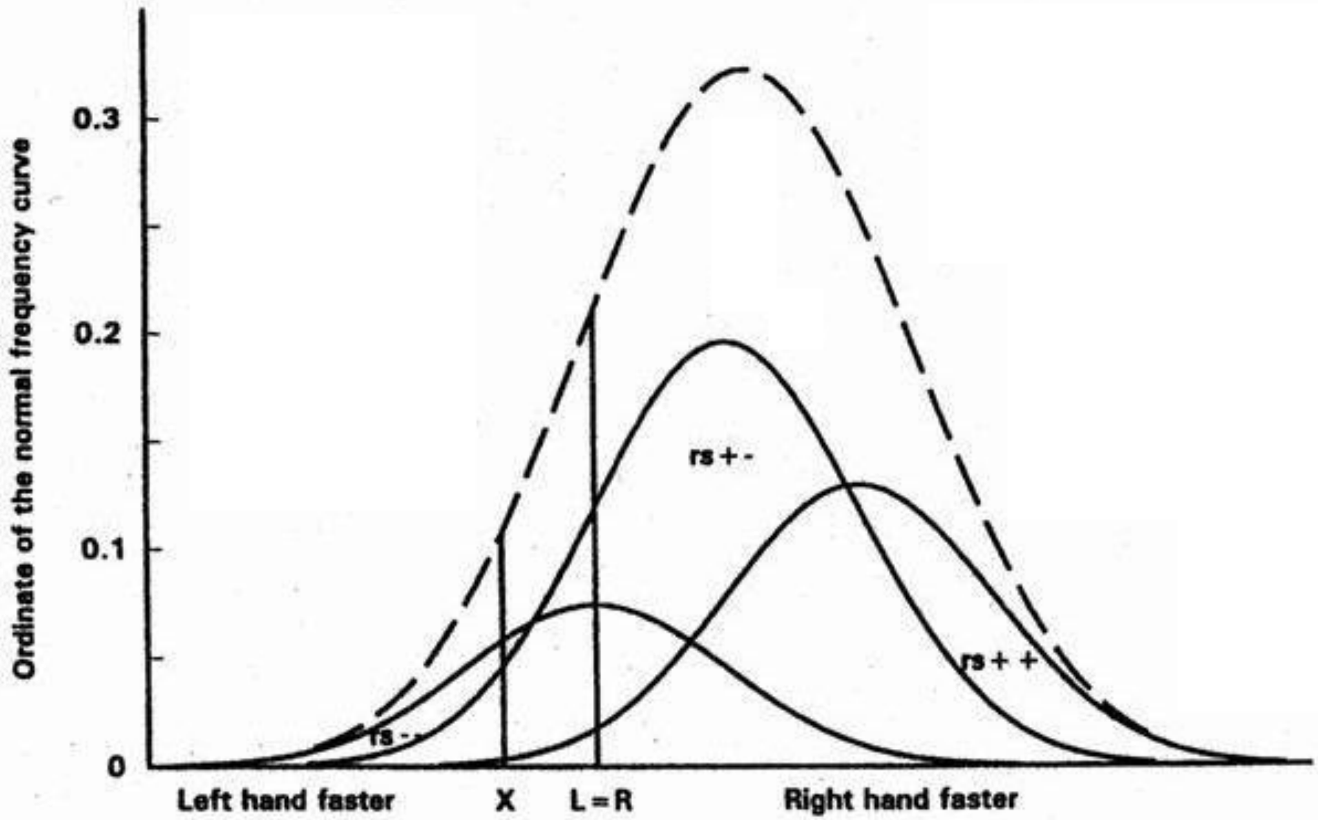


Figure 4. The distributions of R-L hand skill estimated for the three genotypes of the rs locus. A possible threshold for left-handedness is marked 'X', equivalent to a frequency of about 10 percent left-handers in the population.

How Is Handedness Defined During Infancy?

During infancy, identification of hand-use preference seems to depend on:

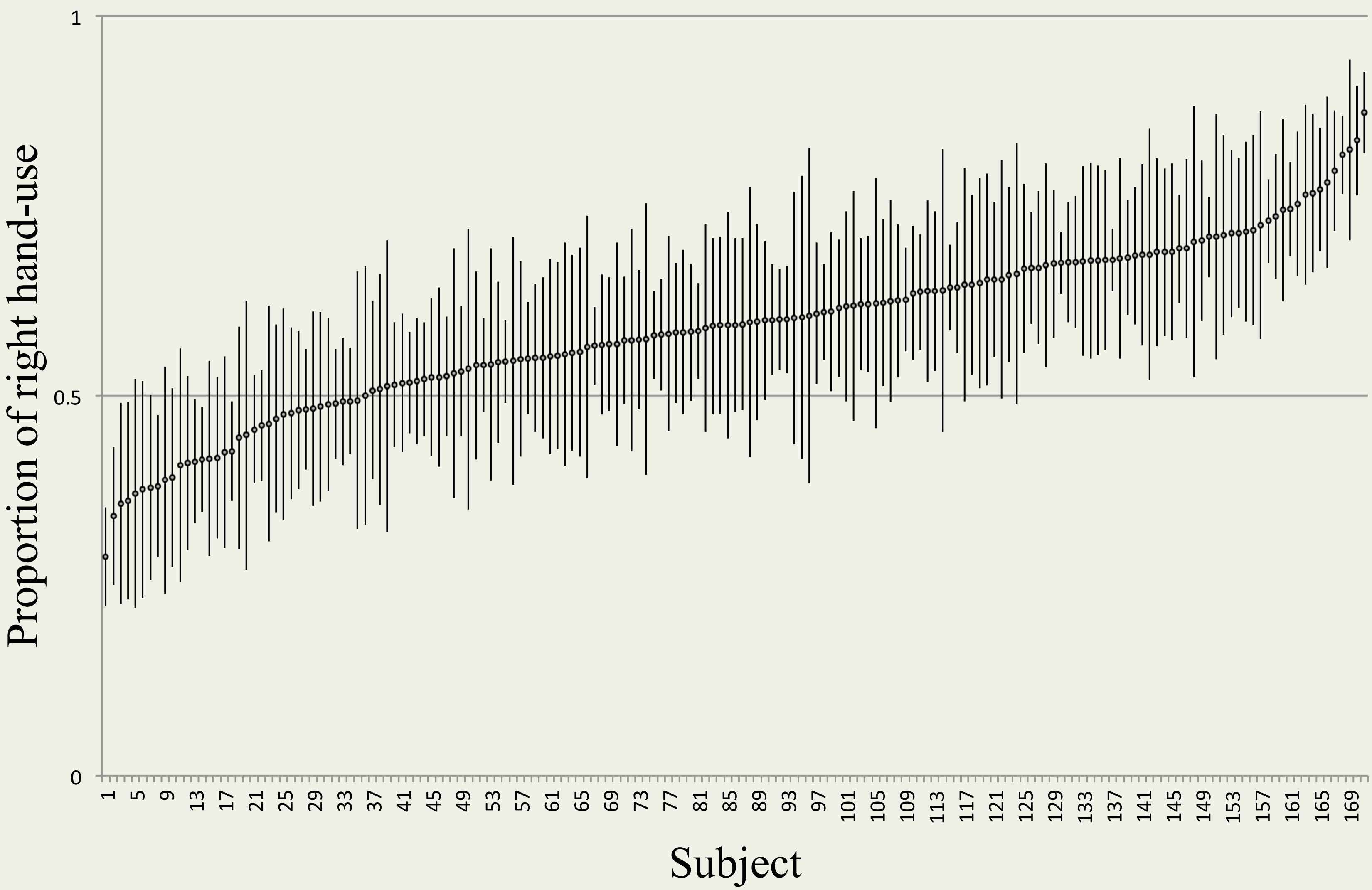
1. How preference is defined (e.g., differential frequency of use, differences in complexity of action patterns employed, and/or differences in sophistication of manifest skill),
2. Whether preference is determined by simple difference of use between the hands (a handedness index – HI) or by statistical estimates of whether that difference is unlikely to occur by chance (a z-score – $(R-L)/(R+L)^{1/2}$),
3. The type of skill that is examined (reaching, unimanual manipulation, bimanual manipulation).


Kk
Mm

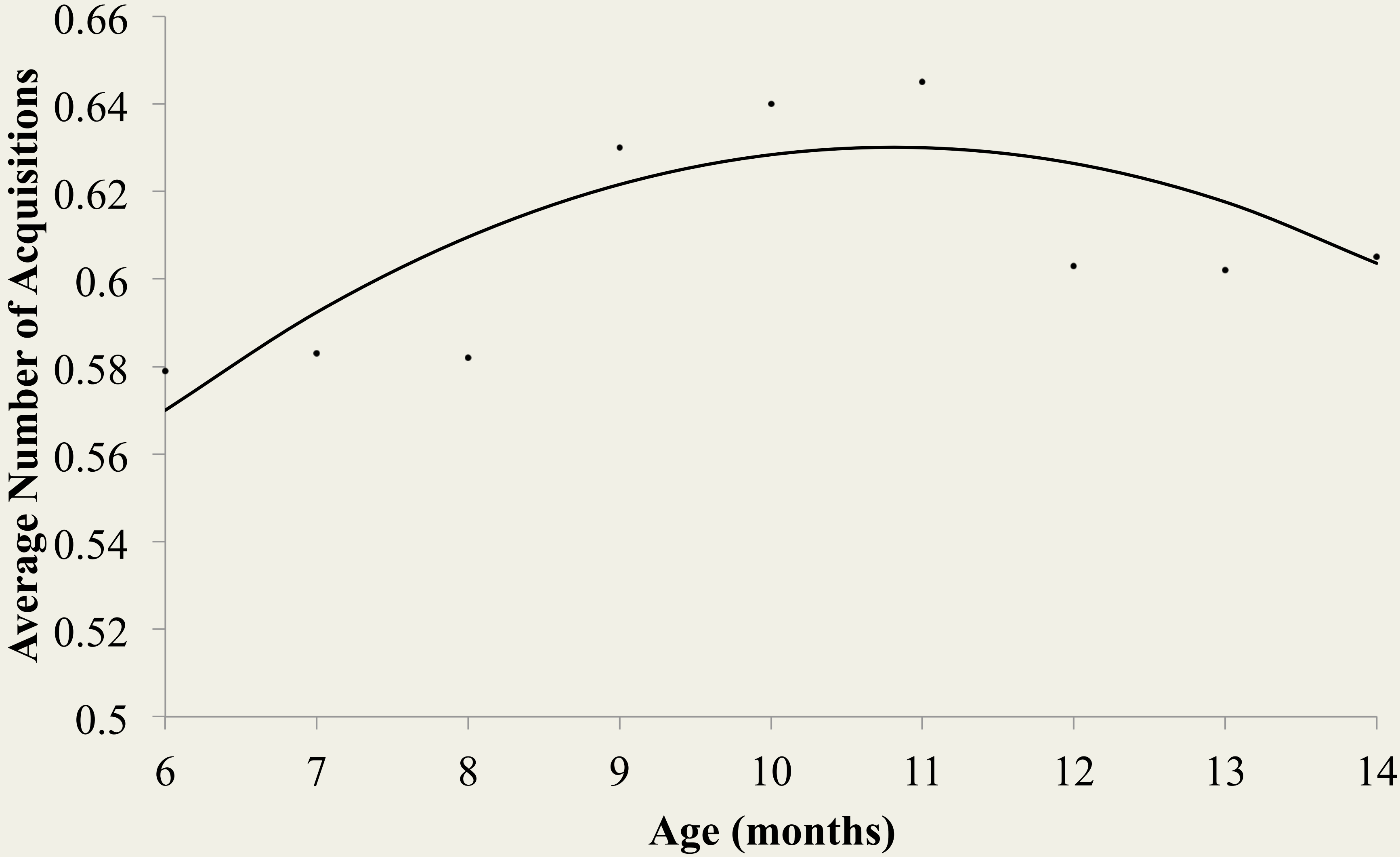
Assessing Infant Handedness

- Recorded hand-use preferences for acquiring objects of 171 infants (93 males) monthly from 6 to 14 months.
- 26 toys were presented for a total of 34 presentations. Each infant provided hand-use data for at least 24 presentations.
- Frequency of right hand use relative to total frequency of hand use was calculated for each infant at each age period (HI).

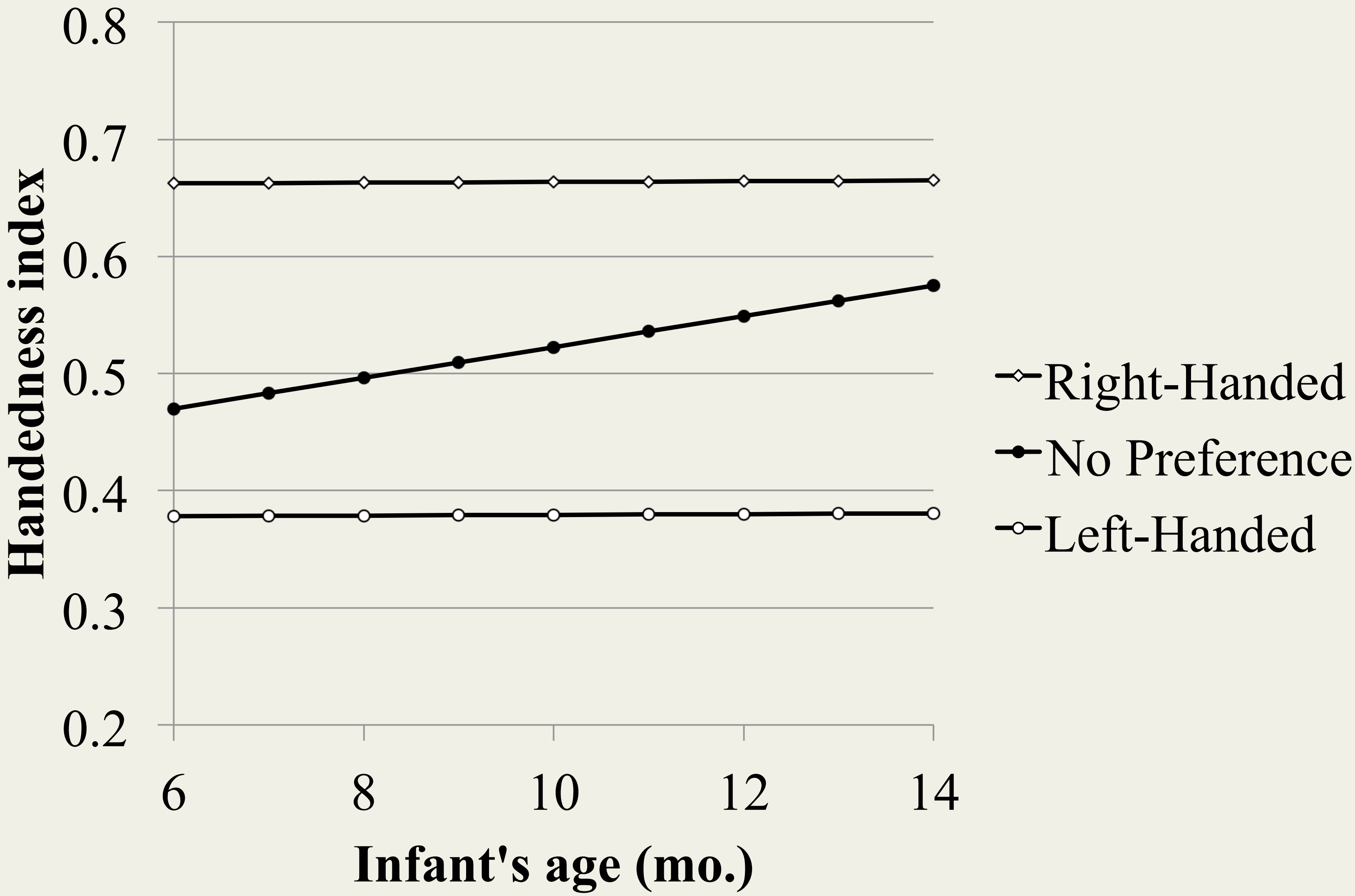
Mean HI and 95% CI for each infant's 9 monthly assessments (ordered from smallest to largest Mean)



Average population change trajectory for quadratic model of acquisition handedness



Average trajectories of lateralized hand-use



Handedness Distribution

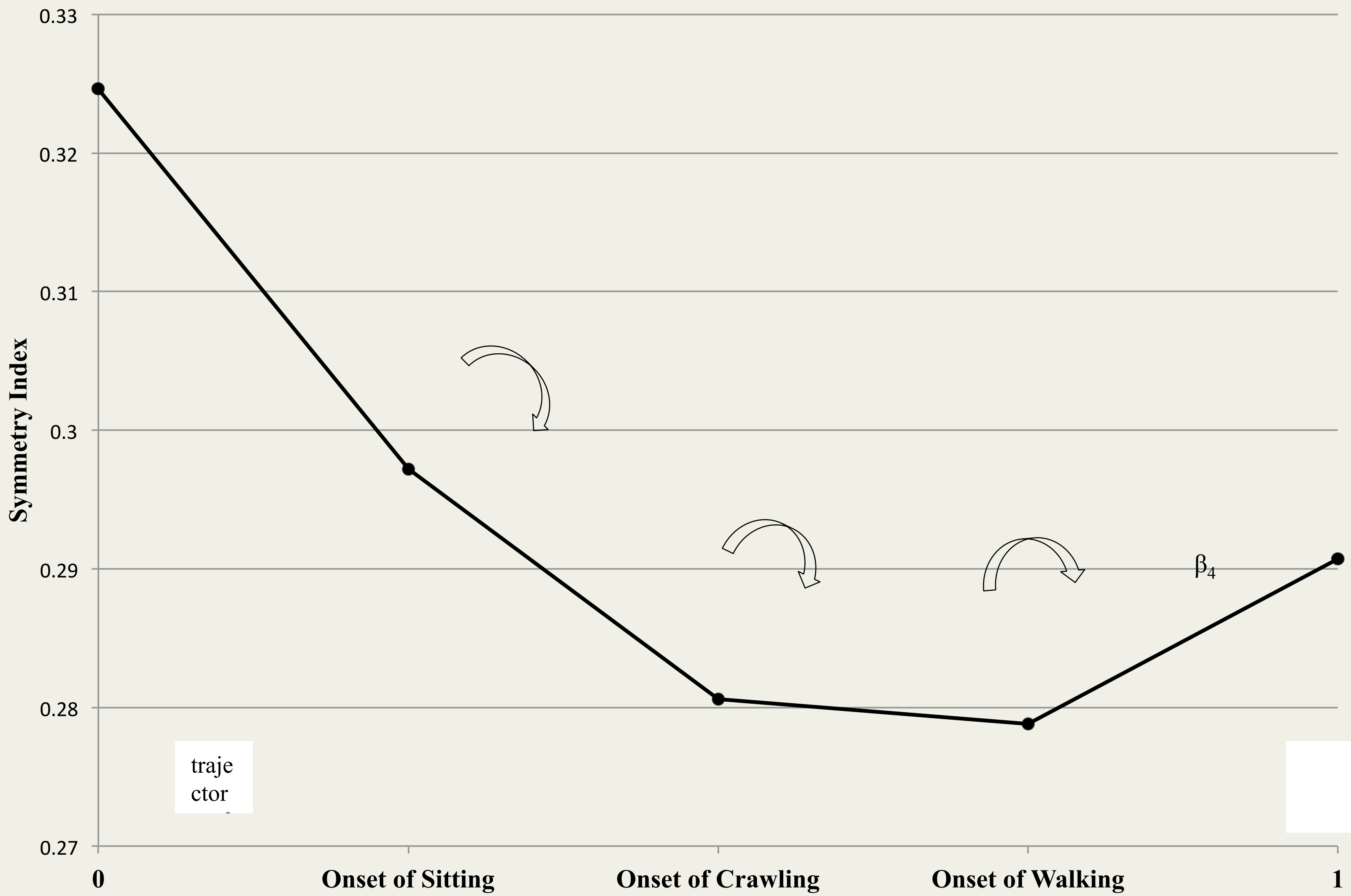
Using the 95% CI for the HI, we find that a majority of infants (62%) manifest a reliable and stable hand-use preference: 54% are right handed and 8% are left-handed.

Those without a stable hand-use preference for acquiring objects exhibit a significant trend toward right hand use across this age period.

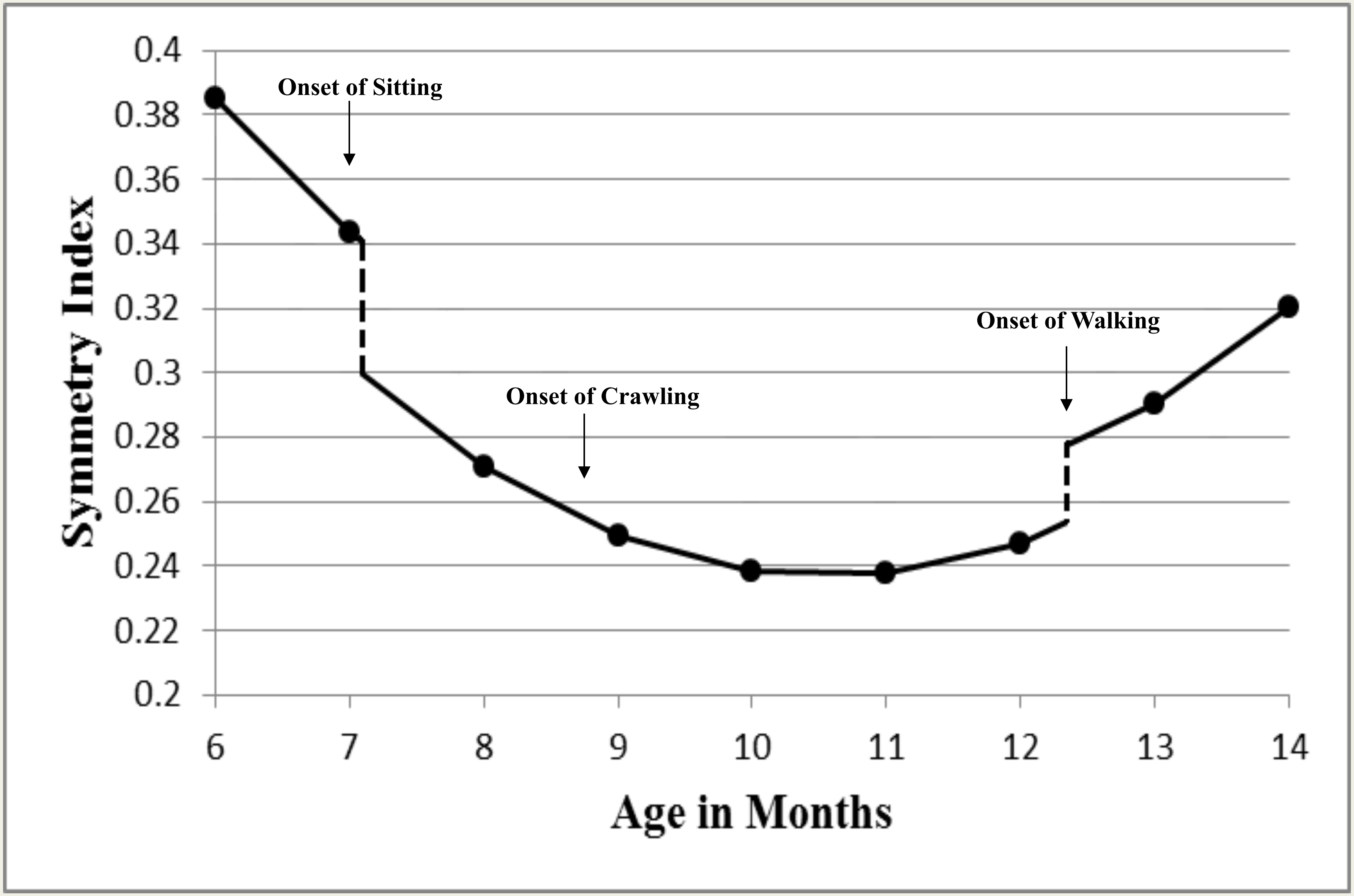
Does development of locomotor skills during this age period account for the curvilinear trend in acquisition handedness?

No, but locomotor skills affect the manifestation of the use of both hands to acquire objects.

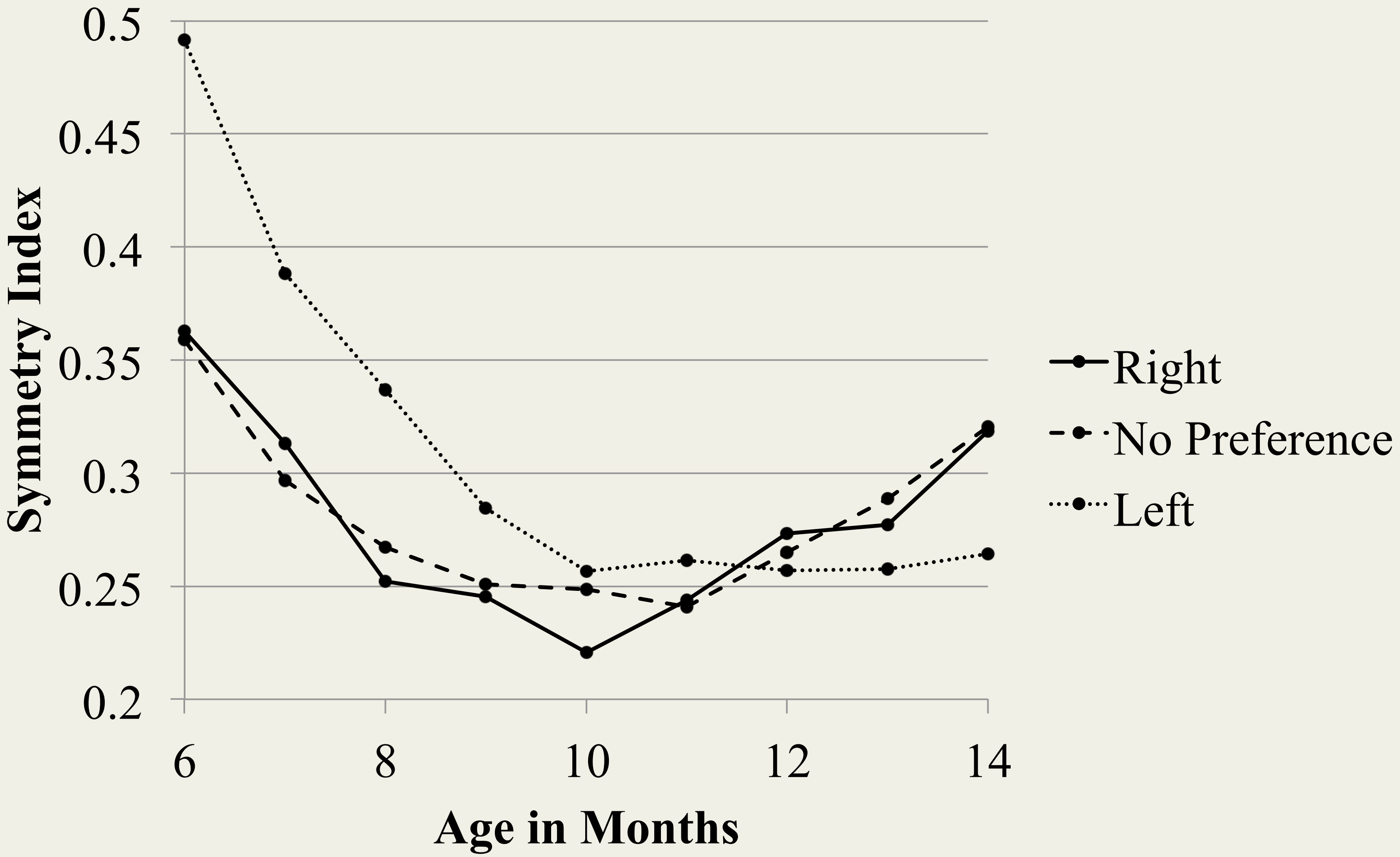
Trajectory of non-lateralized hand-use



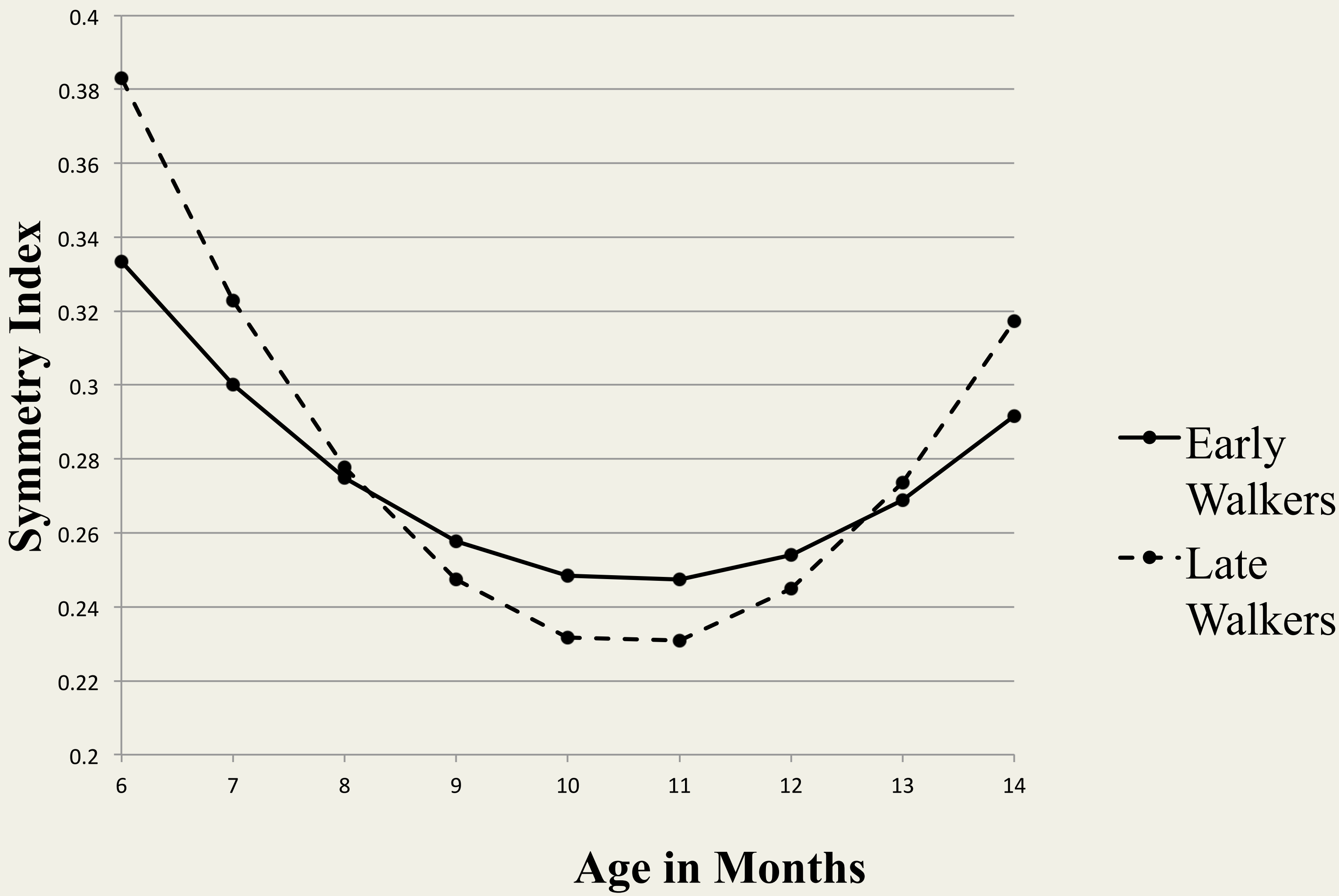
Locomotor skill and trajectory of non-lateralized hand-use



Trajectories of non-lateralized hand-use for groups of infants with different handedness



Non-lateralized hand-use in early and late walkers



Conclusions

1. A majority of infants (62%) manifest a reliable and stable hand-use preference: 54% are right handed and 8% are left-handed.
2. Hand-use preference does not vary according to developing locomotor skills.
3. Use of both hands when acquiring objects does vary with developing locomotor skills but not as predicted.
4. Some other factor must affect manifestation of the curvilinear function in the development of a hand preference for acquisition.

What about Annett’s right-shift factor?

(Latent class analysis)

BIC (Bayesian information criterion) and 2 Delta BIC for Latent Class Analysis.

Number of groups	BIC	2 Delta BIC
1	2929.32	-
2	2860.34	137.96
3	2848.77	23.14
4	2854.67	-11.80
5	2861.36	-13.38

Parameter estimates of the 3-group model.

Group	Parameter	Estimate	S. E.	Group membership (%)
1	Intercept	3.914	2.005	
	Linear	-0.948	0.420	14.96
	Quadratic	0.046	0.021	
2	Intercept	-0.056	1.026	
	Linear	0.030	0.221	57.46
	Quadratic	0.004	0.011	
3	Intercept	-3.702	1.591	
	Linear	1.128	0.349	27.59
	Quadratic	-0.054	0.018	

Annett's predicted genotype proportions and observed proportions for three latent classes in infant handedness (S.E.).

Annett's genotypes:	rs -/- (S.E.)	rs +/- (S.E.)	rs +/+ (S.E.)
Predicted adult population proportions	0.185	0.490	0.324
Latent class proportions of infants	0.150 (0.043)	0.575 (0.075)	0.276 (0.083)

Infants distributed by handedness group and latent class

Growth curve handedness groups	Latent Class Analysis Groups			Total
	class 1 (rs-/-)	class 2 (rs-/+)	class 3 (rs+/+)	
No preference	10	53	1	64
Right-handers	1	47	45	93
Left-handers	14	0	0	14
Total	25	100	46	171

Conclusions

- Comparing the three latent groups with the three classes of infant handedness status (as defined by the CIs for their HI) revealed a highly significant relation
- All 14 left-handed infants and only one right-handed infant were classified as Annett's rs -/- individuals and 56% of the rs-/- infants were classified as left-handed, as was predicted by Annett
- Nearly all (99%) of right-handed infants were classified in the rs +/+ and rs +/- groups and the right handed infants accounted for 98% of the rs+/+ group and 47% of the rs+/- group

Conclusions

- 84% of "no preference" infants were classified as Annett's rs+ factor (83% rs+/-, 2% rs+/+, and only 15% rs-/-). Remember the “no preference” infants did exhibit a significant age trend toward right handedness
- Our left-handedness measure specifies the presence of rs-/- with a probability of 56% and our right handedness measure specifies the rs+ factor (in rs+/- or rs+/+ forms) with a probability greater than 63%.
- During infancy, a hand-use preference for acquiring objects can provide reliable estimates of presumed differences in a genetic influence on an infant's hemispheric specialization.

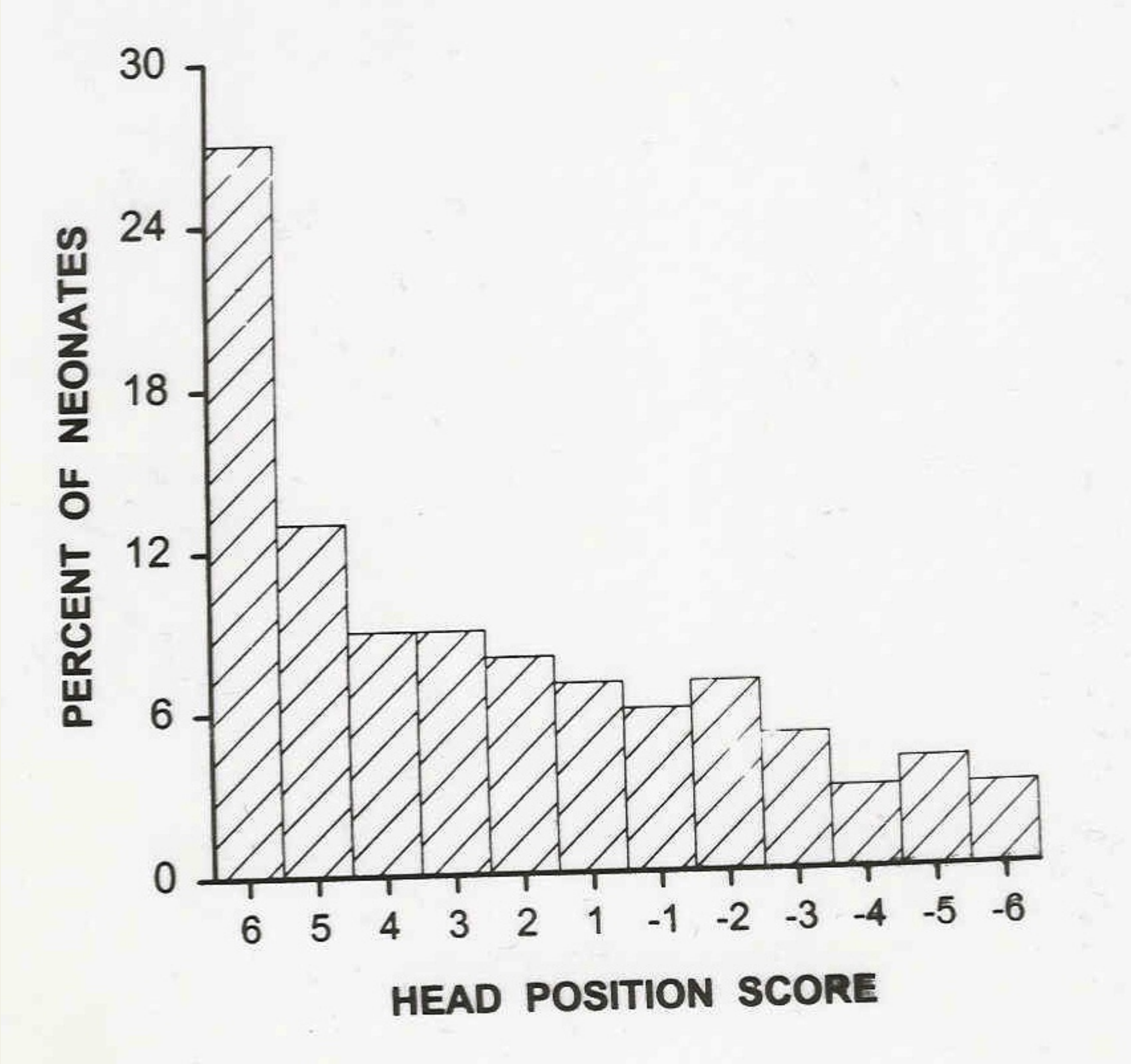
What are the Developmental Origins of Handedness?

Fetal right hand preference highly controversial

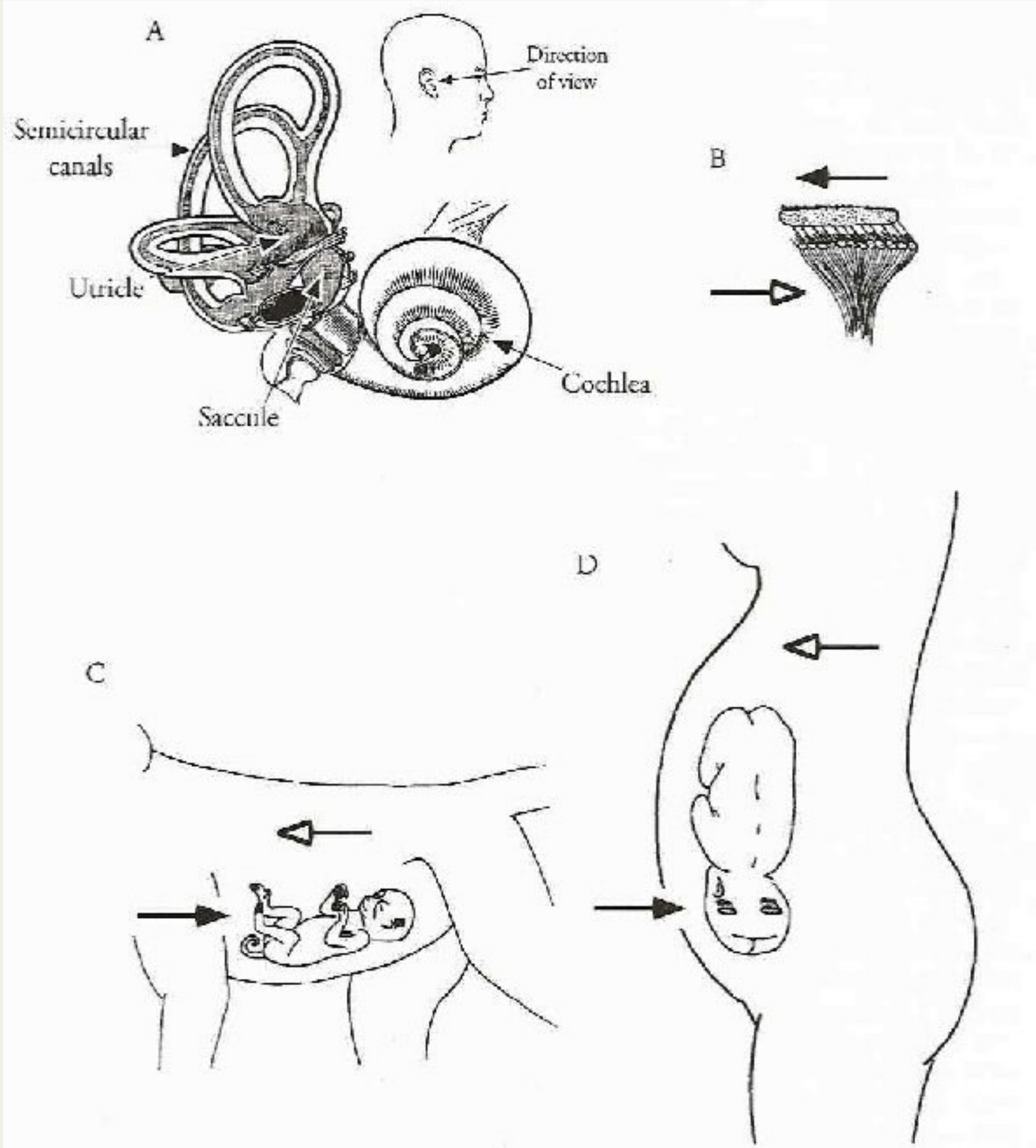
Neonatal rightward head-orientation preference is a robust phenomenon particularly after left occiput anterior birth position

Rightward head orientation is a consequence of vestibular/medulla mechanisms affecting neck muscle activation. These do not appear to be influenced by “higher” level brain mechanisms presumably associated with hemispheric specialization of structure and functions.

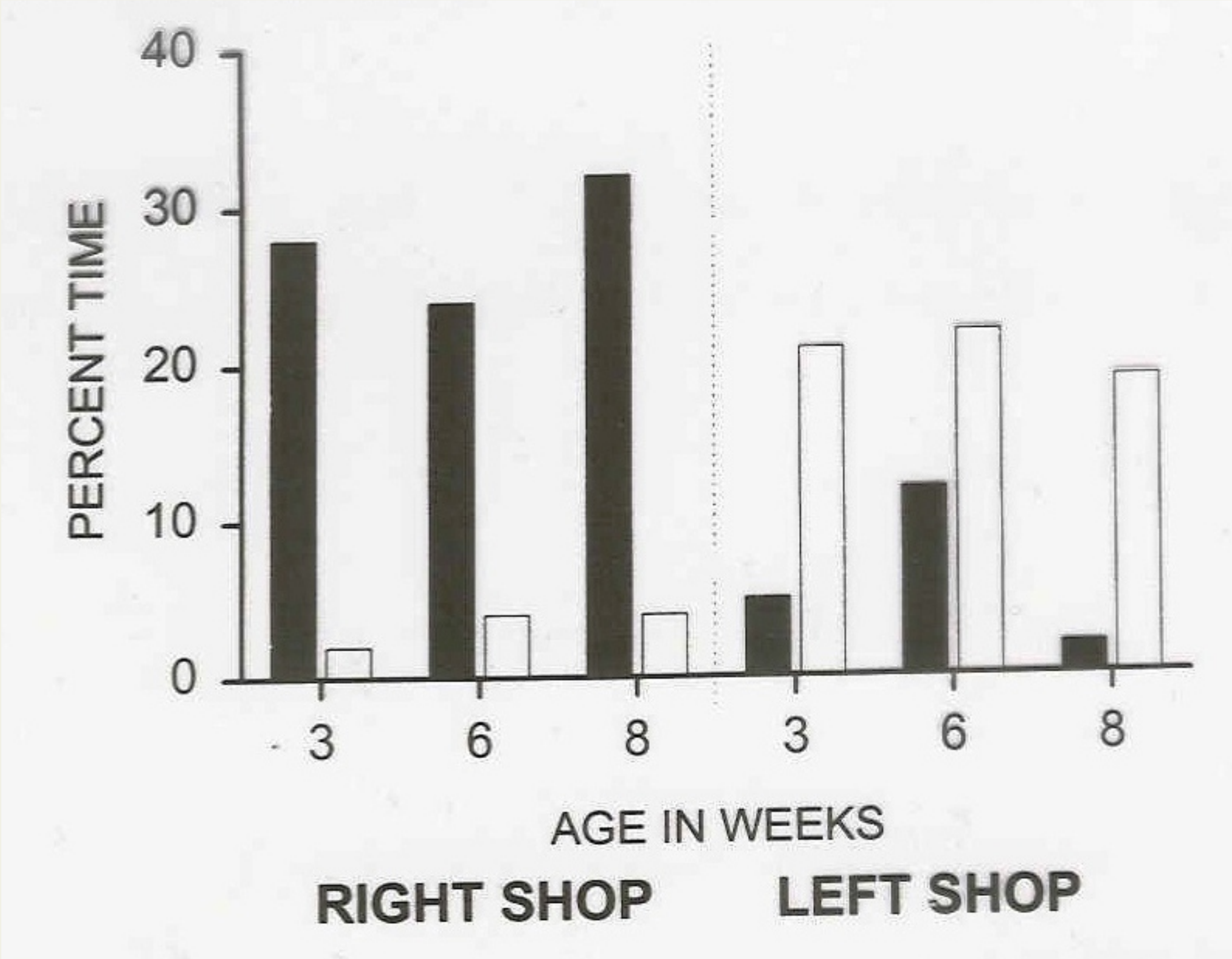
Distribution of Neonatal Head Orientation Preferences (n=150)



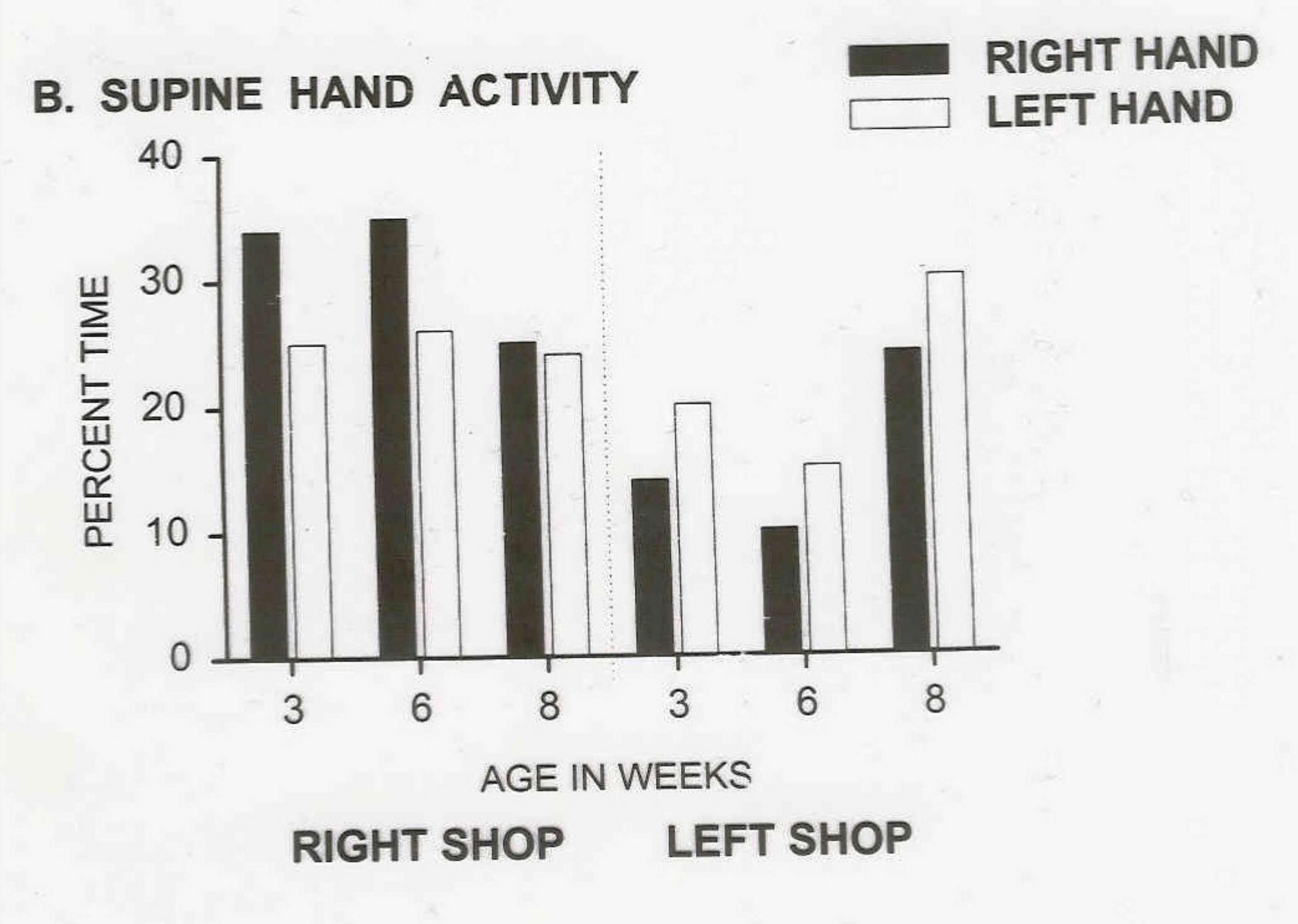
Intrauterine Position and Upright Posture



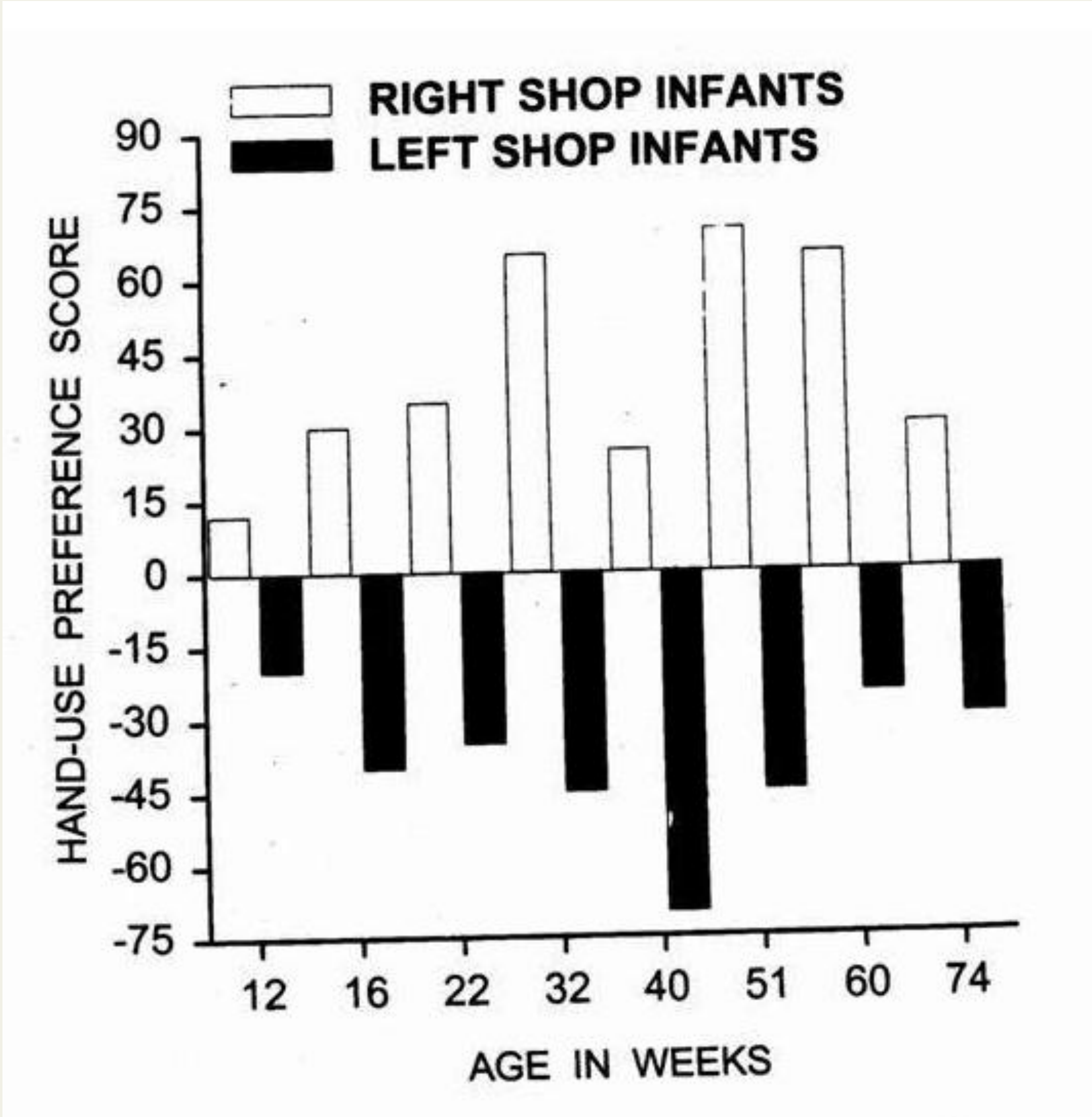
Head-Orientation Preference Affects Hand Regard for First Two Postnatal Months



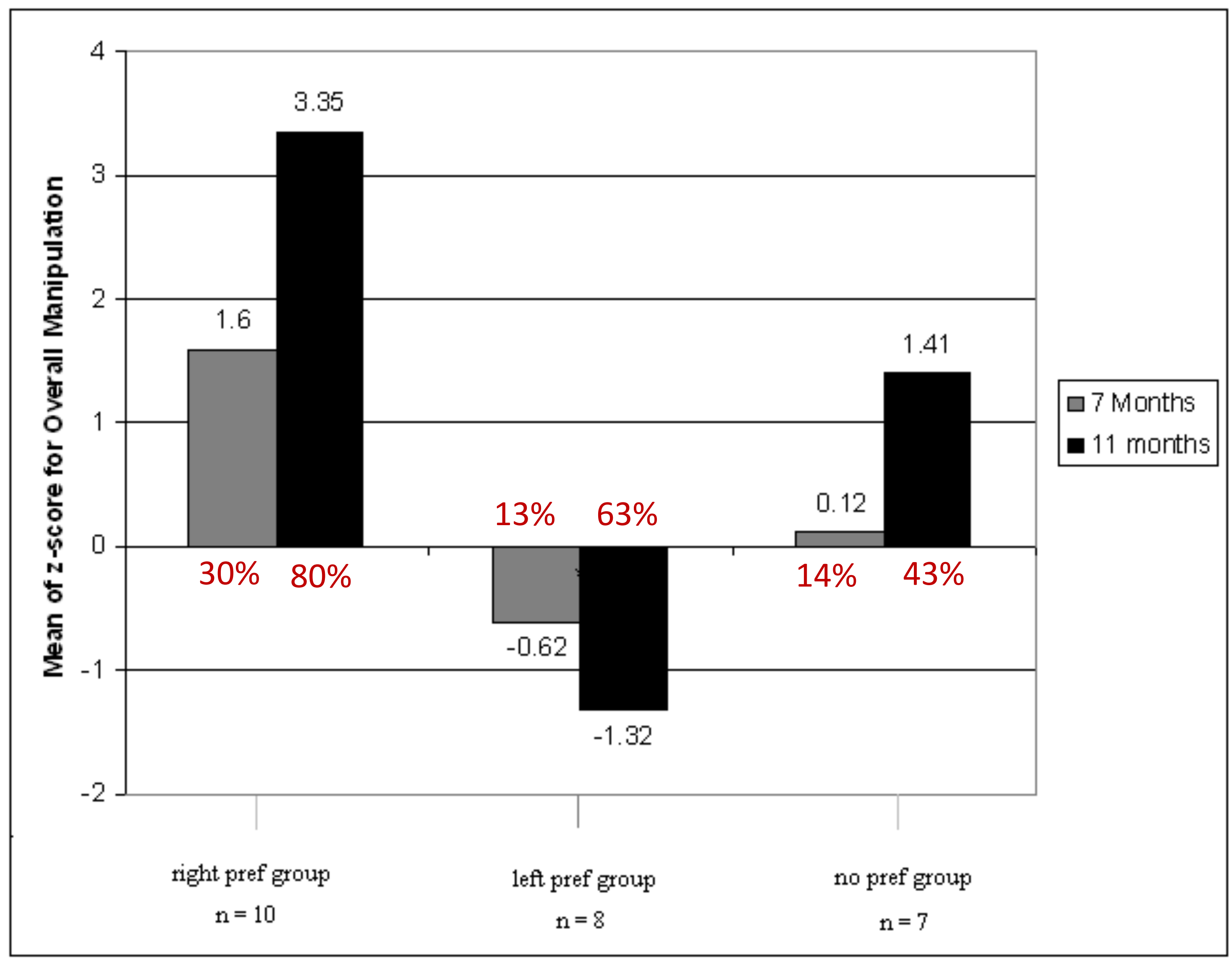
Head-Orientation Preference Affects Hand Activity for First Two Postnatal Months



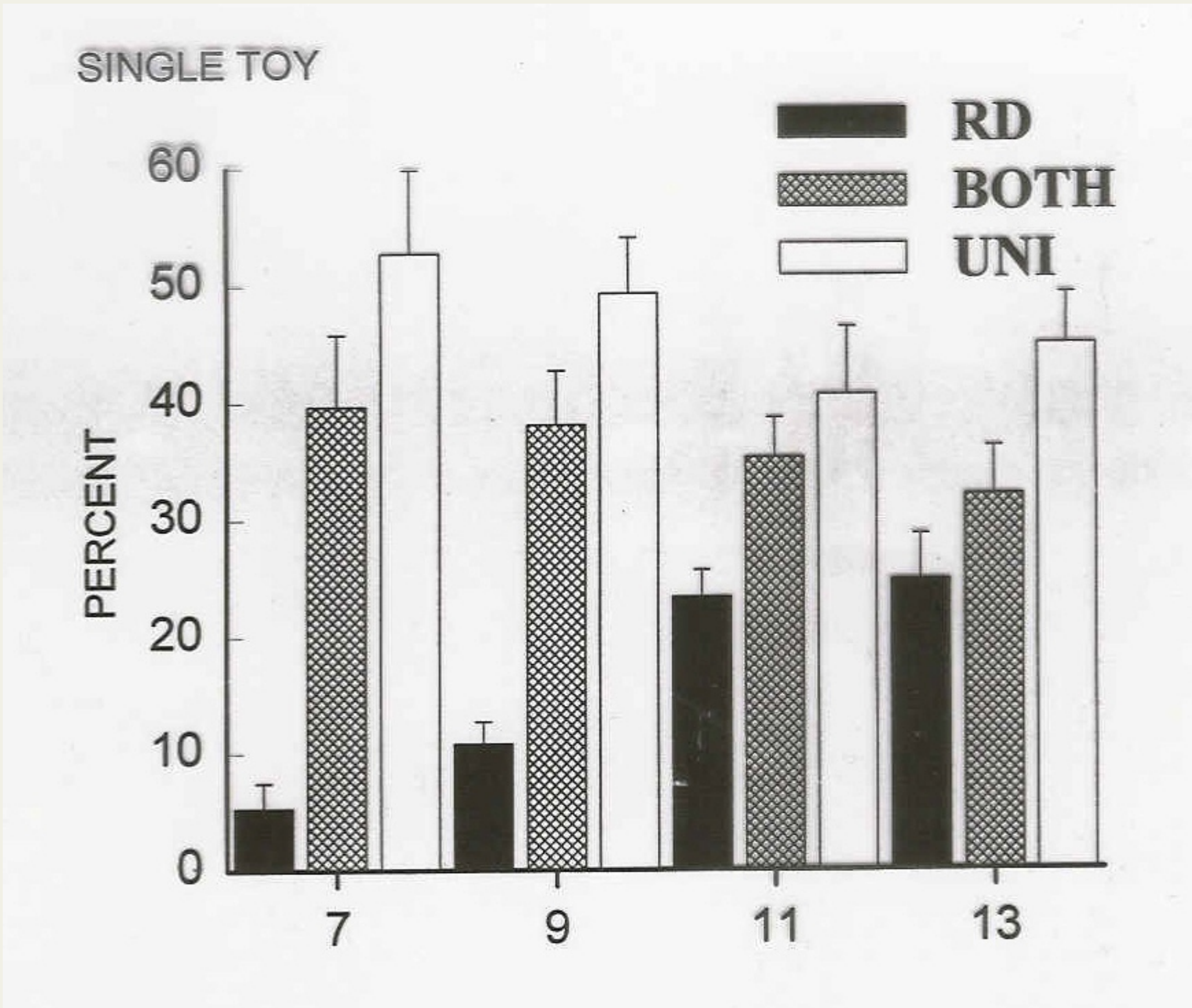
Head-Orientation Preference Predicts the Hand Preferred for Reaching from 3 to 18 Months



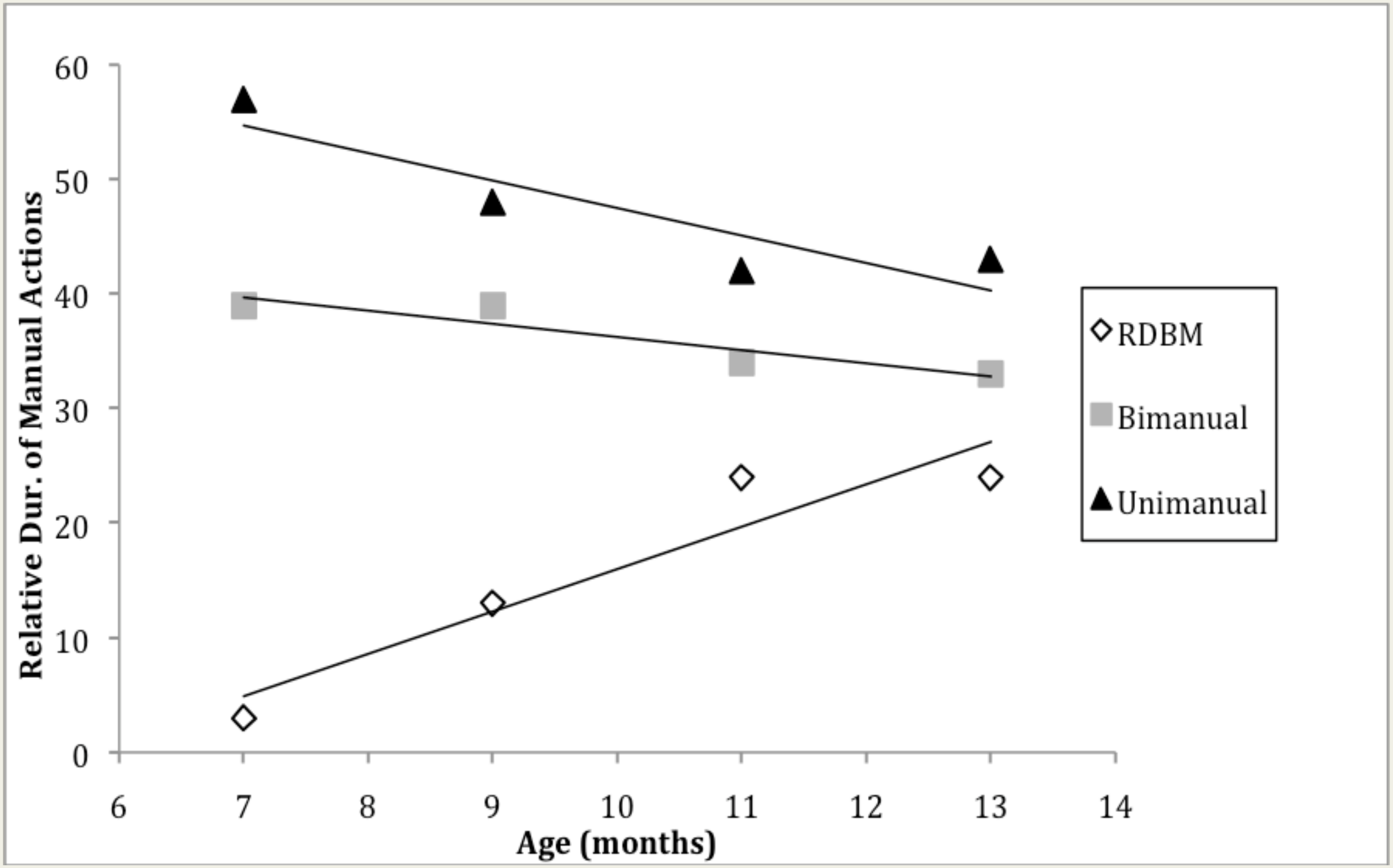
Reaching Preferences Affect Manipulation Preferences only in 11 Month-old Infants



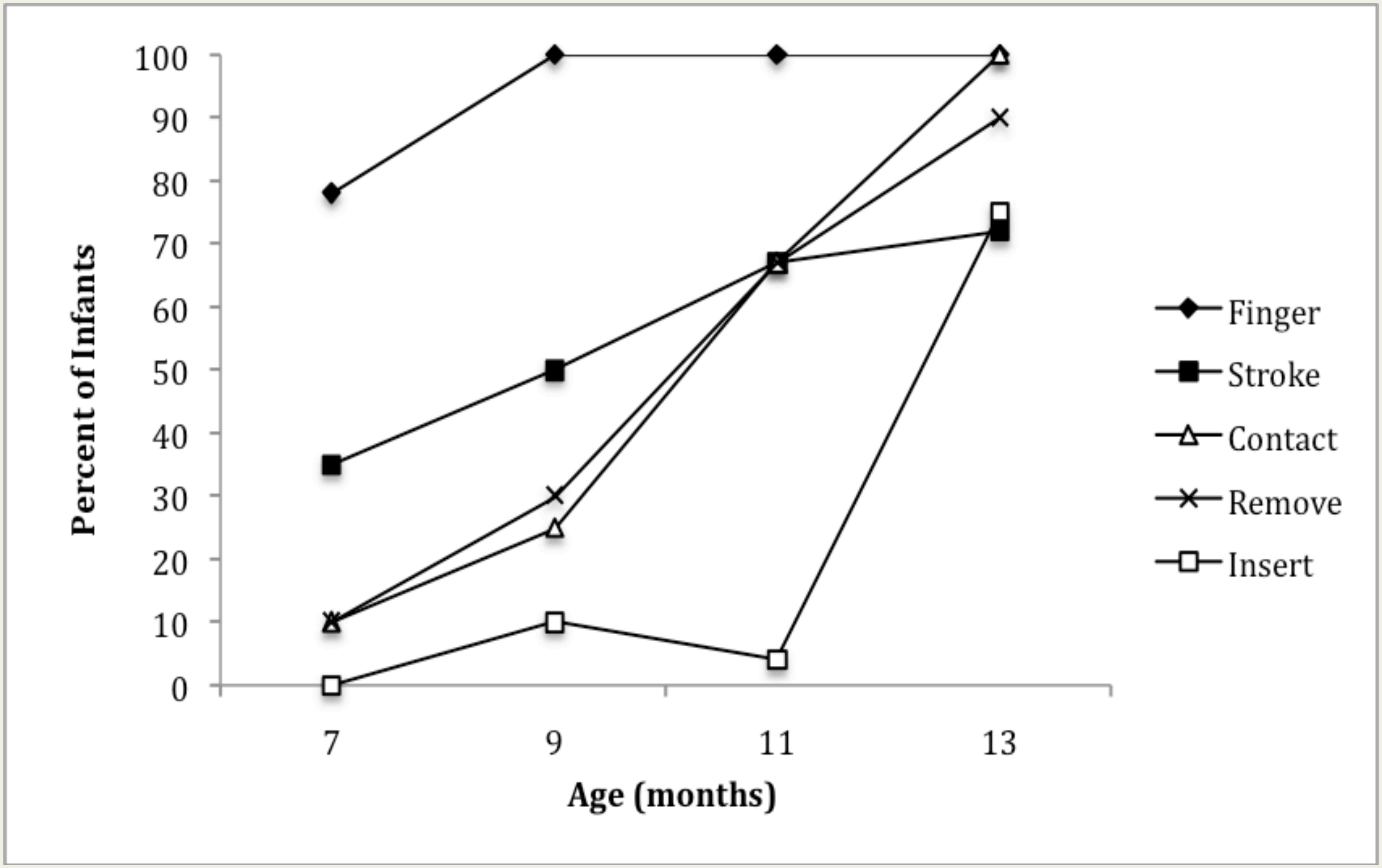
Role-differentiated bimanual manipulation (RD) in the manual repertoire of infants 7-13 months of age



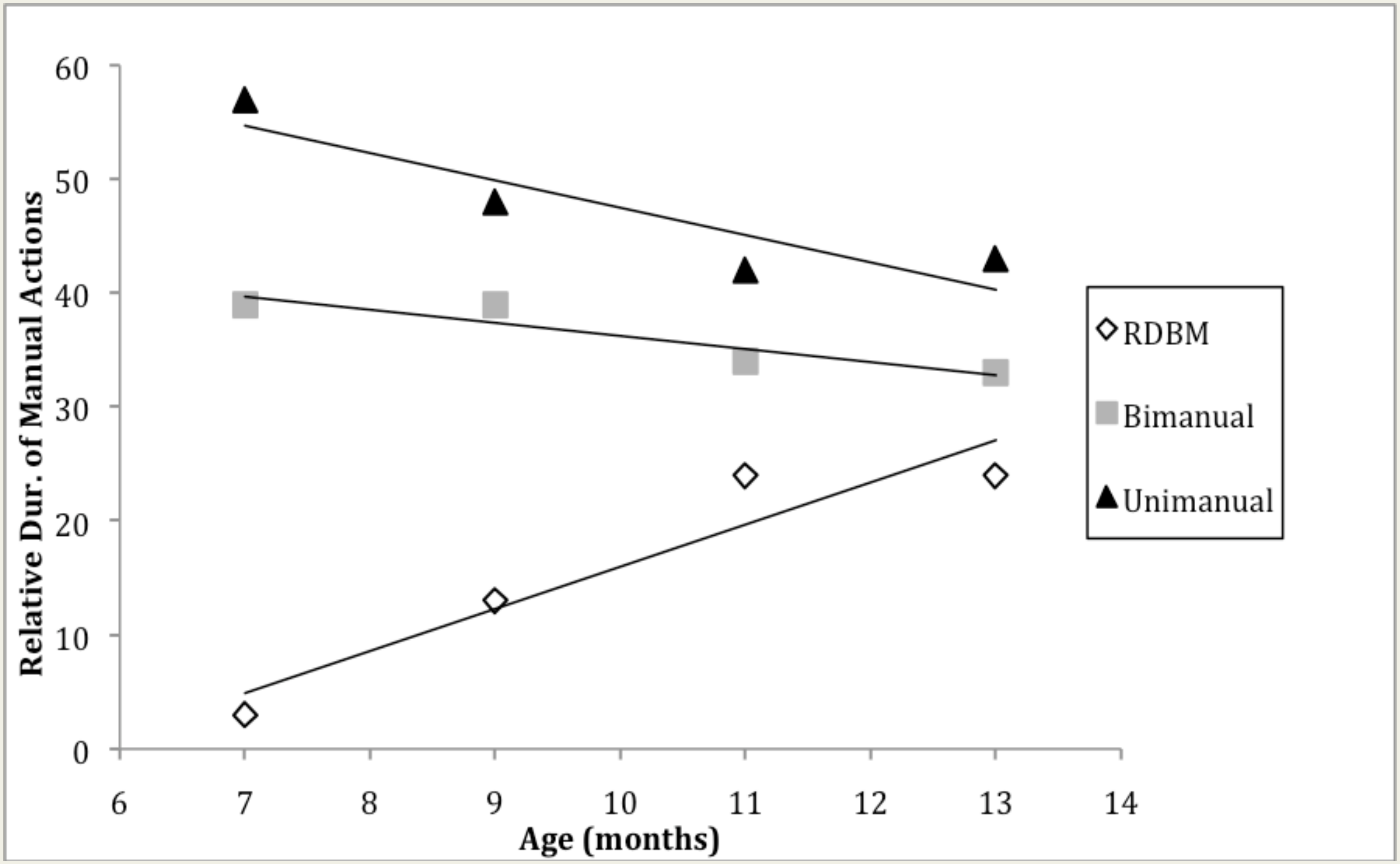
Relative duration of RDBM, bimanual, and unimanual actions



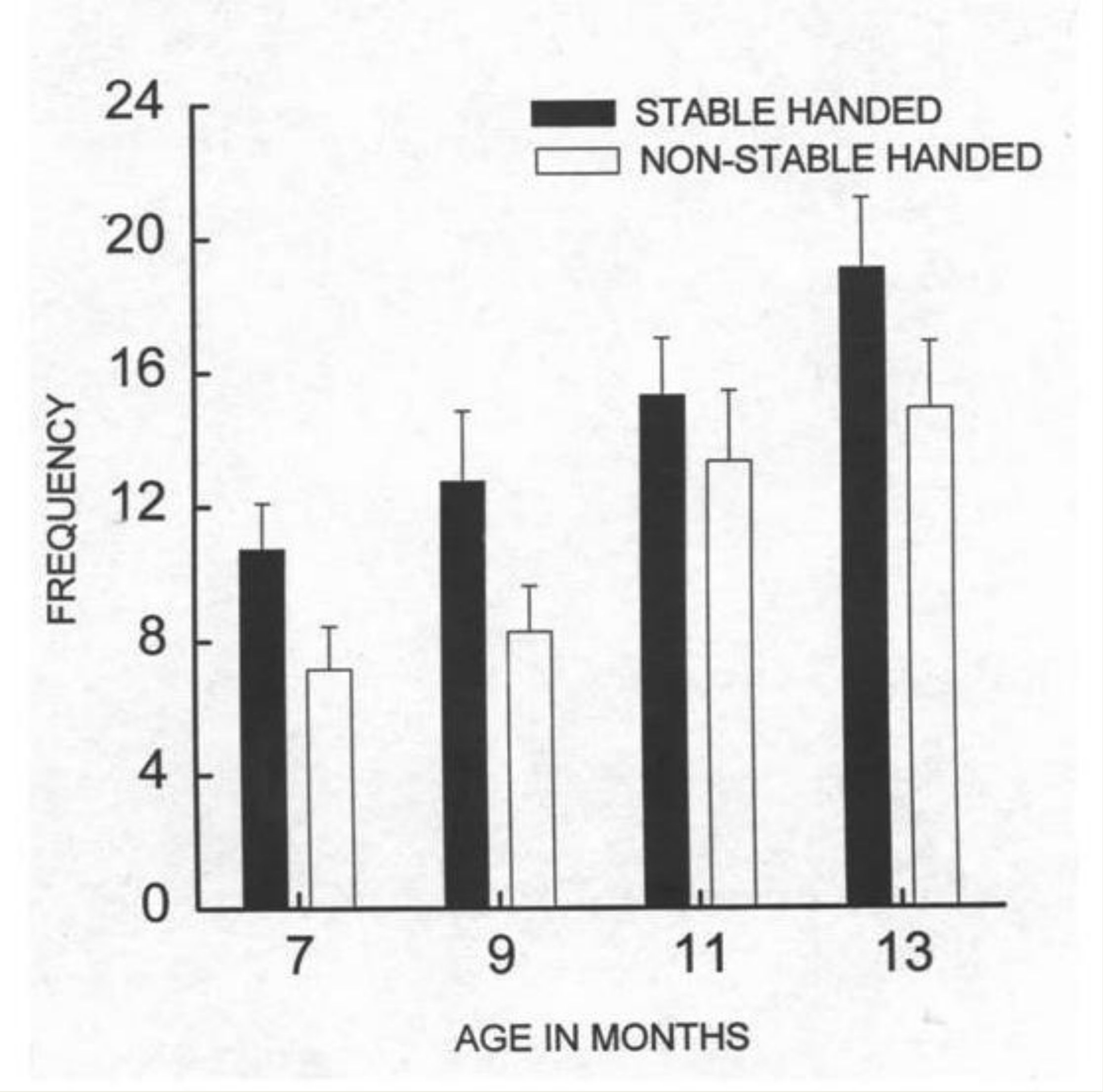
Cumulative percentage of infants demonstrating each RDBM category



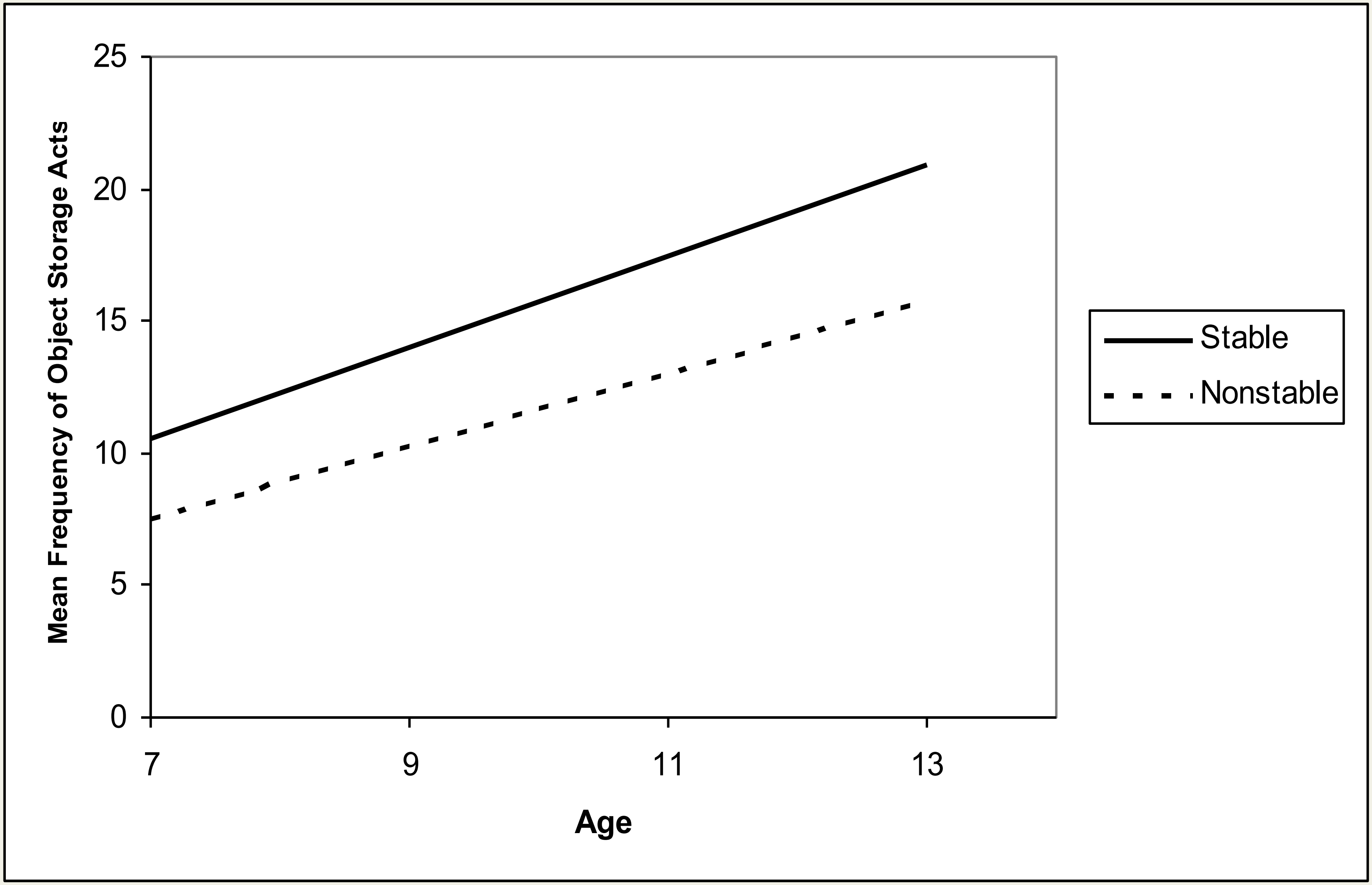
Relative duration of RDBM, bimanual, and unimanual actions



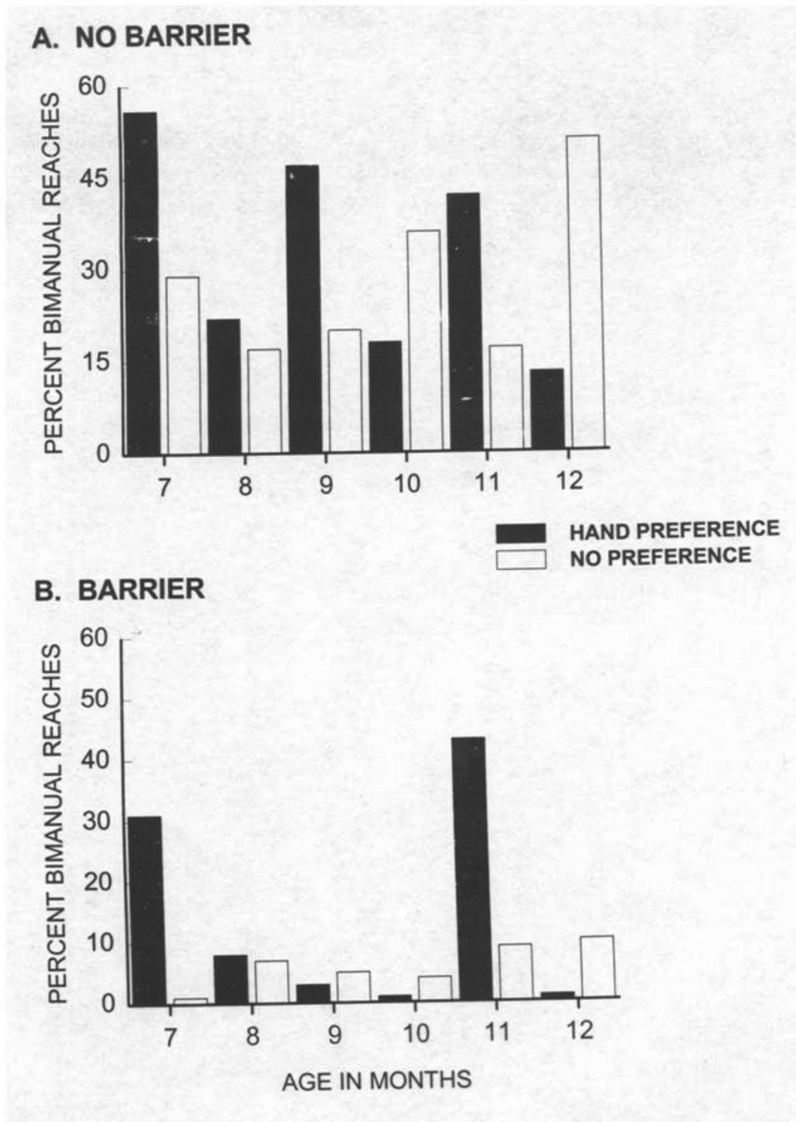
Consequence of Infant Handedness - Storage



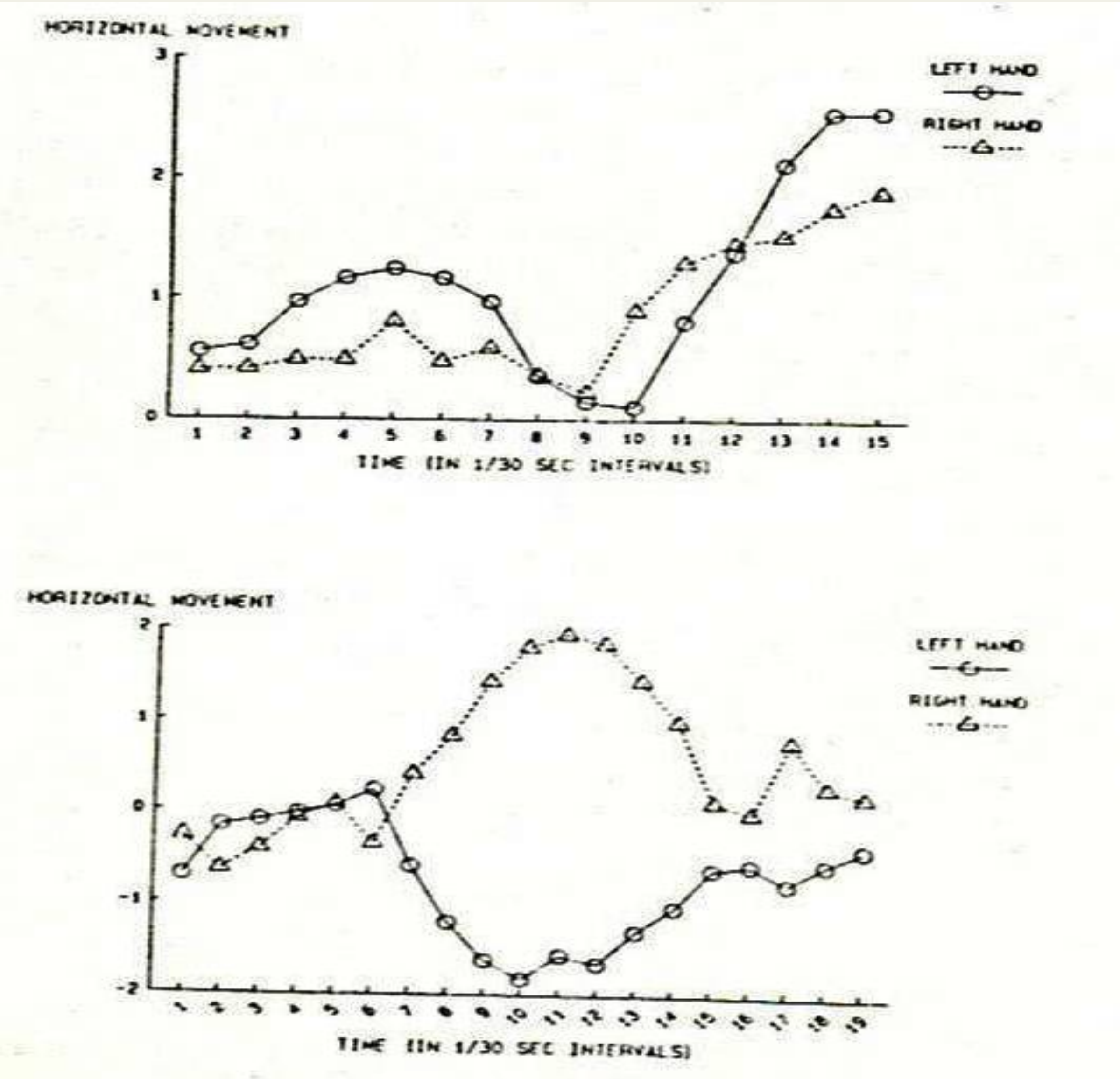
Handedness and Storage Skills



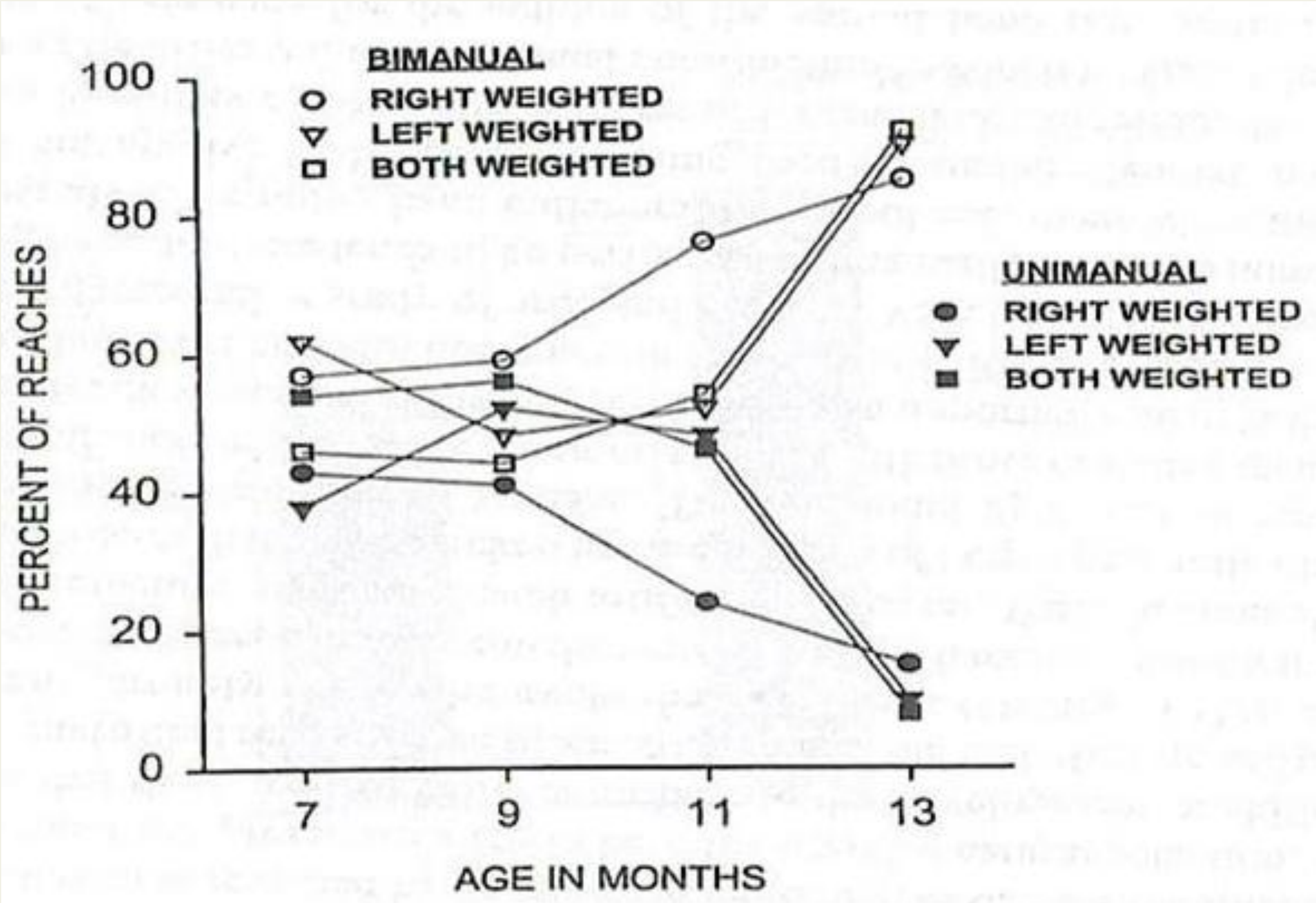
Consequence of Infant Handedness - Trajectory



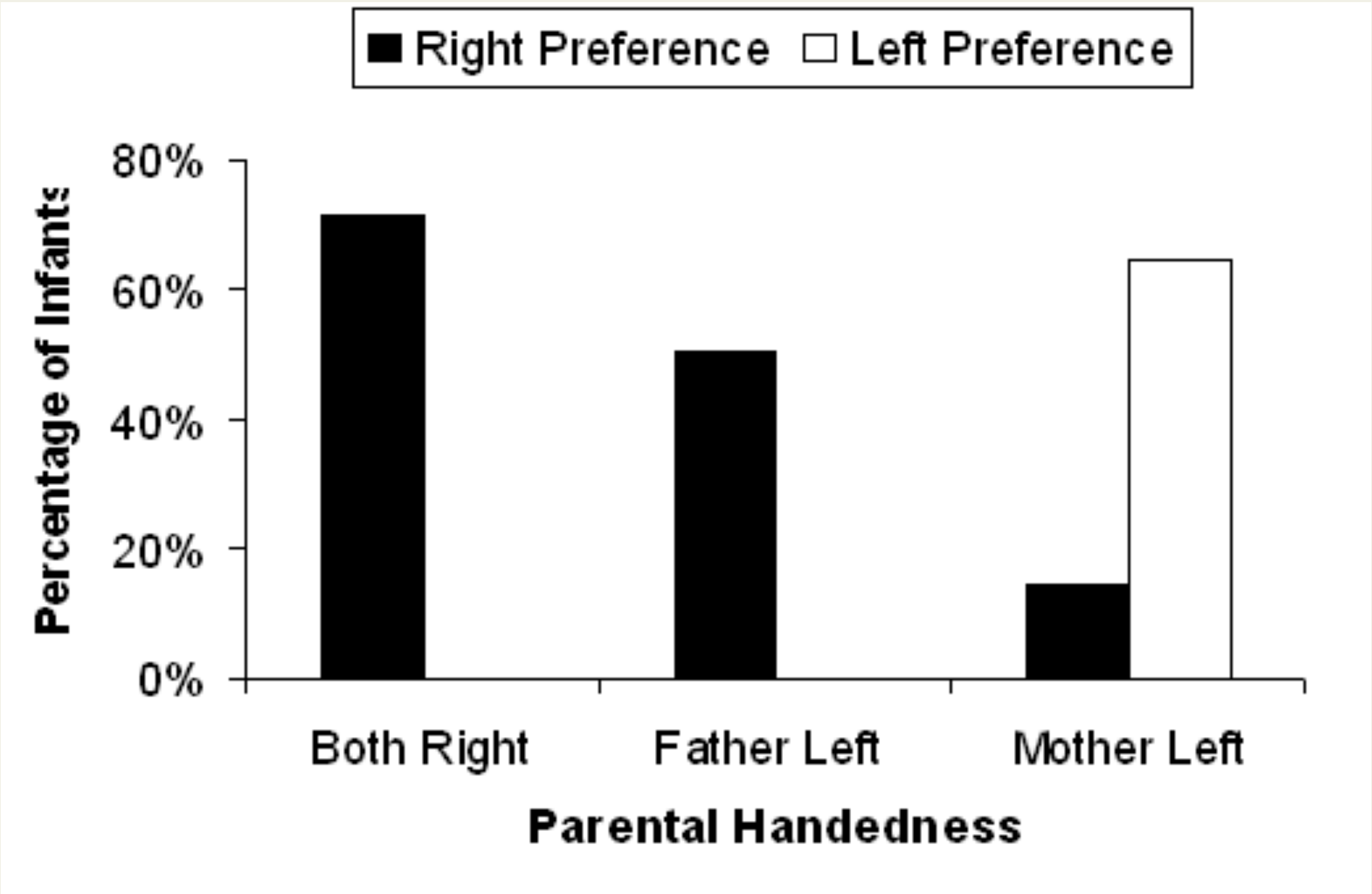
Functions of Infant Handedness – Bimanual Reaching Patterns at 7 and 11 Months



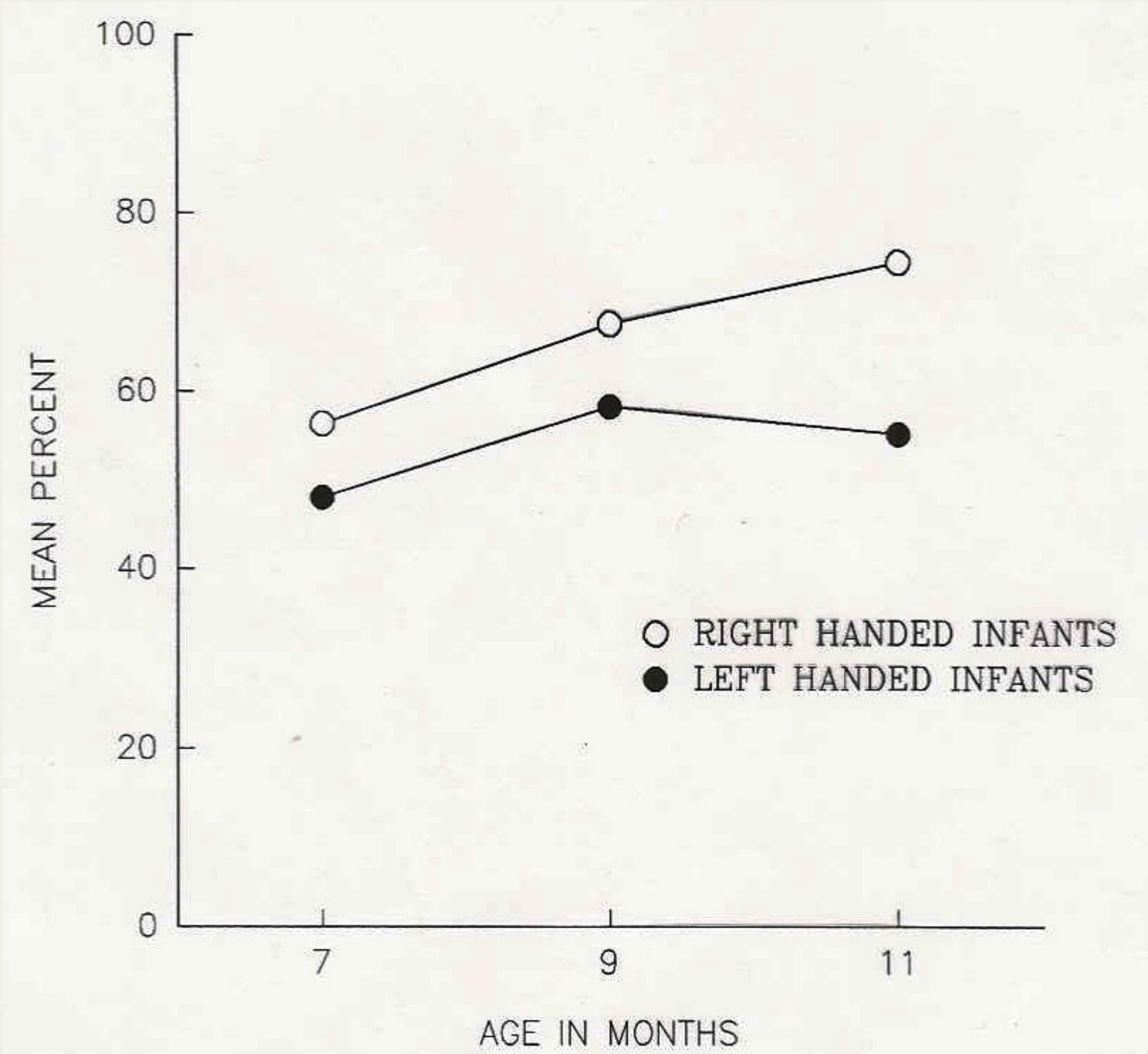
Function of Infant Handedness – Force



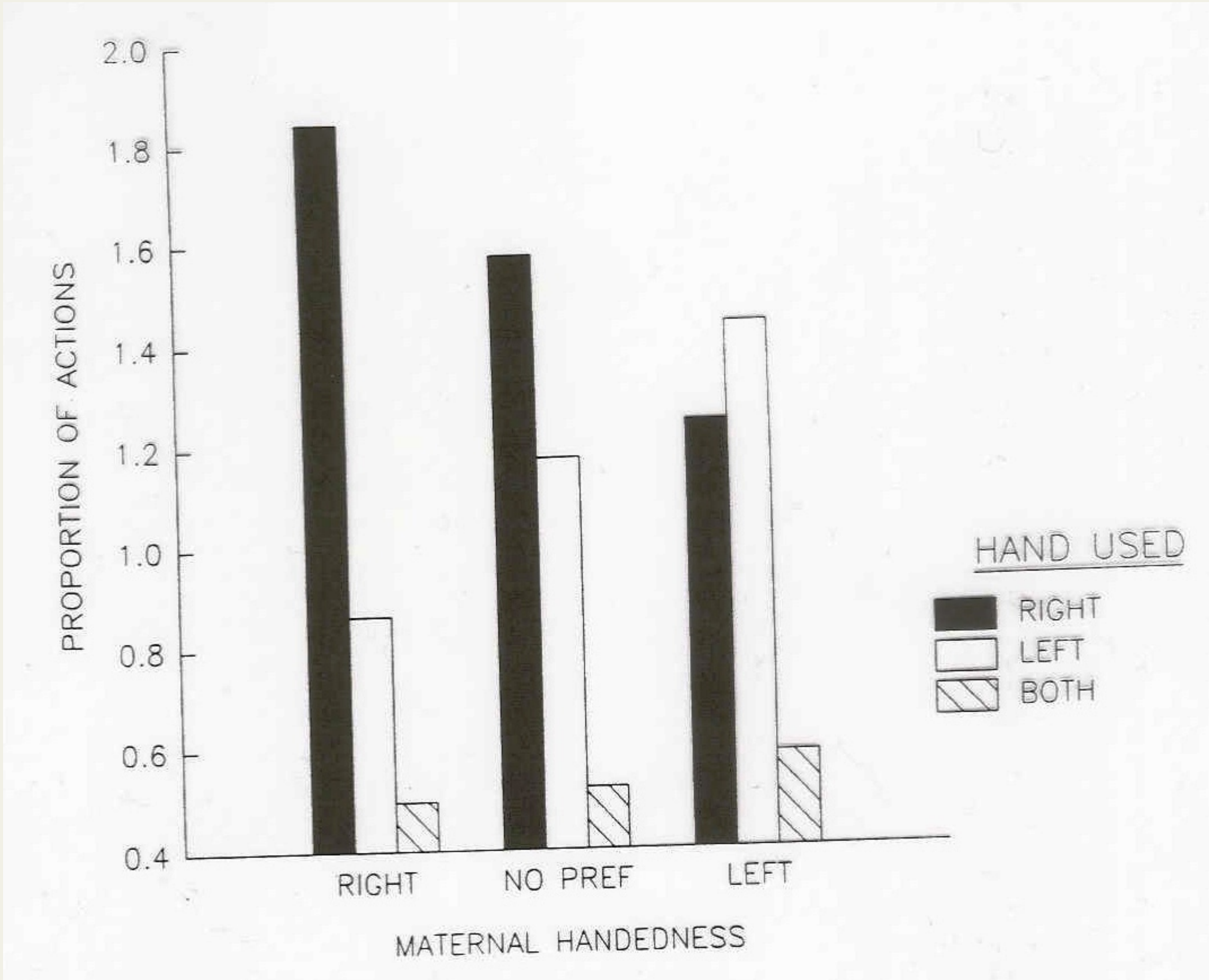
Relation of Infants Hand-use Preferences to the Handedness of Their Parents



Effect of Right-handed Mothers on Infant's Handedness



Relation of Maternal Handedness to the Hand She Uses to Play with Her Infant



Concluding Remarks

- There is insufficient evidence to conclude that handedness in primates is homologous to handedness in humans
- Right-handed bias is species-typical to humans
- Handedness bias is an expression of, and an influence on, the lateral asymmetry of brain organization
- Handedness bias is influenced by parental (maternal) handedness but not determined by it
- Handedness bias may be related to a genetic homology
- Handedness bias may be related to intrauterine position and its effect on vestibular system development

Concluding Remarks

- Handedness Bias has functional consequences on manual skill
- Neonatal head-orientation preference likely predicts infant reaching preferences because of its effect on asymmetry of hand regard and activity
- Early reaching preferences concatenate into later manipulation preferences
- Handedness development is a spreading cascade across different manual skills rather than simply an increase in handedness within a skill.
- Early hand-use preferences are likely developmental precursors for, but not homologous to, adult handedness

Concluding Remarks

- Moreover, the asymmetries within any skill can interact with the caregiver's handedness to further shape the individual's hand-use such that by their 18 months, most children have a hand-use preference across a range of unimanual and bimanual skills that will form the basis of all future hand actions and hence their "handedness".
- We need good systematic comparative developmental research using precise definitions of handedness (appropriate for different stages of development) before we can consider the homology of handedness.
- If handedness can be used analogously, I would argue against using homology in developmental research of any sort.

Reminder: Constraints and Homoplasy

Because morphological variation is limited by constraints dependent on lineage, developmental, physical and biochemical mechanisms, not all possible morphologies for a particular organism are realized or expressed.

Such inherent limitations on form increases the likelihood of homoplasy.

These limiting conditions apply to other traits (e.g., physiology, behavior), as well as form.

Form can limit function – similarity of behavior may simply reflect homology of structure – each type of joint has limited degrees of freedom.

<u>Comparative Developmental Research</u>

<u>Comparative developmental research</u> (not of model organisms but of taxonomically related organisms) is essential for identifying and defining the processes responsible for similar phenotypes across diverse taxa.

Comparative developmental research is essential for identifying similarities based on convergence versus parallelism.

Modern developmental research has demonstrated that the mechanisms responsible for generating phenotypic similarity can be found at different organizational levels - the phenotypic or whole organismal level, developmental, epigenetic, and genetic levels.

Criteria for Behavioral Homology

Ethologists added two criteria specific for behavior:

4. Peripheral structures. Movements employing homologous structures in similar ways are homologous (but form constrains function -> homoplasy)

5. Nervous system. Behavior associated with established homologous regions of the brains are homologous (again, form constrains function -> homoplasy)

Although 40 years ago, Atz (1970) argued that these criteria had not solved the problem of homology of behavior, modern research has simply ignored these criticisms when considering behavioral homologies.

Thanks to:

Infants and their parents

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Audience: You

What is a Developmental Psychobiological Approach?

- Systematic description of some species typical trait
- Examine the trait with four questions:

1. What function does the trait serve?
2. What factors, internal and external, enable the expression of the trait?
3. What is the phylogenetic history of the trait?
4. How does the trait develop?

EDINBURGH HANDEDNESS INVENTORY

Surname.. Given Names..

Date of Birth.. Sex..........................

Please indicate your preferences in the use of hands in the following activities *by putting + in the appropriate column*. Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, *put ++*. If in any case you are really indifferent *put + in both columns.*

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

		LEFT	RIGHT
1	Writing		
2	Drawing		
3	Throwing		
4	Scissors		
5	Toothbrush		
6	Knife (without fork)		
7	Spoon		
8	Broom (upper hand)		
9	Striking Match (match)		
10	Opening box (lid)		
i	Which foot do you prefer to kick with?		
ii	Which eye do you use when using only one?		

L.Q.		Leave these spaces blank	DECILE	

MARCH 1970

Annett's Handedness Inventory

Indicate Hand Preference - Right or Left:

- To Write legibly
- To throw a ball or dart to hit a target
- To hold a tennis racquet, fishing pole, or paint brush
- At the top of a push broom to sweep dust from the floor
- At the top of a shovel to move snow or dirt
- To hold a match when striking it
- To hold scissors to cut paper
- To guide thread through the eye of a needle (or to guide a needle on to thread)
- To deal playing cards
- To hammer a nail into wood
- To hold a tooth brush while cleaning teeth
- To unscrew the lid of a jar

Indicate Hand Preference:	Always Right	Usually Right	No Pref.	Usually Left	Always Left
1. To Write legibly					
1. To throw a ball or dart to hit a target					
1. To hold a tennis racquet, fishing pole, or paint brush					
1. At the top of a push broom to sweep dust from the floor					
1. At the top of a shovel to move snow or dirt					
1. To hold a match when striking it					
1. To hold scissors to cut paper					
1. To guide thread through the eye of a needle (or to guide a needle on to thread)					
1. To deal playing cards					
1. To hammer a nail into wood					
1. To hold a tooth brush while cleaning teeth					
1. To unscrew the lid of a jar					