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The Electroencephalogram (EEG) as a Research Tool in Human Behavior Genetics: Psychological Examinations in Healthy Males With Various Inherited EEG Variants

III. Interpretation of the Results

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Summary. Interpretation of the results from psychological examinations of 298 probands with inherited EEG variants requires (1) critical evaluation of previous literature on psychological EEG correlates, (2) knowledge of the main concepts and experimental approaches for elucidating the basic mechanisms of EEG rhythms, (3) discussion of previous attempts to link psychological variation in human populations with corresponding variation in brain function, and (4) interpretation of results from considerations at these three levels with the data from our own study.

At the first level (previous psychological studies), comparison with Schmettau's study proved to be especially revealing: Her conclusions about personality correlates with high α-index and with "flat" EEGs were very similar to ours with the monotonous α-(R) and low-voltage (N) EEGs, respectively. Her EEG type with high β-index overlaps with our β-diffuse (BD) type; a tendency to psychasthenia and low resistance to stress is less obvious in our group, but is expressed indirectly by reduced speed and accuracy in tests requiring attentiveness and persistence. The correlation between α-frequency and intelligence found in other studies was confirmed by the especially high intelligence scores of our group with occipital fast α-variants (BO).

At the second and third levels of the discussion (EEG mechanisms; neurophysiological theories), the cooperation of cerebral cortex (EEG battery), thalamus (pacemaker), and ARAS (tonic arousal) is discussed, and the personality typologies of Eysenck and Claridge are mentioned. From this and other evidence, the following hypotheses are discussed:

1) The personality profiles of the R group are influenced by high activity and efficiency of the thalamic α-pacemaker(s), which leads to a high degree of modulation, selection, and amplification of afferent stimuli.

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2) In the countertype of this EEG variant, the N EEG, a low modulation and amplification by the thalamic α-pacemaker is assumed. This leads to relatively low intensity of feeling and to low spontaneous activity, but to faster information processing. Combined with an increased level of tonic arousal in the ARAS, it may cause certain 'neurotic' complaints (our low-voltage borderline (NG) group).

3) The EEG with diffuse β-waves (BD) is caused by a high level of tonic arousal in the ARAS, which tends to disturb the thalamocortical circuit. This leads to reduced stress resistance and to impairment of intellectual functions, especially space perception.

Due to limited evidence, the next two hypotheses are advanced only tentatively:

4) α-rhythm with very high frequency (16—19 c/s) leads to improvement of information processing and, hence, to high intellectual performance and motor dexterity.

5) Probands with frontoprecentral β-groups (BG) show no psychological signs of increased tonic arousal; therefore, these β-groups are caused not by increased tonic arousal of the ARAS, but by a genetic variant of a thalamic subsystem.

1. EEG and Behavior: Aspects of the Problem

In this contribution, the third of this series, the results of our studies, described in Vogel et al. (1979b), will be interpreted in the light of the available literature on EEG associations with psychological parameters and of the evidence on the neurophysiological mechanisms producing the EEG.

Many studies on associations between EEG and psychologically defined parameters have been performed. However, not all of them are relevant for the problem examined here: the association of genetically determined EEG variation with performance, feeling tone, attitudes, and behavior. Therefore it may be useful to explain which kind of EEG variation in connection with behavior is of little or no significance for our problem.

1.1. Transitory EEG Changes in Certain Psychological States

An individual resting EEG can be obtained only if the proband relaxes and closes his eyes but neither drouses nor sleeps. Ever since Berger (1929; cf. Berger, 1938) published his classic descriptions, it has been known that visual or accoustic stimulation (most notably opening of the eyes) leads to EEG changes: The α-waves disappear and are replaced by waves with faster frequency and lower amplitude, which Berger called β-waves (for ref., see Jung, 1953; Christian, 1975). We do not intend to review the abundant evidence on EEG changes in various types of mental activity; in the context of our study, it is important to remember that emotional experiences may also lead to EEG alterations (cf. Becker, 1972). Various kinds of stimuli may change the EEG in different ways.

1.2. Transitory EEG Changes due to Physiological Alterations and Diseases

Apart from psychological influences, the resting EEG may be altered by changes in the physiological and metabolic steady state of the individual. For example hyploglycemia, O_2 deprivation, severe disturbance of liver function, or various endocrine diseases may lead to transitory or even long-lasting EEG changes. Many of these conditions are also associated with psychic alterations. This is even more typical for brain diseases, such as the various forms of epilepsy, in which—apart from EEG anomalies (Christian, 1975; Janz, 1969)—mental and emotional alterations are found. Most specialists consider these alterations as consequences of the epileptic seizures; they are in principle independent of whether the epilepsy is genetic or nongenetic in origin. EEG anomalies similar to those seen in epileptics when they are free of seizures have often been described in individuals diagnosed as psychopaths or law offenders, even if these persons had never had epileptic fits. Family data suggest a genetic component for some of these EEG anomalies (Høncke et al., 1949); but so far, detailed knowledge of modes of inheritance and physiological mechanisms seems to be lacking.

An unusually large proportion of patients with chromosomal aberrations, especially those involving the sex chromosomes—most notably XXY, XXX, and XYY patients—show mild to severe EEG anomalies (Züblin, 1969). Also, their mean performance in intelligence tests and their success in school and occupational careers are impaired; they suffer from a variety of emotional disturbances; and their social adaptation may be poor (Züblin, 1969; Murken, 1973; Witkin et al., 1976). Here, although the genetic basis of the anomalies is obvious, the neurophysiological basis is not, as chromosome aberrations lead to multiple disturbances of embryonic development in general and especially brain development. Besides, much too little work has been done on brain morphology of patients with chromosomal aberrations.

In conclusion, the situations mentioned tell little about the information that the genetically determined variation of the normal EEG may provide for a better understanding of the genetic variation influencing human behavior.

1.3. Advantages and Shortcomings of Some Earlier Studies on Associations of EEG Parameters With Psychological Results

In many, if not most, studies on associations between EEG parameters and variations in psychological condition and behavior, no attempt has been made to exclude the above-mentioned factors: Are we concerned with the individual resting EEG or with a transient alteration induced by sensory stimulation, by a special emotional state, or by the effects of a transient physiological anomaly? Is there a brain disease that influences both brain physiology and behavior? In many of the studies, the authors did not intend to make this distinction. In fact, they did not even realize that associations between EEG parameters—especially those of the "normal" EEG—and psychological results may be important for behavior genetics.

Even so, some reports contain valuable information for our problem. The conditions for including them in the discussion are (1) that the EEG parameters are clearly defined, if possible using quantitative criteria; (2) that the proband samples are not only large enough but—much more important—uncontaminated by overt psychological drug effects (In- and out-patient populations will, in most cases, be useless); and (3) that quantifiable methods for psychological examinations, preferably acknowledged test methods, have been used.

Quite a few studies, in spite of the different intentions of their authors, provide very valuable information for our problem.

2. EEG and Behavior: Our Results Compared With Those of Other Reports

Our research project differs in design from all other reported projects on EEG and psychology in two aspects:

1) Our probands were not a random sample of the normal population but were selected for having special EEG variants. In certain aspects, these variants represent extremes within the variability of the normal EEG. There are almost no indications that other investigators have realized the analytical possibilities offered by comparison of such extreme groups. Only Schmettau (1969), in the

discussion of her own study, regarded investigation of strongly contrasting extreme groups and probands with rarer EEG types as possibly rewarding.

2) Our investigations were confined to genetically well defined features of EEG variability (cf. Vogel, 1970). Schmettau (1969) correctly remarked that all studies carried out until then, including her own, had left open the question of whether the aspect of brain function that can be observed in EEGs is the precondition for the psychic variation, whether the differences in psychic attitudes determine the EEG, or whether both depend on an unknown third factor. Because we examined genetically determined EEG variation, we can answer this question: Any difference between EEG variants in psychological parameters that might be detected can now be traced back with confidence to genetic variability in brain function, which expresses itself directly in EEG variability and in a much more indirect way psychologically.

In the following, our results will be compared with relevant data from the literature.

2.1. Intelligence

2.1.1. Overall Intelligence Test Results

Many authors seem to agree that apparently little or no correlation exists between normal EEG variation and overall intelligence as measured by the IQ (Shagass, 1946; Hill, 1955; Ellingson et al., 1957; Schmettau, 1969; Ellingson and Lathrop, 1973). Even mentally retarded individuals may have a normal EEG (Vogel and Broverman, 1964; Ellingson and Lathrop, 1973). Birbaumer (1975) regards it as naive to expect such associations because the origin of intelligence as measured by IQ is much too complex. On the other hand, according to many authors the IQ shows a relatively high heritability (cf. Vogel et al., 1979a). Moreover, factor analysis has pointed to a common factor in most—if not all—measures of intelligence, Spearman's G. Therefore, it may, after all, be worthwhile to look for EEG features showing a correlation with overall intelligence. The evidence from the literature is equivocal; a number of authors described some positive correlation between IQ and α-frequency (cf. Mundy-Castle, 1958; Mundy-Castle and Nelson, 1960), whereas others failed to find any association. Ellingson and Lathrop (1973), examining a small group of psychiatric patients, found correlations ranging between 0.08 and 0.52 for 11 subtests of the WAIS (Wechsler) as well as for the full scale ($r=0.27$), verbal scale ($r=0.30$), and performance scale ($r=0.24$). However, only one of these correlations was significantly different from zero[1]. The authors concluded that there is no or, at best, a trivially weak correlation between α-frequency and IQ.

If α-frequency influences the overall IQ, then one would expect the highest IQ in our BO (occipital fast α-variant) group: In this genetically determined and dominantly inherited (Vogel, 1966) variant, the α-waves, which normally have a frequency of ~8—13 c/s, show a frequency of ~17—19 c/s. Comparing this prediction—which has also some foundation in neurophysiological hypotheses on the function of the α-rhythm (paragraph 3)—with our results (Vogel et al.,

1 For a group of Down syndrome patients, no correlation with Binet results was described

1979b, Tables 1 and 3), we find that the BO group achieved, indeed, the highest overall intelligence score in the IST test as well as in the Raven. Our sample, which is relatively small ($n = 15$) due to the rarity of this variant (~ 0.6% of males), scored especially well in all tests of abstract thinking. Whether the outstanding performance of this group in motor skills (two-hand coordination; pursuit rotor) has anything to do with this result is a different question.

The picture is quite different for the BD (diffuse β-group). In most intelligence scores, this group scored the lowest, especially in spatial ability. As explained before, this was partly because raw results were evaluated in the LPS test; the average age of this group was the highest. However, their IST scores showed the same tendency in spite of this test being standardized for age.

2.1.2. Spatial Ability

Ability for spatial orientation was shown to have high heritabilities in twin and family studies (De Vries et al., 1976); also it indisputably shows a pronounced sex difference, women achieving lower average scores than men (cf. de Vries et al., 1977; Jarvik, 1975). In another study, our group (Friedl and Vogel, 1979b) showed that spatial ability is correlated positively with occipital α-activity and negatively with β-activity. These correlations were found mainly in women; also there is a normal sex difference in the EEG in the same direction, women showing on the average less α-waves and more β-waves. In women with the Turner syndrome, ability for spatial orientation is especially poor. In a series of 39 Turner patients living outside an institution, 17 (46%) showed "an increased amount (more than 50%) of 14—18 c/s β-waves" (Tsuboi and Nielsen, 1976). Results in patients with chromosome aberrations have to be regarded with caution, as various EEG abnormalities and borderline results may be found. Still, the deviation is in the expected direction.

All these results strongly suggest a real relationship between the pattern of the (especially occipital) EEG and spatial ability and, more specifically, a genetically determined interindividual variability in brain function that influences both the EEG and the ability for spatial orientation. Discussion of the possible nature of this variability will be postponed.

2.1.3. High Test Performance and Low-Voltage EEG

Especially interesting from the point of view of α-wave function is the excellent performance of the low-voltage group in intelligence tests in general and specifically in spatial orientation. This result must be considered when hypotheses on the function of α-waves are discussed. Diminishing of the occipital α-pattern by intermixture of β-waves is something quite different physiologically from the absence of α-waves without other activities.

2.2. Personality

2.2.1. Personality Scores and Genetics

Unlike the intelligence tests, for most of the „personality" measures, little evidence for genetic determination on the basis of twin and family studies is available. As noted by Vogel et al. (1979a), twin studies with personality questionnaires—also including our own—have given, for the most part, inconclusive results. Heritabilities tended to be rather low, especially in series of adult twins. Partly, this may be due to the special conditions under which twins—and especially MZ twins—develop their attitudes. However, the main reason seems to be that the observed interindividual variability within the 'normal' range in many if not most of those aspects of feeling tone, attitudes, and other psychic activities that can be measured by personality questionnaires indeed depends much more on environmental differences than on genetic variability. This does not mean, however, that genetic variability is without influence. For example, it is well known that extreme variants of behavior, such as mental or affective disease, psychopathy, criminal behavior, and even neuroses, depend in part on the individual's genetic makeup (cf. Anastasi, 1958; Fuller and Thompson, 1960; v. Bracken, 1969; Schepank, 1974; Ehrman and Parsons, 1976; and many others). Furthermore, functional differences of the endocrine glands and of the brain at various levels may influence personality (Vogel and Motulsky, 1979).

One disadvantage of the methods of quantitative genetics, including the twin method, is that if the studies are carried out with a random sample of twins, only very common genetic types will influence the genetic variance appreciably. The lower the prevalence of the deviant type in the population, the smaller its influence, for example, on heritability estimates. The EEG variants examined here have prevalences of about a few per cent (or even less) (Vogel and Fujiya, 1969; Vogel, 1970). Hence, even an appreciable mean deviation in personality characteristics between carriers of such a variant and the population majority would lead to a very small contribution to heritability, because even a twin or family sample of fair size would contain at most very few probands with this variant. And vice versa, even if heritability for measurable personality characters were low, an appreciable association between certain personality scores and a fairly rare genetic variant would still be possible. However, in the long run, a reverse research strategy would be more rewarding: First, find a genetic variant and define its influence on brain physiology. Then, develop a hypothesis about its possible influence on behavior. Finally, try to test your prediction by comparing personality variables of your probands with those of controls, using either established methods or even new methods, developed specifically to demonstrate the suspected difference.

At the present state of the problem, sufficiently detailed hypotheses for actually following the strategy could not be formulated. In fact, one purpose of this study was to formulate such hypotheses.

2.2.2. Personality Differences Between EEG Variants; Our Results

Our results on personality scores can be found in Tables 6—8 of Vogel et al. (1979b). There are a number of statistically significant differences between single EEG variants and controls, as well as between certain variants. In spite of their overall number being higher than expected by pure chance, i.e., than if the EEG had no influence at all, the conclusion is still possible that the study failed to give convincing evidence of an influence of the inherited EEG type on personality. However, with this conclusion we risk overlooking real differences in certain aspects of personality. This risk can be minimized by showing (1) that some of the differences found coincide with the correlations between EEG variables and personality characteristics from the literature and (2) that interpretation in terms of known neurophysiological EEG mechanisms is possible. Both approaches will be tried: the first one, in the following paragraph; the second one, in paragraph 4.

The present study is the first on genetically well defined EEG variants. Therefore, direct comparison with data reported by others is impossible. To the best of our knowledge, only the study of Schmettau (1969, 1970) is sufficiently similar to ours to permit a more detailed comparison. Her method was described in the first contribution of this series; she examined a sample of 118 male students, ages 18—32, unselected for EEG types.

Using correlation methods and factor analysis, she tentatively delineated three EEG syndromes, for which she gave personality descriptions based on her test results, especially from personality questionnaires. From the MMPI, she evaluated the standard scores used in our study and some additional scores. However, she did not include intelligence test results in her description; her selection of intelligence test scores was much smaller than ours; she failed to find convincing correlations with EEG parameters; and she mentioned that, according to the majority of authors, there is little if any relationship between EEG and intelligence test performance. In Tables 1a—c, Schmettau's (abbreviated) personality descriptions are compared with our results.

2.2.2.1. The R Group (Monotonous α-Waves). Schmettau's first EEG syndrome comprises individuals with high α-index, which correlates negatively with variability of frequency. This syndrome—especially in its more extreme expression—obviously overlaps very strongly with that of our R (monotonous α-) group. Indeed, our psychological descriptions are strikingly similar. The average proband in this group is sthenic, stable, and well controlled. In our study, the sthenic component is most clearly expressed by a high mania (Ma) score in the MMPI; it was significantly higher in the R than in the N (low-voltage) group. In the MMPI handbook (Dahlstrom et al., 1972, p. 222f.), normal individuals with high Ma scores are described as "frank, courageous and idealistic. The high energy level of this group is also shown in the common use of the terms talkative, enthusiastic and versatile." Here, the high energy level and the sthenic component fit best with Schmettau's and our impression. The high energy level is controlled, however, by a high level of stability and self-control, expressed in our study by a low I score in the 16 PF, which indicates toughmindedness, and by above-average precision (= low errors per cent) in three performance tests (d-2 and KLT; practical arithmetics in the IST). Apparently, these results were easily attained by these probands because of their excellent short-time memory.

It apparently helped them to avoid flight accidents in service, but not car accidents in civil life; driving a car may be regarded as easier, and here, a sthenic and a little ebullient ('hypomanic') temperament may lead to occasional carelessness.

Most of our probands were unusually successful soldiers. As evidenced by the intelligence and performance test results, the R group seem to owe their success in the military field to their energy and precision more than to formal intelligence and swiftness.

Table 1. Comparison of personality descriptions for three EEG types according to Schmettau (1969) with results from the present study

EEG description	Personality description (Schmettau)	Our results
a Monotonous α-waves		
Schmettau (1st syndrome)		
Individuals with high α-index (correlates negatively with variability of frequency)	Sthenic, stable, well controlled	Sthenic: high activity (high MMPI, Ma (mania) score)
	Sthenic: activity, efficiency, initiative, independency, vitality	
	Stable: dependable, realistic, but experimenting rather than conservative	Stable and well controlled: above-average precision in concentration tests (d-2 and KLT); good results in short-time memory and calculation (IST)
	Well controlled: endurance, superego strength, discipline, psychic maturity	Resistant to stress: low scores in the I scale. Pointing to toughmindedness in the 16 PF
Present study:		
Monotonous α-waves	(No special data on intelligence test performance)	Average performance in most intelligence test scores
	(A tendency to 'neuroticism')	(Low incidence of flight accidents; higher incidence of 'civilian' accidents)
	(Skepticism toward other people)	(Low paranoia score in the MMPI)

b Low voltage EEG		
Schmettau: 'flat' EEG (low α-index, variable basic rhythm)	"Represents the negative of individuals with high α-index" (our R group).	High intelligence scores but relatively poor results in concentration tests (d-2 and KLT).
(Also probably cases which we regarded as 'low-voltage borderline (NG)') Present study: Low voltage (N)	"Relaxed and carefree; they have a playful attitude toward life." Remarkable is stability of the sympathetic system. They rarely get exited about anything, are self-confident and optimistic. They rarely take anything in bad part. In a group, they are popular but rarely elected as leaders. Extravert and group oriented. Their interests are more person oriented and less fact oriented; therefore, they often impress as feminine; they are basically passive and conservative; their lively social participation makes them appear more active and energetic than they really are.	Low MMPI scores; especially low in D (depression), Mf (male-female), Pa (paranoia), Pt (psychasthenia), Sc (schizothymia), Ma (mania), and Si (intraversion) scores, indicating a conspicious degree of 'normality' in these aspects. Description of probands as 'relaxed' and 'carefree' fit these results. Extraversion and group orientation certified by low Si score. High factor-G score (superego strength) in the 16 PF points to a conservative, authority-dependent attitude. A relatively high incidence of flight accidents (compared with few other accidents) contrasts with the high intelligence scores. A more 'feminine' direction of interest not testified by our sample: Mf score is low. However, it is high in the NG group.
c EEG with diffuse β-waves		
Schmettau: 2nd syndrome: High β-index, positively correlated with fast α-frequency Present study: Diffuse β-waves (BD)	Hypersensitivity and psychasthenia; neurotic tendencies and anxiety; caution and reserve are the predominant attitudes. Narrow mental horizon; probands remain within the conventional and so avoid taking risks. They depend on the group and expect help from others. Thus, a certain philistine touch. On the other hand, they suffer from continuous internal tension, show little resistance to stress, and tend to neurasthenic and hypochondric symptoms and to depression. Behavior poorly controlled; the Mf scale gives high feminity score.	Personality scores (MMPI and 16 PF are rather inconspicious. Clear signs of hypersensitivity and psychasthenia lacking. Remarkably low performance in spatial ability and arithmetic scores of intelligence tests, the high error percentages in the two concentration tests (d-2 and KLT) combined with low working speed and relatively long reaction time. A relatively high tendency to 'neurotic' complaints testified by high values in 8 of 10 'clinical' MMPI scores found in the NG (low-voltage borderline) group which may be part of Schmettau's 2nd syndrome

Since Schmettau based her conclusions on a relatively small and unselected sample of probands and on mostly nonsignificant correlations, it is amazing, indeed, how well her description fits our results. We were able to enlarge her description of performance (precision; good short-time memory). There can be little doubt that it has been possible to identify a fairly clear-cut personality dimension related to an inherited variant of the EEG. How this personality dimension can be explained neurophysiologically remains to be shown.

2.2.2.2. The N (Low-Voltage) Group. For this group, the essentials of Schmettau's description are contained in Table 1 b. The relaxed and carefree attitude and the low tendency to neurovegetative complaints find their counterpart in the low 'clinical' MMPI scores of our study, i.e., their high degree of 'normality.' That they are group oriented and sociable was also obvious in both studies. Their relatively low Ma score in our study, significantly lower than that of the R probands, corresponds with the 'basically passive' attitude described by Schmettau. Unlike Schmettau's probands, ours had no 'feminine' color. On the contrary, their Mf (masculinity-femininity MMPI) scores were low. However, this discrepancy may be explained by the origins of the two series: Schmettau's probands were students. Group conformity in a student's group favors widespread cultural interests, which give a high Mf score in the MMPI. Our probands were soldiers; here, typical 'male' interests such as sports and technics are favored. Hence, the different Mf scores may express group conformity in both series. Moreover, Schmettau's series very probably also contained EEGs classified as NG (low-voltage borderline) in our probands. However, they are quite different from the N group; among other features they had high Mf scores.

Considering these differences and the small size of Schmettau's and our own series, it is amazing how well our results coincide with her descriptions. Our data, however, permit some additional conclusions. For example, our probands performed very well in intelligence test scores, especially those testing spatial orientation. This has implications for hypotheses on the biological function of α-rhythm (cf. below). Surprisingly enough, many of our probands had achieved the rank of officer. This may be due to their carefree attitude, social conformity and intelligence, rather than their energy and leadership qualities.

2.2.2.3. EEG With Diffuse β-Waves. Schmettau's personality descriptions are compared with ours in Table 1 c. At first glance, there seems to be little correspondence between her results and ours: She found hypersensitivity and psychasthenia, anxiety, and little resistance to stress in her probands. In our series, on the other hand, personality scores proved inconspicuous. Our most prominent results were the low scores in intelligence tests, especially in spatial and arithmetic tasks, and the high error rates in the concentration tests in spite of low working speed. The latter result could, indeed, point to low stress resistance. The discrepancy in personality scores might be explained by the different origins of the materials: Whereas Schmettau's students were relatively free to admit their emotional tensions in the questionnaires, such tensions—and psychasthenic symptoms—contradict the professional self-image of the soldier. Moreover, overtly psychasthenic individuals with low stress resistance very probably would have been forced to leave the army before they were included in our study. Hence, our series was probably strongly selected against these characteristics.

Interesting enough, the BD EEG type is especially common in women, and its prevalence increases with increasing age in both sexes, but in women more than in men (Vogel and Götze, 1962; Friedl and Vogel, 1979a). Moreover, a negative correlation between α-activity and neurovegetative complaints and a positive correlation with aspects of β-activity has repeatedly been described, especially in women (Friedl and Vogel, 1979b, cf. this paper for further references).

In our series of soldiers, a relatively high tendency to neurotic complaints was found in the NG group, which often could not be distinguished unambiguously from the BD group. However, our NG group was relatively small; therefore, the differences were not statistically significant.

2.2.3. Other Data on EEG Personality Correlations Discussed in the Light of Our and Schmettau's Results

This discussion of most of the remaining literature—apart from Schmettau's study—is made difficult or even impossible by a number of shortcomings: In EEG evaluation and psychological examination, a great variety of methods were used. Their reliability was often disputable. Often, the established rules of statistical sampling were disregarded. Therefore, some of the conclusions lack sufficient foundation. Understandably enough, this is especially true of studies carried out in the early, and often overenthusiastic, years of EEG research. Therefore, the following discussion will be brief.

2.2.3.1. High and Low α-Index. This measure overlaps with Schmettau's first syndrome and with our R group. Some authors described individuals with high α-index as passive, dependent, receptive, rather than active, not very energetic, nonproductive, tending to avoid risks and responsibilities. The probands were said to tend to daydream and to be inhibited and withdrawn.

On the other hand, individuals with low α-index were described as independent, striving for dominance and leadership, productive, extravert, and ready to take risks. This hypothesis was discussed by a number of authors in the early stages of EEG research (Saul et al., 1959; Rubin and Bowman, 1942; Rubin and Moses, 1944; Knott et al., 1939, 1941; Ostow, 1950; Palmer and Rock, 1951; McAdam et al., 1952, 1954). It was not confirmed by Sisson and Ellingson (1955), Gastaut (1957), Werre (1957), and Schmettau (1969). The studies in which this association was claimed were extensively reviewed and criticized by Schmettau (1969). Suffice it to say that most of the psychological data were based on short interviews and on the personal impression of the investigators.

Our results, like Schmettau's (1969), strongly contradict this hypothesis. Our study showed that individuals with the R type are especially active and sthenic. Therefore, the hypothesis that such individuals are passive and dependent can definitely be refuted. The same holds for the complementary hypothesis, namely that individuals with low α-index are especially active. At least for their extreme type, with low-voltage EEG, this is certainly not true.

In view of these discrepancies, one might ask how some authors could arrive at wrong conclusions during the first decade of EEG studies. One explanation may be that these investigators did not succeed in providing their probands with the relaxing conditions necessary to obtain true, individual resting EEGs.

2.2.3.2. Low-Voltage EEG. Gallais et al. (1957) concluded from their series of 113 young soldiers that a 'flat' EEG has no relationship to any special psychological pecularities. Rémy (1949), on the other hand, concluded that a flat EEG is most often found in passive personalities with little interest in their environment. Brazier et al. (1945) and Hill (1950) regarded a flat EEG as typical for increased anxiety. Our and Schmettau's results partially confirmed Rémy's conclusions: Individuals with low-voltage EEGs tend to be somewhat passive and not very energetic. However, this does not mean that they are uninterested in their environment; on the contrary, they seem to be rather friendly and group dependent.

On the other hand, we did not find a high tendency to anxiety in our probands with typical low-voltage EEGs. Rather such an inclination could be concluded from the test results of our NG group and, incidentally, of a group of individuals with poorly developed and easily disturbed α-rhythm who appear to have an increased tendency to alcoholism (Propping, 1977, 1978). From the frequency of 'flat' EEGs in these studies, which was usually much higher than in our series, in which strict categories were applied, it can be concluded that all reported series (including Schmettau's) were mixtures of these—physiologically apparently different—EEG variants. Hence, the results were expected to differ, depending on which of these variants happened to be primarily represented in these series.

2.2.3.3. Increased β-Activity. According to some authors, increased β-activity is correlated with activity, extraversion, cyclothymia (McAdam and Orme, 1954; Schmettau, 1969), and social insecurity. High extraversion scores in probands with high β-activity were also found by Schmettau (1969). Comparison is again impaired because none of these authors tried to differentiate between various types of β-EEGs. In our series, three different β-types were distinguished: the BG category, in which β-waves in spindlelike groups are found in frontal and precentral leads (24 individuals); the BD variant, with diffuse β-waves in all leads (65 individuals); and the BO category, with occipital fast α-variants, which was included in all previous series among the EEGs with a high amount of β-waves.

Our BG group showed especially low MMPI scores and the lowest Si scores of all groups, i.e., high extraversion was confirmed for this group. Moreover, the second, most numerous, β-category, BD had the second-lowest Si score. The difference between the three β-categories combined (BG + BD + BO) and the controls is significant. Moreover, the same three categories showed high extraversion in the 16-PF Q_I second-order factor. This result also confirmed (and extends) the reports from previous authors that extraversion increases with β-activity. Schmettau described the type of extraversion found in her probands as 'specific wakefulness which means more defense than participation.' A counterpart of this defensive attitude may be found in the significantly increased L (lying) score of the MMPI for the three β-categories combined. However, we cannot go as far as Schmettau in our conclusions; psychological differences between her and our probands, especially in the (most numerous) BD category, can be explained by selection: Her probands were students; ours were soldiers. This might also be one reason why we did not find any clear-cut indication of 'social insecurity.' In this connection, it might be interesting to note that the BG category shows the lowest MMPI scores, and this means the highest degree of psychic 'stability' of all EEG groups.

2.3 Sensory and Motor Performance

There are only a few studies the results of which can readily be compared with ours.

2.3.1. Sensory Abilities

Rémond and Lesèvre (1957), reporting on 46 drafted soldiers and 38 truck drivers, found three EEG types: The first one, a complex EEG rhythm with few α-waves and many β-waves, seems to overlap with our BD type. Their group performed poorly in psychotechnical tests (reaction time to auditory stimuli; motor speed); our BD group showed average to good performance in sensory tests and average to poor performance in motor tests. Their poor standing in intelligence test scales for spatial orientation, which, according to many psychologists, predicts technical skills, has already been mentioned. On the other hand, our low-voltage group showed significantly lower simple reaction times to red than the R group—a result without precedence in the literature. The high motor skills of the BO group, which was mentioned with the results of intelligence tests, seems also to have been reported for the first time. In a certain way, this result seems to coincide with Mundy-Castle's finding (1955, 1957) that mean α-frequency is correlated with unstructured, indiscriminate motor speed: The BO group also shows the highest tapping speed.

Schmettau (1969) used a sensorimotor test spectrum similar to ours, but she mentioned very few results. She reported a significantly negative correlation ($r = -0.22$) between α-index and missed reactions in the mixed reaction experiment and a number of correlations of reaction-time parameters with degree of 'flatness' of the EEG. Our N probands, on the other hand, have short (= good) reaction times for colors. For the β-categories (β-index and β-amplitude) Schmettau did not describe consistant correlations with EEG parameters; nor do our results point to consistent difference. Remarkable in our data is the poor performance of the NG group in almost all motor test parameters. Some of the data on sensorimotor tests will be mentioned again under neurophysiological mechanisms.

3. Possible Neurophysiological Mechanisms of Inherited EEG Variants and Their Significance for Interindividual Psychological Differences

Here we shall discuss experimental data on the neurophysiological basis of the EEG insofar as it may be significant for inherited EEG variation. Then, the very few attempts to explain interindividual psychological differences in terms of neurophysiological mechanisms will be reviewed in the light of experimental evidence. Finally, we shall advance some testable hypotheses for the nature of the genetic variability underlying the EEG variants and their psychological correlates.

3.1. The Neurophysiological Basis of 'Normal' EEG Phenomena

The neurophysiological mechanisms of the normal EEG, especially the α-waves, were elucidated mainly by experiments on cats and other animals. However, these experiments were supplemented by studies on humans (For reviews cf. Andersen and Andersson, 1968, 1974; Creutzfeldt, 1971; Creutzfeldt and Houchin, 1974). Three levels have to be considered: The EEG waves are produced by a 'battery' (Andersen and Andersson, 1968) in the cerebral cortex; their pacemakers are found in the thalamus; and the EEG is modified by input from lower-level brain structures, especially the ascending reticular activating system (ARAS) and the limbic system.

3.1.1. The Battery of EEG Waves in the Cerebral Cortex

In his first papers on the human EEG, Berger (1929, 1931) stated that EEG waves must be produced in the cerebral cortex. Bremer (1938) described the α-waves as signs of synchronous electric activity of several neurons in the deeper layers of the cortex. The β-waves seen when α-activity is blocked—especially during opening of the eyes—he regarded as being caused by asynchronous activity of cortical elements. Eccles (1951; cf. Creutzfeldt, 1971) proposed the hypothesis that EEG waves are summated postsynaptic potentials of cortical pyramidal neurons. Experimental evidence for this hypothesis was first presented by Creutzfeldt et al. 1974). They and others showed by intracellular recordings of postsynaptic potentials (PSP) that the barbiturate spindles of the cat—which neurophysiologists regard as very probably homologous with the human α-rhythm—are caused by summation of the excitatory postsynaptic potentials (EPSP) of many neurons. In principle, the same seems to apply for slower waves in the ϑ- and the δ-range. For the exact mechanism of how the EPSPs are transformed into EEG waves, only hypothetical models are available, for example the dipol model of Jung (1963). This problem is of little immediate interest for the present study. According to Creutzfeldt (1971), more or less α-rhythm, higher or lower amplitudes of single

α-waves, correspond—with certain qualifications—to the rhythmic activation of larger or smaller populations of neurons in the cortex and the corresponding thalamic structures.

3.1.2. The Pacemakers of EEG Waves in the Thalamus

According to Derbyshire et al. (1936), barbiturates in small doses produce in cats a rhythmic activity similar to the spontaneous activity with drowsiness and to the α-activity of man. As mentioned above, these 'barbiturate spindles' are in wide use in experimental neurophysiology as an animal model for human α-rhythm. In 1935 Bremer showed that identical activity is found in cats without barbiturate treatment after dissection of the brain at the level of the superior colliculi, i.e., behind the thalamus (cerveau isolé preparation). On the other hand, various investigators (Morison and Basset, 1945; Jasper, 1949; Kristiansen and Courtois, 1949) reported that removal of the entire thalamus leads to almost complete loss of spontaneous rhythmic activity. Widespread cortical activity could be provoked by continuous electric stimulation of medial thalamus areas, especially the so-called intralaminar nuclei. These and other results (cf. Andersen and Andersson, 1968, 1974) contributed to the foundation of a hypothesis by Morison and Dempsey (1942, 1943), that structures in the medial thalamus serve as pacemakers for the spontaneous rhythmic cortical activity. This concept was elaborated by numerous experiments, which were reviewed by Andersen and Andersson (1968, 1974). At present, it looks as if the thalamus contains numerous facultative pacemaker regions that can influence activity in corresponding cortical areas. "Rhythm generation is assumed to occur in many independent thalamic locations and each nuclear group is supposed to be able to produce rhythmical activity of various intraspindle frequencies. Via the specific thalamo-cortical fibres the burst discharges of the thalamic rhythmical entity are imposed on a cortical area . . . (Andersen and Andersson, 1974). These authors estimated the number of rhythm generators in the cat thalamus to be 30,000–40,000; however, "the high degree of synchrony of rhythmical activity usually found in thalamic and cortical areas indicates that the activity of individual generators of rhythm is coordinated into larger units. This may be done by 'distributor neurons'. . . ." A number of hypotheses about the exact mechanisms for the production of rhythmic activity in these thalamic pacemakers were discussed: "There seems to be agreement, however, that long-lasting inhibition is important as a phasing device . . . ."

3.1.3. Synchronization and Desynchronization. The Influence of Structures at Lower Levels, Especially the ARAS

One of the first observations of Berger (1929) was that the EEG may be changed by sensory input, for example opening of the eyes: The well-synchronized α-waves are replaced by more poorly synchronized β-waves. Then a few years after Berger's first description, it was discovered that the EEG is thoroughly changed —and primarily synchronized—during sleep (Loomis et al., 1936). The decisive hint for the origin of desynchronizing and synchronizing impulses was proved by Bremer's experiments, which were mentioned in part before. We mentioned that the mesencephalic transection (cerveau isolé preparation) leads to a continuous slow rhythmic activity similar to that observed after slight barbiturate anesthesia. Contrary to the normal spindle activity, however, this activity cannot be disturbed by stimulation of visual or olfactory afferents still connected to the brain. Transection between spinal cord and medulla oblongata (encéphale isolé), on the other hand, rendered an EEG in which spindles alternated with periods of fast rhythms. Arousal was possible by stimulation of afferents. Bremer explained these results by assuming that the sensory afferents reaching the brain between these two levels were necessary for maintaining the cortical tonus of the waking state.

Moruzzi and Magoun (1949), examining this brain segment in greater detail, found that EEG desynchronization was inhibited especially when its central part was destroyed. On the other hand, electric stimulation of this area led to generalized EEG desynchronization. These and other confirming studies helped to establish the concept of the ARAS. It was soon identified as the 'reticular formation,' a structure consisting of neurons interspersed among apparently undirected fibers, which is widespread in the brain stem. Subsequent studies in the cat led to the subdivision into a more frontally situated desynchronizing region and a more caudal synchronizing segment. Moreover, "posterior hypothalamic structures are necessary for a sustained tonic desynchronization" (Schlag, 1974).

Various areas within the ARAS have different functions in normal sleep, in which phases with highly synchronized EEG patterns are interrupted by phases with desynchronized EEG, eye movement, and dreams, the so-called REM (rapid eye movement) sleep. (For a more detailed description, see Birbaumer, 1975.)

The tonus of the ARAS is influenced by input from the periphery, but also from a variety of cerebral structures. Apparently the problem of whether the tonic activity of the ARAS depends on this input, or is to a certain degree autonomous, i.e., whether some activity is maintained even in absence of centripetal impulses, is not settled (Schlag, 1974). According to Schlag, "EEG fast rhythms correspond to the asynchronous occurrence of graded [membrane] potentials, many of them probably of synaptic nature .... The cortical fast rhythm caused by thalamic and reticular stimulation are indistinguishable although the sets of synaptic events observed at the site of recording are different."

An important question is which events at the level of thalamic neurons are triggered by the impulses from the ARAS. Here, the evidence seems to be fairly good that "the most conspicuous event ... is an elimination of the prominent inhibitory postsynaptic potentials (IPSPs) .... Therefore, the reticular effects on thalamic neurons in general must be due, at least predominantly, to a *disinhibition* ...."

To the best of our knowledge, none of the studies cited above on the EEG battery in the cerebral cortex, its pacemaker in the thalamus, and the influence from the ARAS were performed by scientists interested in genetics. Therefore, nothing whatsoever seems to be known on genetic differences between animals of the same species at any of these three levels, and much less, of possible genetic mechanisms by which such differences could be brought about. *Therefore, hypotheses on possible neurophysiological mechanisms of inherited EEG variants in humans can be based on our general knowledge of EEG mechanisms, but not on any* *specific results in animals. Animal experiments, however, will be necessary for testing such hypotheses.*

3.1.4. Speculations on the Physiological Function of EEG-Waves, Especially α-Waves

Before we propose hypotheses on the physiological basis of EEG variants and their influence on human feeling tone and behavior, some present-day concepts on the physiological function of EEG waves, especially α-waves, should be reviewed. In EEG rhythms, Berger (1937) saw the deepest recognizable cause for the rhythmic activity of the human brain, which is also expressed, for example, in rhythmic oscillations of attentiveness, voluntary movements, and our inclination toward all rhythmic activities. More specific concepts were discussed in the years to follow. For example, Walter (1963) developed the hypothesis that the α-rhythm acts as a scanning device for memory patterns, which are stored somehow in the brain. The α-oscillations are seen as long as this mechanism has not identified a certain pattern. As soon as some specific pattern has been spotted—for example, a visual impression after opening the eyes, or an imagined picture—the oscillations disappear and are replaced by less well synchronized EEG waves. The experimental evidence for and against this hypothesis cannot be reviewed here. Suffice it to say that Walter and his coworkers, unlike most other research workers in this field, recognized the interindividual differences of EEG patterns and corresponding psychophysical reactions and tried to account for them in a (highly preliminary) typology (Golla et al., 1943).

Another, fairly elaborate, hypothesis for the physiological function of α-waves was proposed by Andersen and Andersson (1968):

> It is tempting to propose that the rhythmic thalamic activity is necessary to produce a sufficiently effective impact by the afferent volleys on the cortical system. A single stimulus to the cortex or to certain thalamic nuclei is not sufficient to produce a perceived reaction. ... However, even when a single receptor is activated, the ensuing response is perceived .... It may be conjectured that a single afferent volley from a receptor is transformed to a train of impulses of about 10 c/s by the thalamic recurrent inhibitory mechanism. Such a train may have far greater effect on the cortical synapses than the single excitation .... In this context, it is important to note the greatly increased efficiency of the transmission across many synapses when repetitive stimulation is used instead of a single stimulus.

An increase of EPSPs with increasing numbers of stimuli has been observed in various experimental systems, for example, respiratory and cervical motor neurons. In the autonomous system, "a train of stimuli produces a train of steadily augmenting junction potentials, which probably relates to increased amounts of excitatory transmitter released by each stimulus" (Birnstock and Holman, 1961). In the context of our results, we shall return to this finding.

The hypotheses by Walter (1963) and Andersen and Andersson (1968) are not mutually exclusive: they can be regarded as describing the function of α-waves at two different levels. For example, the Walter hypothesis accounts for the α-blocking after (sensory and other) stimulations, an aspect not covered by the Andersen hypothesis, which attempts to explain the events at the neuronal level. For the latter hypothesis, experiments are important that showed that the efficiency of propagation of artificial electric stimulation of thalamic structures to the corresponding areas in the cerebral cortex varies with the phase of the thalamic spindle rhythm (homologous to the human α-rhythm) in which the stimuli are administered (Andersen et al., 1967). According to these authors, this favors the view that the neurons involved in the spindles are identical with those utilized for the orthodromic volleys after peripheral stimulation.

3.2. Attempts to Relate the Above-Mentioned Mechanisms Leading to Individual EEG Patterns With Interindividual Differences in Personality

To the best of our knowledge, there are little or no attempts in the literature to relate the EEG mechanisms by neurophysiological research with interindividual differences in human personality. At first glance, this is surprising; it can be easily understood, however, remembering that science—and especially technically difficult science such as experimental neurophysiology—advances in closed social communities of scientists, often with relatively little outside contact. Anyway, there are at least two attempts at understanding psychological variability in terms of interindividual differences in brain function, which contribute valuable aspects to our problem, even if the authors did not appreciate either the brain physiology of the EEG or the principles of human genetic variability at a sufficiently up-to-date level. These attempts have been made by Eysenck (1970), and—in modification of Eysenck's concept—by Claridge et al. (1973). In the following, these fairly complex concepts will be reviewed insofar as they are import for the present study.

3.2.1. Eysenck's Two Dimensions of Personality

According to Eysenck (1970) the interindividual variability of personalities may be described using two dimensions that are orthogonal to each other: introversion vs extraversion and neuroticism vs stability. Each of these dimensions can be measured phenomenologically by a specifically designed personality questionnaire. At the neurophysiological level, both dimensions are characterized by a number of parameters such as cutaneous reactions, effect of psychotropic drugs, or the EEG. In the elaboration of this typology, the concepts of excitation (or—not entirely identical—arousal) and inhibition play an important role; they are used in a basically similar, though not identical, way as in experimental neurophysiology. In the context of the present study, the use of the EEG as indicator for the functional state of the brain is especially interesting: Eysenck generalizes the (somewhat contradictory) evidence from the literature by stating that "introverted neurotics tend to have fast EEG activity." Our group confirmed the association between fast EEG activity and neurovegetative complaints, which had been asserted before in a number of studies, in a parallel study on adult females. On the other hand, the correlation between introversion and fast EEG activity was not confirmed; in the contrary, all β-categories showed significantly *low* introversion (= high extraversion) scores in the MMPI and the 16 PF.

Eysenck explained individual differences in personality dimensions and correlated EEG patterns by assuming different functional states of brain areas, especially the reticular system (ARAS) and the limbic system, which he calls 'visceral brain.' According to his hypothesis, introversion corresponds to a high level of activation (arousal) in the ARAS; neuroticism corresponds to high activity in the 'visceral brain.'

Eysenck made a strong point that these basic, and physiologically defined, personality dimensions are largely genetically determined. However, he founded his argument on classic biometric twin and family studies, which were based on purely phenomenological evidence and are for this and other reasons of limited scientific value (cf. Vogel and Motulsky, 1979). The evidence for the genetic determination of the EEG and the genetic basis of some distinct EEG variants was apparently unknown to him. These variants would have served his purposes much better.

3.2.2. The Modified Personality Typology of Claridge

The personality model of Claridge (1967; Claridge et al., 1973) was developed as a modification of Eysenck's typology. To cite Claridge,

at the descriptive level two major personality dimensions are recognized, namely neuroticism and psychoticism, the end points of each being defined by appropriate forms of neurosis and psychosis. Thus, neuroticism is seen as a continuous variable running from dysthymia to hysteria, while emotionally active and withdrawn or retarded psychotics, respectively, define the opposite poles of psychoticism. Since neuroticism and psychoticism are regarded as continuously variable dimensions running through the general population they are also assumed to account for normal personality differences ....

At the psychophysiological ... level the main difference between neuroticism and psychoticism is assumed to lie in the manner in which two important arousal processes interact or covary. These two processes ... have been named *tonic arousal* and *arousal modulation.* The former refers to arousal as conventionally defined by activation theorists and appears to have its major loadings on measures of autonomal reactivity .... Arousal modulation is a more difficult concept but statistically is mainly associated with EEG parameters, such as α-index and α-frequency .... Arousal modulation is regarded as having a CNS regulating function and to be concerned with the monotory and sensory input and with such processes as narrowing and broadening of attention (Fig. 1).

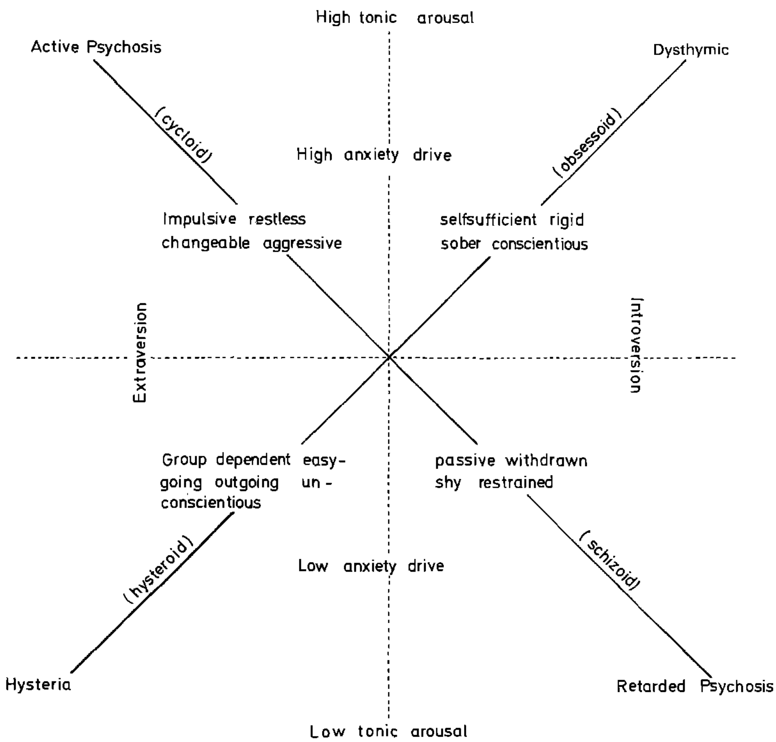


Fig. 1. Personality model proposed by Claridge (1967). Broken lines refer to the two underlying causal mechanisms, tonic arousal and arousal modulation, determining two behavioral criteria of 'neuroticism' and 'psychoticism,' represented by solid lines. Also shown are some features of normal personality expected in individuals at various positions along the two continuums (cf. Claridge, 1967; Claridge et al., 1973)

The model differs from Eysenck's mainly in assuming the personality types to be formed not by neurophysiological dimensions at one level (neuroticism vs stability; introversion vs extraversion), but by assuming interaction between two levels, tonic arousal and arousal modulation; empirically the arousal modulation level is mainly represented by EEG parameters, α-index and α-frequency. Certainly, this concept at two levels agrees with the present state of neurophysiological theory and experimental evidence better than the one-level model of Eysenck: The level of 'tonic arousal' can be homologized with the ARAS (and, in addition, the limbic system), whereas the level of arousal modulation corresponds to the function of the thalamus (or, to put it less simply, the thalamocortical feedback circle).

It is interesting for us that Claridge uses differential reaction to a drug (the sedation level of an intravenously administered barbiturate, amylobarbitone sodium). In our group, another drug, ethanol, the application of which is much easier, was used for a similar purpose (Propping, 1977). Unfortunately, Claridge reduced the EEG information so much that—apart from the α-rhythm—all other information was suppressed. Consequently, he failed to utilize EEG parameters indicative of individual differences at his tonic-arousal level. Compared with his studies, on the other hand, a drawback of our research design is that we failed to include additional independent measures for the tonic-arousal level. We did attempt to organize a cooperative study on regulation of blood circulation on the same material, but due to reasons beyond our influence, this attempt failed. However, we are studying biochemical parameters of possible importance for individual, genetic differences in neurophysiological function; some results will be mentioned below.

4. Results of Our Psychological Studies in the Light of Neurophysiological Evidence

In the second contribution of this series (Vogel et al., 1979b), we described the results of our psychological studies on probands with inherited EEG variants. They are compared with previously published evidence in this, the third, contribution (especially Table 1a–c).

Here we shall attempt to explain at least some of these results in terms of the physiological mechanisms reviewed above. In this context, fairly specific hypotheses about the influence of certain neurophysiological mechanisms on personality, feeling tone, and performance will be developed. These hypotheses will be divided into those supported by apparently good evidence and others, which can be considered tentative.

4.1. The Influence of Neurophysiological Mechanisms on Personality as Revealed by the EEG. Hypotheses Supported by Apparently Good Evidence

4.1.1. The EEG With Monotonous α-Waves (Our Type R)

This EEG variant shows regular α-waves, often with relatively low frequency but characteristically with high amplitudes, over the whole cortex. As explained in

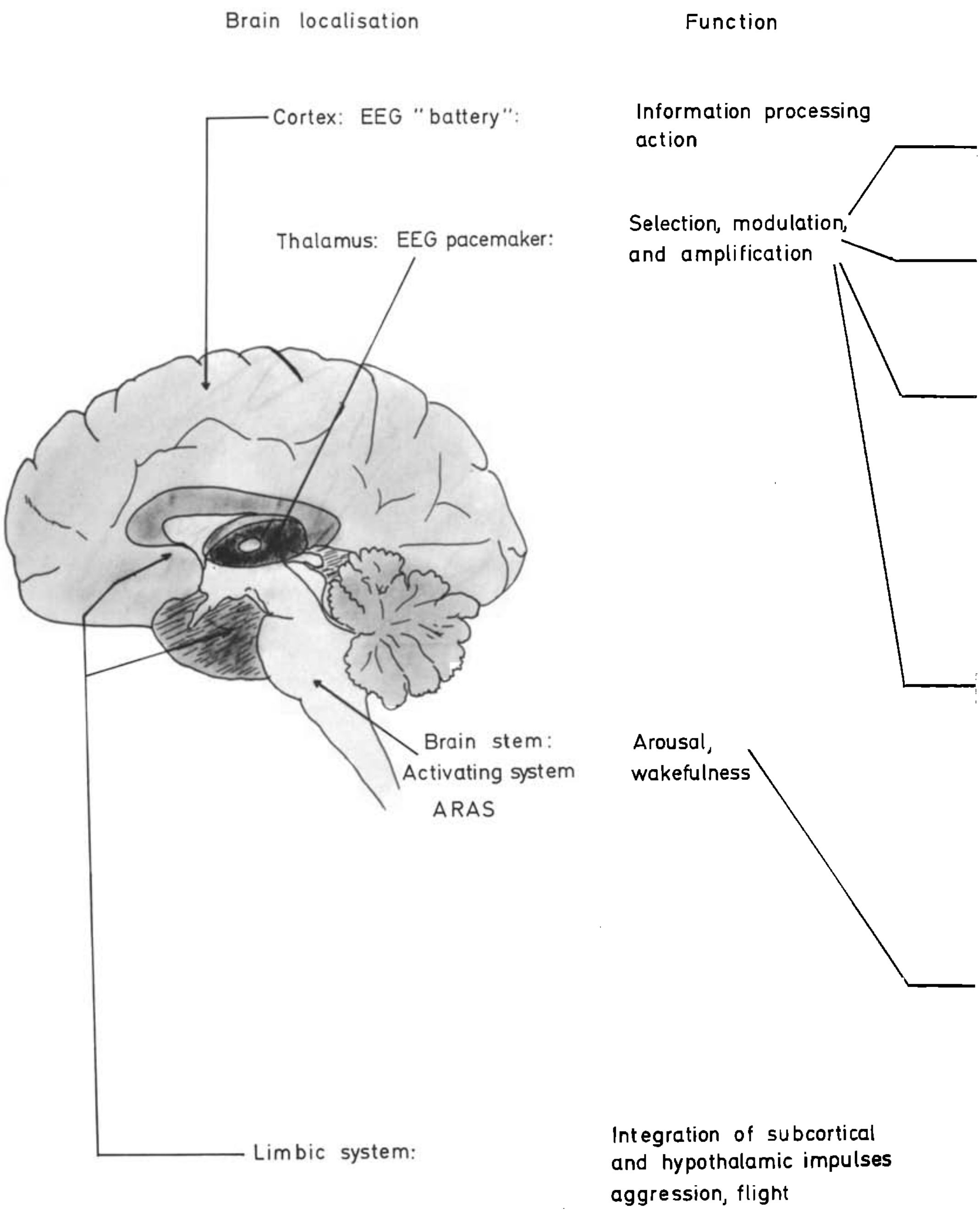
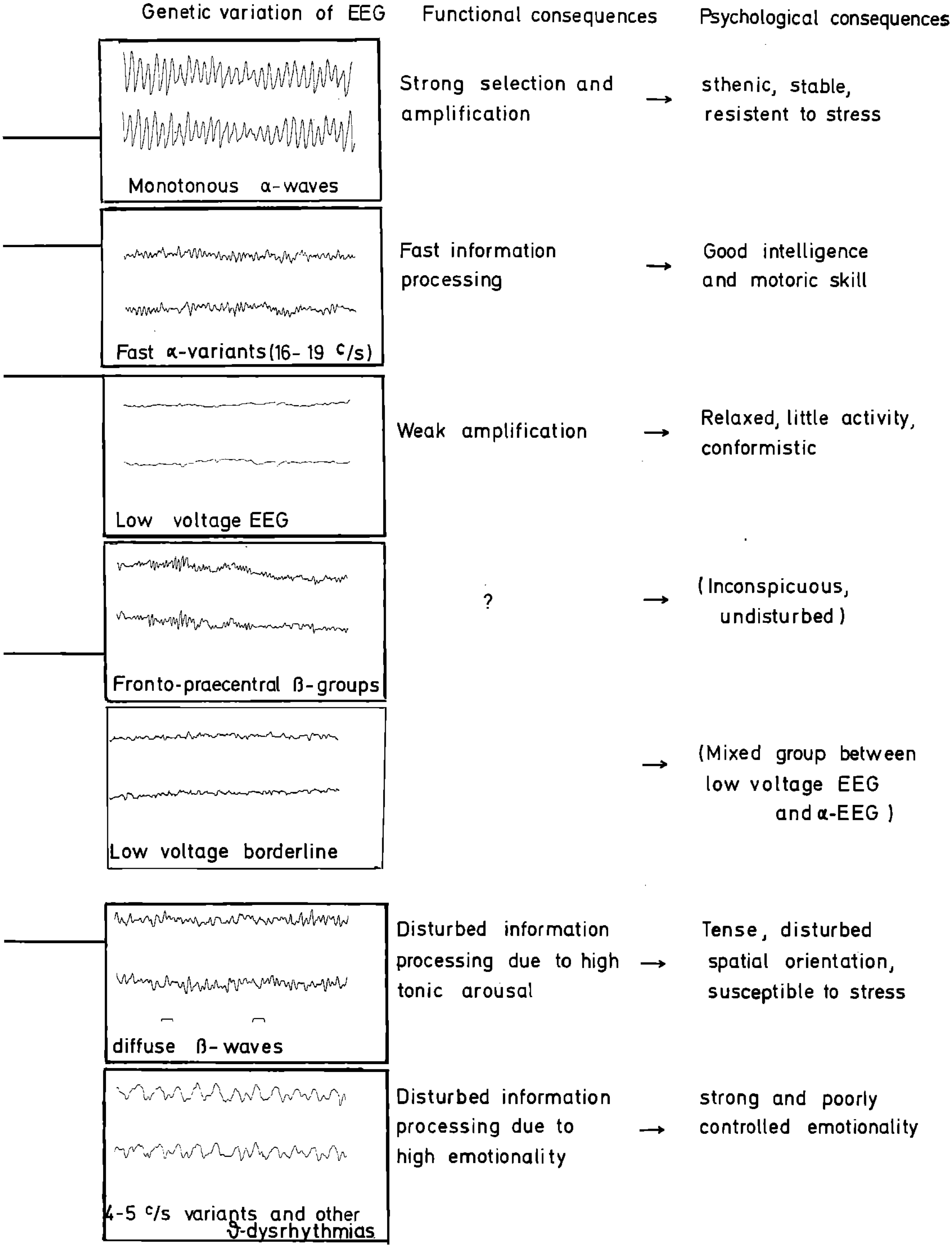


Fig. 2. Synthetic diagram showing the hypothesis explaining psychological differences between individuals with inherited EEG variants. Also shown is a rare (~0.1%) variant not included in this study, the 4—5 c/s variant. Evidence from twin and family studies (Vogel and Götze, 1959; Kuhlo et al., 1969; Neundörfer, 1970) indicates a genetic basis in at least some cases. Emotional disturbances have been described repeatedly (cf. Müller-Küppers and Vogel, 1965)


Genetic variation of EEG
Functional consequences
Psychological consequences
Monotonous α-waves
Strong selection and amplification
→
sthenic, stable, resistent to stress
Fast α-variants (16- 19 c/s)
Fast information processing
→
Good intelligence and motoric skill
Low voltage EEG
Weak amplification
→
Relaxed, little activity, conformistic
Fronto-praecentral β-groups
?
→
(Inconspicuous, undisturbed)
Low voltage borderline
→
(Mixed group between low voltage EEG and α-EEG)
diffuse β-waves
Disturbed information processing due to high tonic arousal
→
Tense, disturbed spatial orientation, susceptible to stress
4-5 c/s variants and other ϑ-dysrhythmias
Disturbed information processing due to high emotionality
→
strong and poorly controlled emotionality

paragraph 3.1.2., this cortical activity is triggered by a pacemaker—or, better, by a group of interrelated pacemakers—in the thalamus. The function of α-activity may be to modulate selectively and to amplify relevant stimuli coming from lower levels of the brain so that the cortex can recognize them better. It could therefore be predicted that brains with especially regular and widespread α-activity would be especially efficient for this function: Such individuals would be especially good modulators and, more specifically, amplifiers. They should process relevant information very efficiently and transform it into well-controlled activity without being overly confused by irrelevant information.

This prediction can now be compared with our results (paragraph 2.2.2.1.): The average personality in this group is sthenic, stable, and well controlled. Information processing seems to be especially efficient as evidenced by above-average precision in short-time memory and in concentration tests. The probands tended to be tough-minded and stress resistant. It might be important for this aspect of personality that the α-activity extends to the frontal and precentral cortex where, in a more average EEG, a mixture of α-, β-, and ϑ-waves can be found. On the other hand, our R group did not excel by high formal intelligence and abstract thinking. This may simply reflect a different selection of probands, i.e., probands in this group have been successful as soldiers not so much because of their intelligence but because of their personality and initiative. As an alternative, we offer the explanation that the strong amplification of stimuli may be connected with a certain time delay; as explained in paragraph 3.1., the transmission of stimuli to the cortex is influenced by the phase of the thalamic rhythm. Moreover, this notion is supported by the observation that the BO group (occipital fast α-variants) was especially good in intellectual tasks and that the N group, whose α-mechanism is much weaker, had low reaction times—especially to simple visual stimuli.

In conclusion, we advance the hypothesis that individuals with monotonous α-waves are strong thalamic modulators and amplifiers, with all consequences for their way of information processing, feeling tone, and behavior.

4.1.2. The Low-Voltage EEG

From the EEG point of view, the low-voltage EEG (N) is the countertype of the R variant. Consequently, one would expect a low degree of modulation and, especially, amplification of stimuli. It is not quite as easy to predict specific personality characteristics for the N as for the R variant. On the one hand, the reduced amplification would be expected to lead to lower intensity of the stimuli admitted to the cortex. On the other hand, it is possible that unfavorable stimuli, for example from the ARAS (or the limbic system), are less efficiently screened and may therefore cause more disturbances.

Our results (paragraph 2.1.1.2., Table 1b) seem to confirm the first prediction. Psychic activities of the N probands tended to show low intensities, especially if compared with those of the R group. In daily life, this low intensity lets the probands appear inconspicuous, and especially 'normal.' Low intensity of afferent stimulation leads to (or is accompanied by) a low level of spontaneous activity; characteristic is the significantly lower Ma score compared with that of the R group. This weak intensity of stimulation and low level of spontaneous activity tend to be combined with a relaxed and carefree attitude. At the level of social contacts and social integration, this leads to conformism; the individual follows the group standards, conforms to group ideals (= high superego strength in soldiers), and often feels comfortable in this situation (= high extraversion scores).

Formal intelligence, especially the ability for spatial perception, seems—at least—not to be impaired by the lack of α-activity. This result does not favor hypotheses, especially that of Walter (paragraph 3.1.4.), according to which the α-rhythm is a screening mechanism for recognition of memory pictures. As mentioned in connection with the R group, a hint as to the special mode of information processes in this group is provided by the low reaction time to simple stimuli of the N group, which is significantly lower than in the R group. Possibly, the strong amplification in the R group needs more time than the much weaker amplification in the N group. According to current theory, however, the α-rhythm not only amplifies but also modulates afferent volleys and helps to screen out unfavorable stimuli. Considering this, one would expect in some probands not the relaxed attitude, which the 'average' N proband actually shows, but rather an increased tendency to be unduly irritated even by average or only slightly above-average levels of tonic arousal in the ARAS.

However, such cases do, indeed, occur. Such an 'irritable'group is represented by our NG (low-voltage borderline) category. Earlier family studies (Reinke, 1966; Vogel, 1970) showed that this group consists of two subgroups: one representing the tail of the distribution of average, multifactorially determined α-EEGs and a second one fitting into the dominant mode of inheritance of the low-voltage EEG but showing a certain amount of β- (and sometimes ϑ-) waves. Moreover, in our early family studies, which established the autosomal dominant mode of inheritance (Vogel and Götze, 1959; Vogel, 1963), occasional individuals without α-waves, but with numerous β-waves (or ϑ-waves), were observed. Hence, many, if not most, of the probands in our series who have been classified as NG probably belong to the N group genetically and have the same, low-energy, modulation and amplification mechanism. However, due to other reasons, their level of tonic arousal may be higher. And indeed, this group shows the highest scores in 8 of 10 'clinical' MMPI scales and low speed with many errors in concentration tests (d-2; KLT). This is exactly what one would expect in an individual with a weak modulation mechanism and a high level of tonic arousal. Moreover, the relatively low energy level of categories N and NG is expressed by their high tendency to social conformity. The probands of the present study were exclusively adult males. However, there is now good evidence that the average level of tonic arousal, i.e., activity of the ARAS, is higher in adult women (Friedl and Vogel, 1979a). It is therefore not surprising that the percentage of 'typical' low-voltage EEGs was somewhat lower in females; here, some of the EEGs which belong to the low-voltage class genetically are classified as borderline or even BD (diffuse β). In conclusion, our study provided evidence that there are two EEG countertypes—the R variant and the N (+ partially NG) variant—which influence a modulating and amplifying mechanism in the thalamus in opposite directions. This leads to variations in personality and performance, which are reflected in the outcome of appropriate psychological tests.

4.1.3. The EEG With Diffuse β-Waves

As mentioned (paragraph 2.2.2.3., Table 1c), our description of this EEG type does not correspond entirely with other aspects, especially Schmettau's (1969) description of the personality correlations with a higher β-index. The amount of β-waves is higher in females than in males, and it increases with advancing age—in women more than in men. Considering the experimental results discussed in paragraph 3, the most likely neurophysiological mechanism is a relatively high level of tonic arousal of the ARAS leading to frequent and repeated disturbance of an α-activity of average or weak strength. Hence, the expected personality correlates would be hypersensitivity and low resistance to stress. Probands with this EEG variant would be expected to avoid excitation continuously, if at all possible. This is exactly Schmettau's description (1969) of individuals with high β-index.

Our own BD (diffuse β) sample, on the other hand, showed inconspicuous scores in personality questionnaires. Hence, there was no direct evidence for the hypersensitivity and psychastheny expected when the tonic arousal level was increased. More indirect evidence, however, was obvious: The probands showed high error percentages in the two concentration tests (KLT and d-2) in spite of relatively low working speed. These tests are generally experienced as stressful. Hence, poor performance is related to low stress resistance. Moreover, the BD probands achieved relatively low scores in the intelligence test scales designed to test spatial orientation. It is remarkable that this deviation is in the same direction as the normal sex difference: Women tend to perform poorer than men in spatial orientation. At the same time, EEGs pointing to a higher level of tonic arousal are more common, and there is a significant negative correlation between measurable EEG criteria pointing to increased arousal and a test scale for spatial ability. These results suggest the hypothesis that a high level of tonic arousal can disturb ability for spatial orientation more than other aspects of intellectual performance.

The data on the BD variant alone could also be interpreted as showing that good spatial performance requires a strong α-mechanism, for example, for screening "memory pictures" according to Walter's hypothesis (paragraph 3.1.4.). If this were true, however, spatial performance should be much better in the R than in the N group. This is not the case; quite the contrary: The N group shows higher average values. Hence, the amplification mechanism revealed by monotonous α-activity in the R group seems not to be necessary for good spatial ability; absence of disturbance due to a high level of tonic arousal of the ARAS, however, seems to be important.

So far, we did not cite the abundant literature on EEG abnormalities in mental disease; there are too many sources of error, for example, difficulties in cooperation of the patient or drug effects. Recently, however, Itil (1978) reviewed the evidence on EEG deviations in schizophrenia. According to his studies, "the EEG of adult schizophrenics is characterized by an appearance of excessive fast activity along with some slow waves and the [relative] lack of α-activity." Similar peculiarities have also been found in the EEGs of schizophrenic children and, most interesting, of healthy children of schizophrenics. These EEG peculiarities overlap strongly with our BD type. They point to a high level of tonic arousal in schizophrenics. Together with the psychological results in our and Schmettau's series, they support the disposition-stress hypothesis of schizophrenia presently referred to by many authors.

4.2. Hypotheses on the Influence of Neurophysiological Mechanisms on Personality as Revealed by Associations Between EEG Variants and Test Results; Weak Evidence

4.2.1. The EEG With Occipital Fast α-Variants (BO)

As mentioned, this EEG variant shows an especially high performance in intellectual and motor tests. It would be tempting to argue that this is due to the high frequency of the α-like waves; this may lead to especially specific amplification of relevant stimuli. This argument has some support from reports on correlations between α-frequency and intelligence test scores (paragraph 2.1.). Unfortunately, however, our series of probands with this relatively rare variant (0.6% in a male population; Vogel and Fujiya, 1969) is so small that most of the differences are not statistically significant. Therefore, more definite conclusions have to be postponed until more observations are available.

4.2.2. The EEG With Frontoprecentral β-Groups (BG)

Contrary to the α-rhythm, there seems to be little if any experimental evidence that could explain at least tentatively the neurophysiological mechanisms of the frontoprecentral, often spindlelike, β-waves in these probands. In spite of the fact that also in the BD type, anterior leads tend to contain more β-waves than occipital ones, it seems unlikely that these frontal groups simply represent another aspect of high tonic arousal in the ARAS: They are completely compatible with an undisturbed, normal α-rhythm with occipital location; occasionally, they can even be observed in combination with a low-voltage (N) EEG. Moreover, our BG probands completely lacked psychological signs of a high arousal level. They had the lowest clinical MMPI scores of our proband groups; their results in spatial perception tests were excellent; and stress resistance as revealed by concentration tests (KLT and d-2) was very good.

One possible origin of these spindles is the thalamus: There is experimental evidence for different kinds of thalamic pacemakers with diverse frequencies and different cortical connections (Andersen and Andersson, 1968). The single autosomal dominant mode of inheritance of this EEG variant suggests that one specific mechanism, possibly involving a limited number of neurons, may be altered. Frontoprecentral β-groups of similar appearance are often seen—sometimes in connection with a more generalized β-activity— after uptake of a variety of drugs, for example small doses of barbiturates. Perhaps someday these drug effects will give clues about the underlying neurophysiological mechanisms.

5. Prospects and Concepts for Further Research

5.1. Attempts to Elucidate the Biochemical Basis of EEG Polymorphism

Genes determine the amino acid sequences of proteins; genetic differences between individuals must therefore—as a rule—be reflected in protein differences. The general rule should also apply for the EEG polymorphisms with single modes of inheritance, for example type N or type R. This raises the question of where exactly such protein differences could be found. As mentioned in paragraph 3.1., recent neurophysiological theory explains the EEG waves as summated excitatory postsynaptic potentials (EPSPs). Such EPSPs are formed by depolarizations of membranes. Therefore, genetic differences in membrane proteins as biochemical causes for EEG polymorphisms is a reasonable possibility. Such membrane differences may, for example, influence pump mechanisms for Na^+, K^+, and Ca^{++} ions, the release or binding of neurotransmitter molecules, or the release of neurotransmitter enzymes. This, in turn, may lead to differences in the efficiency of coordination of rhythmic neuron activity in the thalamus.

Attempts at discovering the expected protein differences in humans are limited because neuronal membrane proteins cannot be examined without severe —and ethically unacceptable—intrusion into the living organism. So far, we have been unable to overcome the organizational difficulties of examining CNS proteins of deceased individuals. However, it was possible that membrane protein differences could be of a more general kind, and could also be detected in membrane material from more easily accessible tissue, for example erythrocytes. However, attempts to find such protein differences in probands with the low-voltage EEG were unsuccessful (Propping et al., 1978). This does not mean, of course, that no such differences exist; the obvious alternative hypothesis is that the differences cannot be recognized by the electrophoretic method used, or that they are expressed only on nerve cells (or certain groups of nerve cells).

In this case, more indirect evidence on different membrane function could be expected. And indeed, Propping et al. (1979) found statistically significant differences in the mean activity of the enzyme dopamine-β-hydroxylase (DBH) between university students with different EEG variants. The mean activity was almost twice as high in probands with the R variant as in those with the N. Very high activities were found only in R-variant probands; however, some of the R-variant probands had very low activities. Thus, the enzyme activity cannot be the direct and only cause of the EEG variant. On the other hand, serum DBH is known to originate not in the brain but in the adrenergic part of the peripheral sympathetic system. Hence, the association with the R EEG variant indicates that this variant reflects some more widespread functional peculiarities of the nervous system.

As shown in other family and twin studies by various groups, serum DBH levels, like levels of MAO and COMT, are largely genetically determined (Weinshilboum et al., 1975; Weinshilboum, 1978; Propping et al., 1978). However, structural deviations of enzyme proteins seem to be rare (Weinshilboum, 1978); they seem not to be responsible for the variation in enzyme activities. This could also point to a membrane factor. Search for such a factor using modern concepts of molecular biology is the next obvious step in the elucidation of genetic mechanisms.

In this connection, the finding of Birnstock and Holman (1961) may be mentioned again: the augmentation of evoked potentials produced by trains of stimuli is probably connected with the release of increased amounts of excitatory transmitters. Possibly, the genetic peculiarity in the R type—whether primarily located in the membrane or not—leads to an increased release of certain neurotransmitters as an important intermediary step.

5.2. Improved Psychological Definition of the Personality Differences Suggested by This Study

The psychological methods utilized in this study were selected with the intention of obtaining as comprehensive as possible a personality description with a one-day examination. The present study did yield some results and permitted formulation of some hypotheses. Hence, new psychological and neurophysiological investigations should be planned in such a way that these hypotheses can be tested more specifically. In part, this can be done by using the same test materials; for the MMPI, for example, apart from the standard scales used in this study, many other scales are available.

Another approach would be to test the hypotheses developed here with other proband groups, for example women, students, or probands with different socio-cultural backgrounds. Inclusions of additional psychological parameters such as evoked potentials, regulation of heart action, or endocrine function may be worthwhile. Comparison of the various EEG variants in psychological function may even help elucidate the central nervous mechanisms that normally influence these functions.

Such attempts, if properly planned, may be successful, as the differences in personality, temperament, and performance revealed by this study seem to be by no means trivial for daily life: Earlier studies showed that probands with β-EEGs (mostly the BD type) seem to marry partners with the same EEG variant more often than expected by chance alone (Vogel, 1962b), and the same seems to be true for the R type (Dieker, 1967). This possible assortative mating (if confirmed) would show that these personality differences can be felt somehow in daily life. The investigators (F.V. and E.S.) had the strong impression that this is, indeed, so. At the moment, however, we cannot prove it. Apparently, such 'biological' differences in temperament are only partially reflected in personality questionnaire responses. Twin studies in the thirties and fourties provided evidence for a much higher concordance of MZ twins in more intuitively recognized properties such as *Antrieb, Empfindlichkeit,* and *Grundstimmung* (drive, sensitivity, and feeling tone; Geyer, cf. Becker, 1958), than have been found more recently by personality questionnaires (Vogel et al., 1979a).

5.3. Concluding Remarks on the Research Strategy of this Study

In the first contribution of this series, we compared the strategy adopted in this research program with the more conventional research strategies in human behavior genetics, comparison of psychological phenotypes between relatives and twins using biometric methods.

The results seem to show that this strategy leads to results that can be interpreted in terms of neurophysiological mechanisms. To avoid misunderstanding, we wish to stress one point: This study does not make the preposterous claim that the whole or even a major part of the genetic variability influencing human behavior has been explained. In the contrary, we feel sure that variability of personality is influenced by many genetic factors, for example, embryonic development of the brain, number of neurons, formation of synaptic connections between neurons, influences on neuronal activity from outside the brain, e.g., hormonal actions, in cooperation with differing environmental influences and interactions during the lifetime of the individual. All our EEG variants showed the whole range of variability of test results; only the means and distribution of test scores differed somewhat. Our study does not contribute to the question of which fraction of the interindividual variability in such test results may be genetically determined, apart from showing that genetic variability influencing psychological test results does, indeed, exist. In our opinion, the study rather shows that such a genetic fraction has little meaning in itself; meaningful, however, is the question of which specific differences may influence behavior of an individual and how they might do so.

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