difference in responses of fibers from the 2 sides of the muscle was observed.

13-15 days after denervation, the number of muscle fibers generating local responses in the extrasynaptic area in the presence of TTX $(5 \times 10^{-6} \text{ M})$ increased from 9 in 30 to 13 in 25 cases (i.e. from 30 to 52%). After the same period from CCh application, the number of responding fibers rose to 17 out of 33 (i.e. also to 52%).

It is known that sodium channels located in the synaptic region of rat muscle are more resistant to TTX than those outside the synaptic area, but all are blocked by raising the toxin concentration2. In our experiments an increase in TTX concentration to 10⁻⁵ M did not eliminate the local re-

The rate of rise of the AP within the synaptic region is higher $(225 \pm 7.8 \text{ V/sec (mean} \pm \text{SE}, 21 \text{ fibers}))$ than that observed extrasynaptically (197±6.4 V/sec, 63 fibers). The difference is significant according to the t-test (p < 0.02). This result supports other data for amphibian¹ and mammalian muscles². It may be assumed that in the synaptic region of frog skeletal muscle there are 2 types of voltagedependent sodium channels; one is nonresistant, and the other resistant to TTX. It is possible that the extrasynaptic muscle membrane has a uniform density of TTX nonresistant channels, whereas in the synaptic region there are additional channels resistant to TTX. This might contribute to the increased density of sodium channels on the postsynaptic membrane thereby affording a more rapid redistribution of charge.

In frog muscle fibers denervation does not cause development of TTX resistant AP⁴. But the present data show that muscle denervation, by nerve cutting or by blocking axoplasmic transport with CCh, leads to an increase in the number of muscle fibers capable of generating local responses on the extrasynaptic membrane in the presence of TTX. This suggests that the localization of TTX resistant sodium channels in the synaptic area is determined by nervous control, as is well known in the case of cholinoreceptors. To eliminate this control it is sufficient to block axoplasmic transport by colchicine, rather than to inhibit the transmission of excitation.

Frog muscle fibers studied in our experiments differ from muscle fibers in mammals in 2 aspects. 1. An increase in TTX concentration does not completely block the development of local AP; 2. In 30% of tested muscle fibers, TTX resistant local responses occur on the extrasynaptic membrane even without denervation.

- W.L. Nastuk and J.T. Alexander, Fedn Proc. 32, 333 (1973).
- S. Thesleff, F. Vyskočil and M.R. Ward, Acta physiol. scand.
- P. Redfern and S. Thesleff, Acta physiol. scand. 82, 70 (1971).
- G.A. Nasledov and S. Thesleff, Acta physiol. scand. 90, 370
- B. Eisenberg and R.S. Eisenberg, J. Cell Biol. 39, 451 (1968). S.A. Krolenko, Nature 221, 969 (1968). J. del Castillo and B. Katz, J. Physiol., Lond. 125, 546 (1954).

- E. M. Volkov, Bull. exp. Biol. Med. USSR 82, 359 (1974).
- A.L. Zefirov, N.P. Resvyakov, G.I. Poletaev, E.G. Ulumbekov and E. M. Volkov, Bull. exp. Biol. Med. USSR 86, 391 (1978).

Face representation linked with literacy level in colonial American tombstone engravings and Third World preliterates' drawings. Toward a cultural-evolutional neurology

Anneliese A. Pontius¹

Harvard Medical School, McLean Hospital, 115 Mill Street, Belmont (Massachusetts 02178, USA), 18 December 1980

Summary. Among colonial North-American artisans, subgroups of South-Americans, Indonesians and New Guineans, a close correspondence exists between illiteracy rates and specifically spatially inaccurate representations of the upper face configuration, a characteristic also seen in the pre-literate period of 'neolithic' art, in early individual development, and in certain pathological regressions. Common to the configuration both of lexical signs and of the face is a specific spatial-relational ratio and orientation. Accurate representation of both configurations appears to be neuro-developmentally linked, within a cultural context, and consistent with a novel position that the 'ontogeny' of such cognitive functions recapitulates their prevailingly culturally determined 'phylogeny'.

This study raises the question of the non-identity between the mental and the graphic representation of a specific object; the human face. The findings here reported will show that pre-literates, i.e. persons untrained in the accurate graphic representation of lexical signs, also showed a significant percentage of inaccurate graphic representations of the human face exclusively. These preliterates were not known to have had problems with the perception and recognition (mental representation) of the face. Other objects were graphically represented without essential distortions. (The characteristic exception of finger misrepresentation only by certain remote cultural groups is of special interest - see later.) Findings from studies of face recognition by Carey et al.^{2,3} and by Yin⁴ also point to the face configuration's quite specific neurological mediation, the existence of which is supported by the present results. In addition, these point to an association between the neurodevelopmental phases of the graphic representation of the face and

of lexical signs within a cultural context. Such a clustering of functions appears to be analogous to that found in the early development of mankind and of the individual, as well as in certain states of pathological regression.

Historical data can be drawn from the pre-literate period of 'neolithic art' that was produced up to about 4 millenia ago. Its most characteristic sign, found world-wide, is a specific and consistent spatial-relational distortion: an obliteration of the narrow or indented area of the bridge of the nose, in short, a depiction of a 'neolithic face' (fig., NGr and NGl). This specific sign persists in historically younger populations within subgroups that have had neither training for literacy nor, it seems, for depiction of the human

On the basis of this clue from historical observation, performance was rated on a task (drawing or gravestone engraving) requiring the pictorial representation of the uniquely oriented human face configuration, containing the complex area of the bridge of the nose. Artisans' performance on this task can be compared with their group's reported performance in literacy tests inasmuch as both tasks require the ability for accurate graphic spatial representation of uniquely oriented patterns - with a distinct ratio among their parts - whether of the subtle human facial features or of lexical signs.

Indeed, a close correspondence will be revealed between lack of literacy and of basically accurate pictorial representation of the human face in a subgroup of colonial North-American artisans⁶, in a contemporary population from South-America, and as previously shown, in contemporary Indonesians⁷ and New Guineans⁷. Literacy is here defined as the learned ability to encode (to write) and to decode (to read) lexical signs, as an analyzing and synthesizing process, not merely as 'sight reading' or 'whole word reading' of overlearned signs, words or phrases.

In such a context, it appears that the evolving ability for complex spatial representation parallels that for literacy. Among all natural things, it is the human face that has these characteristics, particularly in the area which has the most individual patterns (and is therefore hidden by thieves and Mardi Gras celebrants alike); the area around the bridge of the nose. We all encode an enormous multitude of individual faces²⁻⁴ and are able to recognize them after many years and despite paraphernalia. By contrast and characteristically when the human face is less distinctly perceived, as during early infancy, it serves merely as a nonindividualized releaser stimulus for a non-discriminatory automatic 'smiling response'9,10, and during an early subphase up to 18 weeks of age11 infants 'smile' preferentially at 'neolithic face' masks over control masks and the natural

A rating of the folk art of colonial America offered itself as a natural continuation of research^{12,13} to test further the suggested positive correlation between literacy¹⁴⁻¹⁹ and the ability to represent the human face accurately. An alternative hypothesis tested with the colonial American sample (n=1570) posits that body parts other than the upper area of the human face - i.e. fingers and neck - show this postulated close correspondence too, inasmuch as their pictorial representation also marks certain milestones in children's development of general graphic representation²⁰

The sample consists of spontaneously produced engravings and carvings of faces in frontal view on tombstones made by colonial New England artisans during the later sixteenth, throughout the seventeenth and during the beginning of the eighteenth centuries²¹⁻²⁶ as reproduced in photographs. Drawings by subgroups of South-Americans and those previously described from New Guinea and Indonesia are rated as to the presence or absence of the specific distortions of the upper part of the face commonly found during the period of neolithic art (fig.).

Benes²¹ reports that colonial New Englanders were considered to have been 'iconophobic'. Thus, it seems reasonable to assume that they had no particular training in how to depict the face, since these makers of the tombstones were artisans, not specifically highly trained artists. In contrast Europe, with its greater population density, could support trained artists as tombstone engravers. Artisans are more representative of the general population under study than artists would be; the latter could even have been trained by other artists from outside their cultural group.

Populations were chosen for study for which the percentage of literacy had been previously determined by direct methods: signature tests of the colonial North-American artisans^{6b}, or UNESCO's literacy determinations^{14,15} of the other populations under scrutiny here.

A quantitative rating was done on an all-or-none basis (by measurement with a ruler) of the specific two sets of face

distortions shown in the figure. This measurement test had previously been introduced on an empirical basis and found to produce significant results ($p \le 0.01$) in studies of dyslexia and pre-literacy^{6-8,12,13}. Aesthetic judgement was not involved. The longish sub-type 'NGl' (fig.) was judged to be present when a ruler, placed along the upper border of the eyes, indicated that there was an extension of the nose upward over this imaginary horizontal line. The roundish subtype 'NGr' (fig.) was judged to be present when a ruler, placed along the lower border of the eyes, showed at least the same breadth of the nose there as at the tip of the nose, not including flaring nostrils or any bulbous enlargement merely of the cartilagenous, i.e. lowest part of the nose. Two independent workers (Katherine F. Ruttiger and myself) disagreed about the rating in only 0.2% of the cases. The depiction of the fingers and the neck was also rated as to the completeness or presence, respectively, of these body parts.

The results are shown in the table and support the main hypothesis²⁷. The proportions of 'neolithic' face representations and of illiteracy closely correspond to one another (trend analysis, $p \le 0.01$). This finding suggests a specific link between the compared representational abilities, the more so as the alternative hypothesis was not supported: The rating revealed that among those colonial American artisans who depicted the two sub-types of specific face distortions here under discussion, less than 1% also depicted poor finger configurations and/or failed to depict the neck. Note that in adults, mental misrepresentation of the fingers is found in the pathological situation of the Gerstmann syndrome, to be mentioned later on. It includes dys- or acalcu-

'Neolithic' face representations and illiteracy levels

Cultural groups	Proportion of 'neolithic' face representation	Proportion of illiterates
Colonial American artisansa	307 (19.6%) (n = 1570)	77 (20.5%) ^b (n = 375)
Contemporary New Guineans ^c	316 (59.5%) (n=531)	67.8% (n ≅ 3 Million)
Contemporary Indonesians ^c	251 (57.2%) ^d (n = 439)	47.8% (rural) (n ≅ 100 Million)
Contemporary South- Americans ^e	61 (27.9%) (n = 219)	27.3% (n≅25 Million)

Test of heterogeneity: $\chi^2 = 409.4$, df = 3, p \leq 0.01. Test of linear trend of proportions²⁹: $\chi^2 = 388.0$, df = 1, p \leq 0.01.

Population data are from Statistical Yearbook, UNESCO, 1977¹⁴. a Note that - except for colonial American artisans - each one of the Ss made one drawing, while it is possible that some of the (mostly unknown) artisans made several stone engravings during their lifetimes, but only the faces on the stones could be counted, hence there may be some bias, but the direction is unknown. The following authors' photographs²¹⁻²⁵ were measured: Ludwig, n=341; Benes, n = 16; Forbes, n = 80; Jacobs, n = 16; and the Farber collection A-J, n = 1117, T = 1570.

^b The percentage is estimated from Lockridge⁶ (graph 4). The cited percentage is a weighted average of the contributing percentages in the 375 New England artisans sampled over 4 intervals within the period 1650-1791. Inferences must be drawn cautiously since there is a substantial increase in the number of people able to write their signatures during this interval.

^c See previously reported details⁷.

d The Indonesian sample is from remote islands, whose population had even less access to literacy instruction than the general rural population. See previously reported details7.

lia, which was not known to exist in these artisans at least to any significant degree. Characteristically, objects other than parts of the living human body, e.g. animals, crowns, candles, and skulls, were all accurately depicted without distortions of their spatial proportions²¹⁻²⁶. This further supports the previous results⁷ on New Guineans and Indonesians. Thus, there was not general spatial representational disability in this sample of artisans, which is in contrast with their specific distortions of the face only.

Enough data are available to examine the hypothesis that the frequency of neolithic representation goes along with that of illiteracy in diverse cultures. To this end data from contemporary New Guineans, Indonesians (see previously reported details⁷) and South Americans were added to the data from the colonial Americans and analyzed. The sample of Indonesians was taken from remote islands whose populations had less access to reading and writing instruction than the general rural population whose data are presented for literacy. The South American sample was from 4 countries: Peru, n = 144 (data on 38, of these are of special interest)²⁸; French Guiana, n = 33; Ecuador, n = 22; and Surinam, n = 20. Literacy data for the respective populations are found in various sources¹⁴⁻¹⁹.

A Pearson χ^2 test establishes that the sample proportions (see table) are heterogeneous. For 3 df, $\chi=409.4$, highly significant (p \ll 0.01). The question is asked whether the 4 sets of sample proportions (neolithic representations) have a linear relationship to the corresponding literacy rates. A Mantel-Haenszel test for trend in proportions²⁹ was done. $\chi=388.0$, df=1, also highly significant (p \ll 0.01). This is the critical statistic, and shows a strong linear relationship of proportions of neolithic representation to the population literacy proportions. About 95% of the Pearson χ^2 , that is 388.0/409.4, is accounted for by the linear trend relationship. Thus most of the variability in neolithic representation proportions is associated with a linear trend in relation to literacy rates.

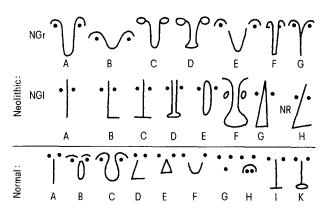
In spite of the strong relationship in general populations, where one state of functioning can be fairly strongly indicative of the other one, in individual cases the 2 states cannot be expected to occur together by necessity. There are no sub-tests available yet to determine where an individual case could be located in either of the two states of functioning, which appear to evolve parallel to each other, albeit not necessarily at the same speed.

The finding that there are no significant or consistently distorted representations other than those regarding the face rules out the alternate hypothesis that there was a general incapacity to depict objects accurately. Thus, it appears that there exists a specific association (a new syndrome?)¹² between the specific distortion of the representation of the face and under- or undeveloped writing and reading ability. It should be noted that such a specific link between signs was detected because of the existence of a natural kind of close correspondence occurring in certain 'experiments of history' or of nature which places constraints on the hypothesis.

The puzzling present and previous^{7,8,30} findings suggest a need to reconceptualize the role of spatial configurational representation in specific subgroups of non-literates. These newly identified and widely diverse cultural subgroups may share an under- or undeveloped, so-called 'paleo-visual-representational mode'⁷, which in the present sample appears to be mainly linked with a paucity of literacy instruction, hindering the actualization of the potential capacity for a refined 'neo-visual-representational mode'⁷. Under other circumstances (for instance in dyslexia, as previously reported^{7,12}) the use of the paleo-visual-representational mode⁷ might additionally be linked with some subtle, spe-

cific neurological dysfunctioning, or underdeveloped functioning. The suggested archaic mode of spatial visual representa-

tion⁷ proceeds in too global a manner, and thus fails to analyze and to synthesize the specific spatial interrelationship among parts of a strictly configurational arrangement characteristic of both lexical signs and face configuration. The present findings can now be viewed within the larger context of those from previous studies^{7,31} and from those still in progress^{8,33}. There emerges a newly-identified class, whose members share a close link between un- or underdeveloped literacy abilities and specifically inaccurate 'neolithic face' representation. Members of this class are found in developmentally early and in pathologically regressive situations: 1) Face representations of the pre-literate 'neo-lithic' period of art^{5,13} (distorting only the human but not the animal face); 2) infants during the phase of the automatic 'smiling response', who smiled preferentially at 'neo-lithic face' masks over control masks¹¹; 3) a third of young children, ages 3-6, who drew 'neolithic faces'⁸; 4) dyslexic youths (39%)^{7,12}. 5a-d) Substantial subgroups of four pre-literate populations tested so far, diverse as to time period and cultural background, who produced graphic representations of the 'neolithic face' distortion, as discussed (table). 6) 22% of chronic alcoholic men (compared with 12% of their controls) tested so far drew 'neolithic faces' and were of a low socio-economic level of functioning, for which a low level of literacy ability can also reasonably be assumed³³. 7) About half of the prosop-agnosic persons reported on in the literature suffer at least temporarily from reading disturbances, as previously discussed^{12,13}. In this state of non-recognition of the individual face, this is experienced as if it was 'flattened out', 'without any relief³⁴ (which also obliterates the bridge of the nose)¹². So far only one report with a face drawing by one of the rare prosop-agnosic persons appears in print (Cohn



Frontal view of forehead-nose-eyes sector of face patterns, measured with a ruler. 'Neolithic face' patterns 'NGr' and 'NGl': continuation of forehead into nose without any indication of a narrowing, indentation or discontiunity at the bridge (root) of the nose, i.e. at the area between the eyes. Thus, a ruler placed at the upper and lower borders of the eyes measures the presence or absence of a neolithic face configuration. Subtype NGr is present if at least at the lower border of the eyes (if not even above it) the nose is as wide there as it is at its tip (NGr: A-G), discounting a bulbous enlargement of the eartilagenous part around the tip of the nose (NGr: D). - Subtype NGl is present if the nose extends above the upper border of the eyes into the forehead (NGI: A-G). A halfprofile type NR is not rated, as it is intermediary between 'neolithic' and normal faces. - Normal face patterns (A-J) are characterized by the indication of a discontinuity between forehead and nose at the bridge of the nose area through a) narrowing or b) indentation, and/or c) a beginning of the nose design only at or below the lower border of the eyes.

et al.35), and this indeed depicts a specific 'neolithic face' drawing. This patient belongs to a larger class suffering from a right or bilateral occipital(-parietal) brain lesion, of which so far two additional cases with 'neolithic face' drawings have been reported in print (without mentioning this distortion) by Weinstein³⁶ and by Luria³⁷, as discussed

The correspondence between the states of literacy and of accurate face representation in culturally diverse populations may not necessarily be based on identical neurological causes. Rather, these two states of functioning can be conceptualized as being structurally analogous.

The data just cited are surprising and need a hypothesis that could explain them a fortiori and that thereby could then be considered to be true along the lines of 'retroductive reasoning' used in pattern detection by Peirce³⁸ and by Hanson³⁹. Such 'abductive inference' does not necessarily lead to the detection of a cause, but rather to the identification of an ordering principle which patterns the observed data³⁹. Herein the following principle is strongly suggested by the data enumerated above - which include observations on early phases of mankind and of the individual as well as states of pathological regression analogous to early functioning; the 'ontogeny' of cognitive functions recapitulates their prevailingly culturally determined 'phylogeny' within a cultural group. If further research data support the existence of this principle, it would open a novel branch of investigation: of cultural-evolutional neurology (including neuro-psychiatry and -psychology).

Additional evidence in support of this concept exists already in two more situations; in the previously identified 'wigmen phenomenon shown by 18-30% of contemporary Enga and Ipili tribesmen living in geographically remote areas of the Western Highlands of New Guinea. While highly functional within the range of the survival needs of their culture, there are certain feature generally considered to be 'developmentally early' kinds of dysfunctions. These are also known to appear in a cluster in the neuro-pathological situation of 'apractognosia'. (Obviously these adult tribesmen do not suffer from such a pathology, and it is again merely the patterning of the dysfunctions that appears in 'phylogenetically' and 'ontogenetically' early situations as well as in pathologically-regressive ones). There are signs of a) impaired orientation in personal space that characteristically pertain only to their culturally important head gear (the 'wig'). This completely replaces the face in a total of 30% of their drawings, and it is the carrier of the facial features in a total of 18% of their pictorial representations. b) Their culture's lack of clothing (which one would get into, rather than hanging it onto the body) is also analogous in pattern to dressing apraxia; and c) visual-constructive dysfunctioning as well as d) visual-spatial dys-gnostic signs have also been identified previously in the 'wigmen phenomenon'31. In the individual's developmentally early stages there also exists analogous behavior; concerning that listed under (a) in particular see Clark⁴⁰, as discussed by Pylshyn⁴¹.

Further, work in progress on finger representation⁴², also tested in geographically remote areas of New Guinea, shows finger mis-representation (as revealed in drawings) to be linked with dys-calculia. This specific cluster of signs is also known to exist in early development and in the pathologically regressive situation of a partial Gerstmann syndrome⁴³, the specific general existence of which has been discussed elsewhere¹².

Thus, within certain cultures, three main specific clusters of cognitive dys-functioning have so far been identified, the appearance of which is consistent with the novel conceptualization of a cultural-evolutional neurology.

- 1 I thank Katherine F. Ruttiger for being an independent rater, and Bernard H. Fox for statistical help.
- S. Carey, in: Explorations of the Biology of Language, pp. 175-242. Ed. E. Walker. Bradford Books, Montgomery, Vermont
- S. Carey and R. Diamond, Science 195, 312 (1977).
- R.K. Yin, J. exp. Psychol. 81, 1 (1969).
- C.A. Schmitz, in: Oceanic Art, p. 42. Harry N. Abrams, New York 1969
- K.A. Lockridge, in: Literacy in Colonial New England, a) p. 19, b) p. 25. W.W. Norton, New York 1974.
- A. A. Pontius, Experientia 36, 83 (1980).
- A. A. Pontius, in preparation.
- E. Kaila, Annls Univ. fenn. åbo. 17 B, 5 (1932).
- R.A. Spitz and K.W. Wolf, Genet. Psychol. Monogr. 34, 57 10 (1946).
- A.A. Pontius, Experientia 31, 126 (1975)
- A.A. Pontius, Experientia 32, 1432 (1976). A.A. Pontius, J. Am. med. Wom. Ass. 29, 435 (1974).
- Statistical Yearbook 1977. United Nations Educational, Scientific and Cultural Organization, Paris 1978, pp. 46-50.
- World Illiteracy at Mid-Century. A Statistical Study. Ed. by UNESCO. Greenwood Press Publ., Westport, Connecticut 1957.
- Statistical Abstracts of the United States. U.S. Dept. of Commerce, Bureau of the Census. Gvt. Printing Office, Washington, D.C. 1979.
- Europa Yearbook, vol.2. European Publications Ltd, London 1979.
- M. Meggitt, in: Literacy in Traditional Societies, pp.300-309. Ed. J. Goody. Cambridge University Press, New York 1968.
- C.S.J. Hunter and D. Harman, Adult Illiteracy in the United States, pp. 27-28. McGraw-Hill, New York 1979.
- F. Goodenough, Measurement of Intelligence by Drawings. World Book Co., Chicago 1926.
- P. Benes, The Masks of Orthodoxy. University of Massachusetts Press, Amherst 1977.
- H.M. Forbes, Gravestones of Early New England and the Men who Made Them 1653-1800. Houghton Mifflin, Boston 1927
- G.W. Jacobs, Stranger Stop and Cast an Eye. Stephen Greene Press, Brattleboro, Vermont 1972.
- A. Ludwig, Graven Images, New England Stonecarving and its Symbols, 1650-1815. Wesleyan University Press, Middletown, Connecticut 1966.
- D. and J. Farber, Collection of New England Gravestones.
- American Antiquarian Soc., Worcester, Massachusetts 1976.
 The slow process of stone engraving is not comparable with spontaneous writing. An inscription has to be planned before it is copied. Even if a copy of an inscription or of faces had been provided by a person other than the artisan, the other one was also a member of the colonial American group under study, though possibly of another occupational subgroup. Furthermore, it is reasonable to assume that the artisan depicting a certain face pattern met with the approval of a corresponding percentage of the population viewing his work. Such a strongly implied approval on the part of the general population then reflects the likelihood that these viewers themselves would have depicted, or at least favored, an analogous kind of face representation.
- Further substantiation of the main hypothesis can be found in my previously reported findings^{7,12}. Out of 200 'Western' dyslexic youths 39% drew these specific face distortions, while only 6% of normal readers did so.
- In the area of the source of the Amazon in Peru, 2 Indian tribes contributed 38 persons to the South American sample. Out of these, 8 teenage boys from the Hibero tribe who had no schooling all drew 'neolithic faces'. Among the Bora tribe 2 settlements were divided by their religious beliefs so that members of one did not attend school on religious grounds while the members of the other did have schooling. All 8 teenage Bora with schooling drew normal faces. Of the Bora without schooling (8 teenagers and 14 adults) only 4 teenagers and 5 adults drew normal faces. The exact status of the schooling of the 5 adults is unknown. In developing countries, information on the relatively sensitive subject of individual literacy is not likely to be given to strangers. - Since these Indian subgroups constituted a special portion of the sample with un-

known representativeness, data are presented excluding them as well as including them. For the latter case see the table. For the case where they are excluded, the 2nd column of the table should be changed so that the proportion of contemporary South-Americans with 'neolithic' face representation is 40 out of 181 (22.1%) instead of 61 out of 219 (27.9%). The test for heterogeneity in the case excluding the 2 Indian tribes above yielded $\chi^2\!=\!418.8,\,df\!=\!3,\,p\!\ll\!0.01,$ and the test for linear trend of proportions²9 yielded $\chi^2\!=\!385.2,\,df\!=\!1,\,p\!\ll\!0.01.$ The proportion of heterogeneity explained by the linear trend is 385.2/418.8, or 92%. Thus, similar conclusions emerge from both sets of samples; most of the variability in 'neolithic' representation proportions is associated with a linear trend in relation to literacy rates.

- 29 N. Mantel, J. Am. statist. Ass. 58, 690 (1963).
- The gravestones of New York City's Trinity Church cemetery (at the foot of Wall Street almost all from the 18th-century show 89 preserved human face images, 17 of which (19.1%) are 'neolithic' faces.
- 31 A.A. Pontius, J. Am. med. Wom. Ass. 32, 247 (1977).
- 32 A reasonable assumption to explain why not all persons tested draw 'neolithic faces' is that some of them are no longer naive as

- to how to draw a face. The naivete as to the face's graphic representation is lost once attention is drawn to the delicate spatial-relational configuration of the forehead-nose-eyes area.
- 33 A.A. Pontius, in preparation.
- 34 J. Bodamer, Arch. Psychiat. NervKrankh. 179, 6 (1947).
- 35 R. Cohn, M.A. Neumann and D.H. Wood, Annls Neurol. 1, 177 (1977).
- 36 E. Weinstein, Behav. Brain Sci. 3, 518 (1980).
- 37 A.R. Luria, in: Higher cortical functions in man, p. 137, fig. 37. Basic Books, New York 1966.
- 38 C.S. Peirce, in: Collected papers, vol.1, p.31. Harvard University Press, Cambridge, Massachusetts 1931.
- 39 R.N. Hanson, in: Patterns of Discovery. An inquiry into the conceptual foundations of science, p. 85. Cambridge University Press, New York 1958.
- 40 E.V. Clark, Cognition 2, 161 (1973).
- 41 Z.W. Pylyshyn, in: Readings in philosophy of psychology, vol.2, pp. 184-185. Ed. N. Block. Harvard University Press, Cambridge, Massachusetts 1981.
- 42 A.A. Pontius, in preparation.
- J. Gerstmann, Archs Neurol. Psychiat., Chicago 44, 398 (1940).

Spatial distribution of signal and adaptive sensitivity in the receptive field surrounds of cat retinal ganglion cells¹

H. I. Cohen and R. W. Winters²

Department of Psychology, University of Miami, Box 248185, Coral Gables (Florida 33124, USA), and William L. McNight Vision Research Center, Bascom Palmer Eye Institute, University of Miami School of Medicine, 1638, N. W. 10 Ave., Miami (Florida 33124, USA), 24 August 1981

Summary. A comparison was made between adaptive and signal sensitivity profiles of the surround response mechanism of cat retinal ganglion cells. The 2 profiles were found to be similar for X cells but the surrounds of Y cells appear to pool adaptation over a smaller retinal region than they pool signals.

Most receptive fields of cat retinal ganglion cells have a concentric organization with central and peripheral zones that are mutually antagonistic³. The response of the cell is thought to be controlled by two spatial overlapping response mechanisms; one that predominates in the middle of the receptive field, the center response mechanism, and one that predominates in the periphery of the receptive field, the surround response mechanism⁴⁻⁶. A response mechanism is an aggregate of photoreceptors and interneurons.

The magnitude of the signal that the ganglion cell receives from a response mechanism is dependent upon the mechanism's adaptation state. Rushton' posited that the effects from field adapting stimuli are physiologically pooled within the retina. The neural substrate, the adaptation pool, serves to reduce sensitivity in regions of the visual field that are not directly stimulated by adapting flux.

are not directly stimulated by adapting flux. There is evidence that both the center stand surround response mechanisms of cat retinal ganglion cells physiologically pool the desensitizing effects produced by steady illumination of their receptive fields. Moreover, for the center mechanism, the adaptive pooling area, i.e., the retinal region over which adaptation is pooled, is the same size as the region over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal pooling area standard over which signals are pooled – the signal standard over which signals are pooled – the signal standard over which signals are pooled – the signal standard over which signals are pooled – the signal standard

The present study was undertaken to assess the spatial relation between the adaptive and signal summing areas of the surround response mechanism of cat retinal ganglion cells. Also, it was our intention to compare the spatial distribution of adaptive and signal sensitivity within these regions. There are 2 major types of cat retinal ganglion cells: X cells and Y cells¹². It was suggested by Cleland et al.¹³ that X cells are concerned primarily with the processing of spatial

information and Y cells may constitute an early stage in the

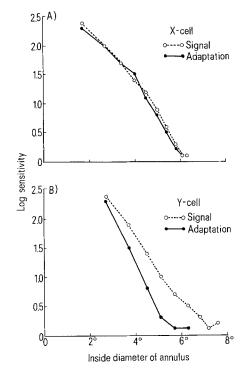


Figure 1. Signal and adaptive sensitivity profiles. Stimuli: $A \times cell$, luminance of 0.2° central adapting spot, 22 candles/m²; luminance of $3.0 \times 3.7^{\circ}$ modulated annulus for adaptation study, 7.3×10^{-2} candles/m²; background luminance, 9.7×10^{-3} candles/m²; $B \times cell$, 0.8° central adapting spot luminance, 1.6 candles/m²; luminance of $3.0^{\circ} \times 3.7^{\circ}$ modulated annulus for adaptation study, 1.7×10^{-3} candles/m²; background luminance, 3.6×10^{-4} candles/m²; all modulated stimuli had duration of 500 msec, at 0.3 Hz.