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17. We are grateful for assistance from the National Geographic Society and Arizona State University Faculty Research Program that made possible the study of these paleo-Indian and other teeth. We also thank D. K. Patterson for assistance and use of the mean measure of distance program. Our Indian and Asian comparisons are based on physical anthropological collections from the American Museum of Natural History, Smithsonian Institution, Academia Sinica (Taiwan), Field Museum, Lowie Museum, Burke Memorial Washington State Museum, and Arizona State University. We thank I. Tattersall, J. L. Angel, Li Chi, H.-M. Yang, G. Cole, F. Norick, and D. Swindler for enabling study of these materials. We are indebted for supplementary information on Siberian anthropology from S. Arutinov, I. A. Mochanov, G. I. Medvedev, N. N. Dikov, R. S. Vasilievsky, R. Ackerman, R. Carlson, and L. Okladnikova, and for other help and views by V. N. Denishchick and D. M. Hopkins. This report is an expanded version of a paper delivered at the 43rd annual meeting of the Society for American Archaeology, Tucson, Ariz., May 1978. It is the seventh in a series of published papers on the peopling of the Pacific basin and adjoining areas. Full description of these paleo-Indian teeth can be obtained from C.G.T.

17 November 1980; revised 27 March 1981

Familial Studies of Intelligence: A Review

Abstract. *A summary of 111 studies identified in a survey of the world literature on familial resemblances in measured intelligence reveals a profile of average correlations consistent with a polygenic mode of inheritance. There is, however, a marked degree of heterogeneity of the correlations within familial groupings, which is not moderated by sex of familial pairing or by type of intelligence test used.*

In 1963, Erlenmeyer-Kimling and Jarvik (*1*) published a summary of the world literature on IQ correlations between relatives. Their finding that the pattern of correlations averaged over independent studies was consistent with the pattern predicted by a polygenic theory of inheritance has been widely cited as strong evidence for some genetic determination of IQ (*2*). Although the accumulation of a great many new data along with the discrediting of Burt's important study on monozygotic twins reared apart (*3*) has outdated that review, the authors' summary or slightly modified versions of it (*4*) continue to be widely reproduced (*5*). Recently Plomin and DeFries (*6*) have reported a comparison of those summary data with the results of several large, recent familial studies of IQ. They conclude that, in general, the recent studies show less resemblance between relatives than do the data reported by Erlenmeyer-Kimling and Jarvik. Their summary is not comprehensive, however, and it does not identify the factors that distinguish the two bodies of data. Roubertoux and Carlier (*7*) have also published a recent review, but it contains only 37 percent of the studies to be cited here.

The purpose of this report is to provide a comprehensive contemporary summary of the world literature on the IQ correlations between relatives. We have updated the 1963 summary, adding recent data and deleting several studies included in the earlier review that do not meet our methodological criteria for inclusion. Although the pattern of averages reported in this and earlier reviews is remarkably consistent with polygenic theory, the individual data points are quite heterogeneous. Therefore, we have also assessed the extent to which the reported correlations are heterogeneous and have attempted to identify some factors that contribute to this heterogeneity.

In our survey of the literature we found 140 studies that reported on familial resemblances in broad cognitive ability. These were reduced to 111 by the application of explicit selection criteria (*8–12*). The 111 studies, which include 59 reported in the 17 years subsequent to the Erlenmeyer-Kimling and Jarvik summary, yielded 526 familial correlations, based upon 113,942 pairings. Figure 1 displays the correlations between relatives, biological and adoptive, in the 111 studies. The median correlation in each distribution is indicated by a vertical bar. The small arrow indicates the correlation that would be predicted by a genetic model with no dominance, no assortative mating, and no environmental effects. Researchers do not subscribe to such a simple model, but it provides a noncontroversial pattern against which to compare the results of various familial groupings. Different investigators will undoubtedly fit different models to the data.

In general, the pattern of average correlations in Fig. 1 is consistent with the pattern of correlations predicted on the basis of polygenic inheritance. That is, the higher the proportion of genes two family members have in common the higher the average correlation between their IQ's.

The data set contains considerable heterogeneity, as indicated by the χ^2 statistics. In an attempt to identify the factors contributing to the heterogeneity, we subdivided the familial groupings into opposite-sex and same-sex pairings (Fig. 2) and male and female pairings (Fig. 3). Among dizygotic twins the IQ's of same-sex twins are more similar than those of opposite-sex twins. This may reflect a social-environmental effect (parents may treat same-sex twins more similarly than opposite-sex twins). The difference between nontwin same-sex and opposite-sex siblings and between same-sex and opposite-sex parent-offspring pairings is trivial. The male-female comparison does not yield consistent trends. For example, the average correlations are larger in male twins than in female twins, but the reverse is true for other siblings. The absence of any demonstrable sex effect is consistent with a polygenic theory of inheritance that does not posit the existence of sex linkage. Environmental theories that emphasize the importance of sex-role effects on general cognitive development are not supported by these results (*13*).

Another possible source of heterogeneity is the intelligence test used. There are many tests that purport to measure intelligence, and they may not be highly interrelated. We found great diversity in test selection. For example, the 34 correlations for monozygotic twins reared together were based upon results from 22 different tests, the 41 dizygotic twin correlations upon results from 25. We do not have sufficient data to determine whether the magnitude of the familial correlation is moderated by the specific test used. We did investigate whether individually administered tests and group-administered tests produced different correlations. For the monozygotic twins reared together the 24 correlations calculated on group tests produced a weighted average of .86, and the 10 calculated on individual tests a weighted average of .84. For the dizygotic twins reared together, the weighted average of 32 correlations based on group tests is .60 and of 9 correlations based on individual tests is .61. In neither case did the distinction between group and individual test produce an appreciable effect.

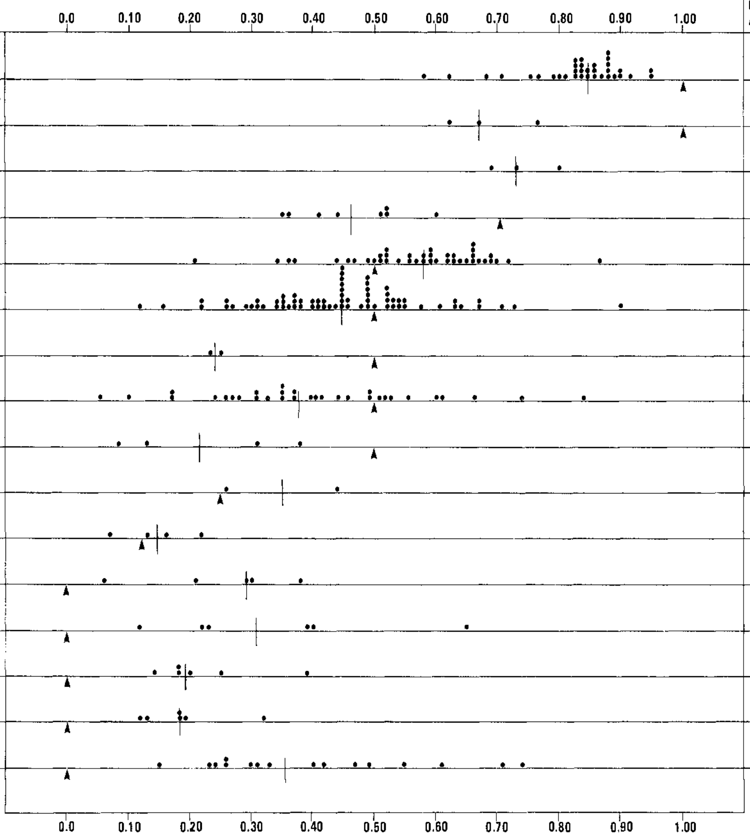
The 34 correlations reported on 4672 monozygotic twin pairs reared together produce a weighted average correlation of .86. This value is very close to those reported in earlier reviews and is approximately the same for male and female pairs. Although the test of homogeneity yields a significant χ^2 value ($P < .02$), the degree of heterogeneity is not extreme and can be seen to result from a few rather low correlations (*14*). The two most extreme values are the .58 reported by Blewett (*15*) and the .62 reported by Nichols (*16*). In both cases the sample sizes are small (26 and 36 pairs, respectively). The observation that 79 percent of the reported correlations lie above .80 convincingly demonstrates the remarkable similarity of monozygotic twins.

After deleting the Burt data we are left with test results on but 65 pairs of monozygotic twins reared apart, as reported in three separate investigations. The weighted average of .72 is much less than that found for the monozygotic twins reared together, the difference suggesting the importance of between-family environmental differences. At the same time, the magnitude of this correlation would be difficult to explain on the basis of any strictly environmental hypothesis.

Three studies give midparent-midoffspring correlations, the weighted average of these being .72. In this case the genetic expectation would depend upon the number of offspring that define the midoffspring value, and is thus indeterminate. The correlation between midparent and individual offspring does have a determinate simple genetic expectation, which is .707. The observed weighted average of .50 is substantially less than that, a discrepancy we discuss later.

The weighted average of the 41 reported correlations in dizygotic twin pairs is .60, considerably larger than for nontwin siblings. Same-sex dizygotic pairs show somewhat greater similarity than opposite-sex dizygotic pairs (.62 versus .57), males being slightly more similar than females (.65 versus .61). As with the monozygotic twins, the test of homogeneity yields a significant value ($P < .01$), although 75 percent of the correlations fall within the narrow range between .50 and .70. The two extreme values were reported in old studies on rather small samples, the lowest being the .21 reported by Wingfield (*17*) in 1928 on 26 pairs, the highest the .87 reported by Merriman (*18*) in 1924 on 51 pairs. The greater similarity of dizygotic twins than of other siblings is most often interpreted as a reflection of greater environmental similarity. It is also likely that bias in the recruitment of dizygotic twins for study is in the direction of increasing psychological similarity (*19*).

The weighted average for siblings reared together is .47, which although close to the simple expectation of .50 is



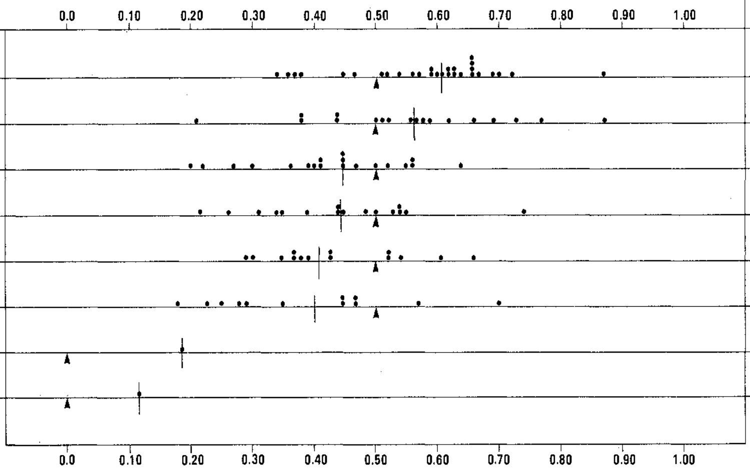
	NO. OF CORRELATIONS	NO. OF PAIRINGS	MEDIAN CORRELATION	WEIGHTED AVERAGE	X^2 (d.f.)	$X^2 \div$ d.f.
MONOZYGOTIC TWINS REARED TOGETHER	34	4672	.85	.86	81.29 (33)	2.46
MONOZYGOTIC TWINS REARED APART	3	65	.67	.72	0.92 (2)	0.46
MIDPARENT–MIDOFFSPRING REARED TOGETHER	3	410	.73	.72	2.66 (2)	1.33
MIDPARENT–OFFSPRING REARED TOGETHER	8	992	.475	.50	8.11 (7)	1.16
DIZYGOTIC TWINS REARED TOGETHER	41	5546	.58	.60	94.5 (40)	2.36
SIBLINGS REARED TOGETHER	69	26,473	.45	.47	403.6 (64)	6.31
SIBLINGS REARED APART	2	203	.24	.24	.02 (1)	.02
SINGLE PARENT–OFFSPRING REARED TOGETHER	32	8433	.385	.42	211.0 (31)	6.81
SINGLE PARENT–OFFSPRING REARED APART	4	814	.22	.22	9.61 (3)	3.20
HALF-SIBLINGS	2	200	.35	.31	1.55 (1)	1.55
COUSINS	4	1,176	.145	.15	1.02 (2)	0.51
NON-BIOLOGICAL SIBLING PAIRS (ADOPTED/NATURAL PAIRINGS)	5	345	.29	.29	1.93 (4)	0.48
NON-BIOLOGICAL SIBLING PAIRS (ADOPTED/ADOPTED PAIRINGS)	6	369	.31	.34	10.5 (5)	2.10
ADOPTING MIDPARENT–OFFSPRING	6	758	.19	.24	6.8 (5)	1.36
ADOPTING PARENT–OFFSPRING	6	1397	.18	.19	6.64 (5)	1.33
ASSORTATIVE MATING	16	3817	.365	.33	96.1 (15)	6.41

Fig. 1. Familial correlations for IQ. The vertical bar in each distribution indicates the median correlation; the arrow, the correlation predicted by a simple polygenic model.

based upon 69 values with a range of correlations from .13 to .90. Opposite-sex and same-sex siblings yield almost identical weighted averages (.49 versus .48), as do female and male siblings (.50 versus .47). The sibling correlations are based on over 25,000 pairs; one large representative study by Record *et al.* showed a correlation of .55 on over 5000 pairs (*20*).

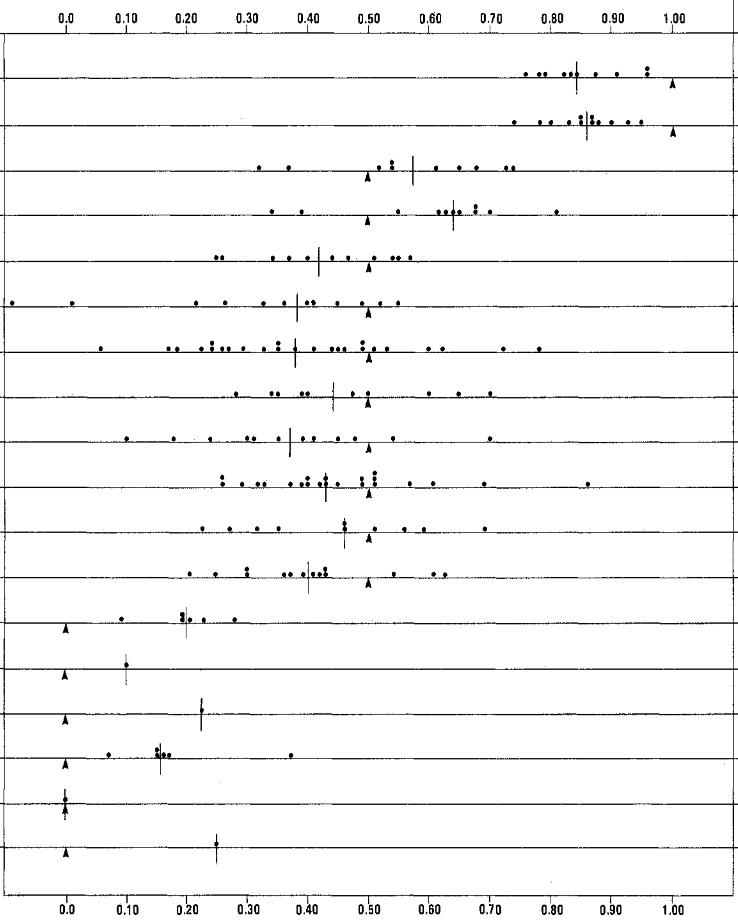
Whereas there is a wealth of information on siblings reared together, there is a dearth of information on siblings reared apart. Only 203 such pairs have been studied, in two investigations yielding a weighted average of .24, much less than the expected value for such pairs and the average value for siblings reared together.

The weighted average correlation between individual parent and individual



	NO. OF CORREL-ATIONS	NO. OF PAIRINGS	MEDIAN CORREL-ATION	WEIGHT-ED AVER-AGE	X^2 (d.f.)	X^2 ÷ d.f.
SAME SEX DIZYGOTIC TWINS	29	3,670	.61	.62	68.14 (28)	2.43
OPPOSITE SEX DIZYGOTIC TWINS	18	1592	.565	.57	58.6 (17)	3.45
SAME SEX SIBLINGS PAIRS	19	6098	.45	.48	84.65 (17)	4.98
OPPOSITE SEX SIBLING PAIRS	16	5127	.445	.49	70.4 (14)	5.03
SAME SEX PARENT–OFFSPRING PAIRINGS	14	4648	.41	.40	55.4 (13)	4.26
OPPOSITE SEX PARENT–OFFSPRING PAIRINGS	12	4476	.40	.39	70.1 (11)	6.37
SAME SEX ADOPTING PARENT–OFFSPRING PAIRINGS	1	460	.18	.18		
OPPOSITE SEX ADOPTING PARENT–OFFSPRING PAIRINGS	1	461	.12	.12		

Fig. 2. Familial correlations for IQ organized by opposite-sex and same-sex pairings.



	NO. OF CORREL-ATIONS	NO. OF PAIRINGS	MEDIAN CORREL-ATION	WEIGHT-ED AVER-AGE	X^2 (d.f.)	X^2 ÷ d.f.
FEMALE MZ TWIN PAIRS	10	869	.835	.86	26.35 (8)	3.29
MALE MZ TWIN PAIRS	12	1,013	.86	.86	24.4 (10)	2.44
FEMALE DZ TWIN PAIRS	10	730	.58	.61	14.73 (8)	1.84
MALE DZ TWIN PAIRS	11	964	.64	.65	20.32 (9)	2.26
FEMALE SIBLING PAIRS	11	1,986	.42	.50	28.34 (9)	3.15
MALE SIBLING PAIRS	12	2,321	.38	.47	54.69 (10)	5.47
MOTHER–OFFSPRING REARED TOGETHER	25	5,660	.38	.41	119.02 (24)	4.96
MOTHER–DAUGHTER REARED TOGETHER	10	1,804	.44	.43	36.80 (9)	4.09
MOTHER–SON REARED TOGETHER	12	2,802	.37	.39	38.52 (11)	3.50
FATHER–OFFSPRING REARED TOGETHER	22	5,497	.43	.41	141.17 (21)	6.72
FATHER–DAUGHTER REARED TOGETHER	10	1,658	.46	.39	33.08 (9)	3.68
FATHER–SON REARED TOGETHER	14	2,843	.40	.38	36.86 (13)	2.84
ADOPTING MOTHER–OFFSPRING	6	1,393	.195	.20	4.28 (5)	0.86
ADOPTING MOTHER–DAUGHTER	1	212	.10	.10		
ADOPTING MOTHER–SON	1	247	.22	.22		
ADOPTING FATHER–OFFSPRING	6	1,279	.155	.18	10.1 (5)	2.02
ADOPTING FATHER–DAUGHTER	1	214	.00	.00		
ADOPTING FATHER–SON	1	248	.25	.25		

Fig. 3. Familial correlations for IQ organized by male and female pairings.

offspring is .42 based upon 32 correlations. There is a marked degree of heterogeneity in the distribution, as evidenced not only by a significant χ^2 value ($P < .01$), but also by the broad range of the correlations. Their extreme heterogeneity cannot be attributed to a sex effect, inasmuch as opposite-sex and same-sex pairings yield equivalent averages, or to a maternal effect, the average correlation of mother and offspring being the same as that of father and offspring. Although the large discrepancies between expected and observed correlations for parent and offspring reared in the parental home ("reared together") may be easily interpreted as a result of a generational (social-environmental) effect, one should not hastily discount the possibility of biological factors. Characteristics that are affected very little by the social environment, such as height and total fingerprint ridge count, show similar generational differences. For example, in one large study of height Wingerd *et al.* (*21*) found a midparent-offspring correlation of .51. Two large studies of total fingerprint ridge count (*22*) yield a *Z*-weighted mean midparent-offspring correlation of .63. The single parent–offspring correlations for height and total fingerprint ridge count are .42 and .42 (*21–23*).

As with parent and offspring reared together, correlations for parent and separated offspring are quite heterogeneous. The weighted average is .22, much less than the simple expectation of .50. As suggested by McAskie and Clarke (*24*), one possible explanation could be that parents and offspring are not given the same test. In fact, roughly 50 percent of our intergenerational correlations were based upon data from cases in which parents were given different tests from those given their offspring. The lower-than-expected morphological correlations found in these studies, however, suggest that scaling may not be the only problem.

Two familial pairings that are rarely studied are half-siblings and cousins. Two half-sibling correlations, both reported by Nichols (*16*), produce a weighted average of .31. The four reported correlations for cousins are quite homogeneous; their average, .15, closely approximates the simple genetic expectation.

A number of recent adoption studies have added considerable knowledge. Enough studies are available to permit comparison of two sets of nonbiological sibling pairs—adopted/natural and adopted/adopted. Other things being equal, the adopted/natural correlation should be higher than the adopted/adopted correlation, because the former would contain a component for the covariance of genotype and environment (*25*). The present review finds the reverse (Fig. 1).

The weighted average correlation of adoptive midparent and offspring is .24, and that of adoptive parent and offspring is .19. Genetic theory requires the biological midparent-offspring correlation to exceed the biological single parent–offspring correlation, and it does, although not by much (.50 versus .42). Some environmental theories predict the same effect (*24*); the failure to find any difference in the adoptive case must be considered surprising from an environmental point of view.

Unlike the case in natural families, adopted offspring are somewhat more similar to the same-sex adoptive parent than to the opposite-sex adoptive parent (Fig. 2). This conclusion is based, however, on a single study (*26*). Overall, adoptive mothers are no more like their adopted children than adoptive fathers are.

The last row in Fig. 1 gives assortative mating coefficients. There is marked similarity between mates, but the weighted mean of .33 is much smaller than the .50 sometimes reported (*27*). The marked heterogeneity of the distribution indicates the sample-specific nature of these indices.

As in the earlier review, the pattern of averaged correlations is remarkably consistent with polygenic theory. This is not to discount the importance of environmental factors; monozygotic twins reared apart are far from perfectly correlated, dizygotic twins are more similar than other biological siblings, and adoptive parents' IQ's demonstrate a consistent relation with the IQ's of their adopted offspring. Although the data clearly suggest the operation of environmental effects, we found no evidence for two factors sometimes thought to be important—sex-role effects and maternal effects. That the data support the inference of partial genetic determination for IQ is indisputable; that they are informative about the precise strength of this effect is dubious. Certainly the large amount of unexplained variability within degrees of relationship, while not precluding attempts to model the data, suggests that such models should be interpreted cautiously.

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8. The reports that met the following criteria were selected: (i) The research was reported in the published literature or as a doctoral dissertation. (ii) Familial resemblance was indicated by a correlation coefficient, or the information provided permitted the determination of the correlation. In excluded studies results were typically reported in terms of *F* ratios or within-pair variances. (iii) The cognitive measure employed was a widely accepted, standardized measure of intelligence, or such a measure could be derived from the test battery (for example, the first principal component as a representative of the g factor). In most studies excluded on the basis of this criterion either a single measure of special ability or a subjective rating of intellectual level was used. (iv) In twin studies, the procedure for zygosity determination was both objective and valid. Use of a validated questionnaire was considered an acceptable procedure. Many of the early twin studies depended on subjective procedures, for example teacher ratings. In such cases only the opposite-sex twins (necessarily dizygotic) were included in our data. (v) The sample reported on did not overlap with another sample reported elsewhere. For example, the sample reported on by Jones (*9*) was not taken because it is included in the larger sample reported on later by Conrad and Jones (*10*). (vi) Because of the controversy surrounding the samples reported on by Burt and some of his colleagues (*3*), all data based on them were excluded.

   For each selected study the reported correlations were classified into the relevant categories of familial relationship. If for any single sample several correlations were recorded within the same category, a single index of association was determined as follows: (i) If correlations were reported for several measures of intelligence one of which was an individually administered test, the correlation for the individually administered assessment was selected. If all measures were group intelligence tests, their average correlation was used. Averaging was on the Fisher *Z* transformations of the correlations. (ii) If several correlations were reported in a longitudinal sequence, then the correlation recorded at the highest age level was selected. (iii) If statistical corrections were applied (correction for attenuation, correction for range restriction, correction for age, or the like), only the age-corrected correlation was used. If no age-corrected correlation was reported, then the uncorrected correlation was used. (iv) If several dependent samples reported on in the same study were relevant for the category, then the weighted average of the correlations was used (weighted average of *Z* transformations, with sample size used as the weight). For example, few studies reported a single correlation between parent and offspring; instead separate father-offspring and mother-offspring correlations were given. In such cases the parent-offspring correlation was determined as the average of the two correlations with the number of pairings equal to the sum of the pairings for the two correlations.

   Application of the above rules resulted in the inclusion of only independent correlations within any single classification category. For each category the total number of pairings reported is actually the minimum number of pairings, as in several studies results were reported in terms of the number of families used. The weighted average correlation was determined by taking the weighted averages of the *Z* transformations with the inverse of the variance used as the weight and is thus the maximum likelihood estimator (*11*). The weights employed were $N - 3$ for interclass correlations and $N - 3/2$ for intraclass correlations. The χ^2 statistic can be used to test the hypothesis of homogeneity; that is, all sample correlations were drawn from the same population (12). The χ^2 statistic divided by its degrees of freedom has an expectation equal to 1.0 under the homogeneity hypothesis and can be used to compare the relative heterogeneity of different categories.

Detailed information about the data presented here and a list of studies included and excluded are available from the authors.

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27. A. R. Jensen has reviewed this literature and found a weighted mean of .42 [A. R. Jensen, in *Human Variation*, R. T. Osborne, C. E. Noble, N. Weyl, Eds. (Academic Press, New York, 1978)]. His review is less selective than ours.

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Modular Segregation of Functional Cell Classes Within the Postcentral Somatosensory Cortex of Monkeys

Abstract. *The distribution of two functionally distinct cell types, presumably related to slowly and rapidly adapting mechanoreceptors in the skin, was explored within the representation of the glabrous hand in area 3b of the somatosensory cortex of monkeys. The two cell classes lie in relatively segregated alternating anteroposterior bands within the middle layers of the cortex.*

One of the most basic and fundamental concepts of how the brain is organized is that the major subdivisions—the cortical areas and subcortical nuclei—are further divided into partially isolated local circuit units or modules of neurons united by a common task. This concept was first formalized when Mountcastle (*1*) proposed that the somatosensory cortex is divided into a mixture of different types of narrow vertical columns, 0.5 mm or less in diameter, extending perpendicularly through the cortical layers. Each column was characterized by neurons having similar overlapping receptive fields on the body surface and responsiveness to a single submodality of somatosensory stimulation. It was suggested that a single or small group of thalamocortical fibers, activated by a single type of peripheral stimulation (such as joint rotation, manipulation of "deep" body tissue, hair movements, or pressure on the skin) at a single body location in turn activates a narrow vertical column of cells, and that adjacent cortical columns are activated by different types of stimulation. The observations that led to this formalization were that vertical microelectrode penetrations in the somatosensory cortex of cats consistently encountered cells responsive to the same submodality of somatosensory stimulation and had overlapping receptive fields. Slanting electrode penetrations, however, revealed short progressions of neurons activated by one submodality interrupted by short progressions of neurons activated by another submodality, as well as shifts in receptive field locations. Such observations have been made repeatedly by many investigators for cortex responsive to sensory stimuli, and there is wide agreement that the sensory cortex is organized into "columns" or "modules." The question that remains is, How is any particular cortical area divided into columns? More specifically, What are the types of columns, what are the sizes and shapes of these columns, and how do the different types of columns relate to one another?

The region of the cortex where this question has been best answered is the striate cortex (area 17) of monkeys, where the precise distributions of ocular dominance columns and orientation columns have been demonstrated (*2*). In regions other than the striate cortex, investigations of modular organization have been hindered to some extent by a lack of detailed knowledge of how sensory surfaces are represented in the particular cortical region (*3*). Until recently, for example, the postcentral somatosensory cortex of monkeys containing the four architectonically distinct zones—areas 3a, 3b, 1, and 2—was thought to contain a single representation of the body and a complex mixture of somatosensory submodalities. It now appears that each architectonic field constitutes a separate representation of the body receiving input from a limited subset of peripheral receptor types (*4*, *5*). Area 3a seems to receive thalamic input related to muscle receptors, and area 2 is activated by thalamic input related to joint and other deep body receptors. Areas 3b and 1 each form detailed topographic representations of the body surface, and each appears to be exclusively or nearly exclusively activated by various types of cutaneous receptors.

Because the somatotopic organizations of areas 3b and 1 are now known in detail, it is possible to perform experiments designed to reveal the modular organization of these areas. Our limited start in this direction has been to explore systematically all of the cortex in area 3b devoted to a single finger of the hand to see how neurons activated by particular receptor types are distributed. We hoped that an understanding of how these inputs are represented in the cortex devoted to the glabrous skin of a single finger would generate a testable hypothesis of how these inputs are organized throughout area 3b.

The two basic receptor types in the skin of primates are slowly adapting (SA) receptors, which respond tonically to a maintained indentation of the skin surface, and rapidly adapting (RA) receptors, which respond phasically only at the onset and offset of applied steady stimuli (*6*). Our mapping studies revealed that areas 3b and 1 of monkeys contain input from both classes of receptors. We found two types of neurons (Fig. 1A). Both types have phasic responses at stimulus onset and often at offset; one type also has tonic responses while a stimulus indents the skin for a maintained period of time. This type of neuron must receive significant input from peripheral SA receptors and is termed an SA cortical neuron. The other type can be most easily related to RA receptors and is termed an RA cortical neuron. In detailed single and multiple unit studies of the representation of the glabrous hand digits in area 3b, we have found that SA and RA neurons are grouped separately in largely anteroposterior