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Relation of Olfactory EEG to Behavior: Factor Analysis

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Rabbits were conditioned to lick (CR+) in response to one odor (CS+); another odor (CS−) served as a discriminative control (CR−). Electroencephalograms (EEGs) were recorded from arrays of 64 electrodes on the olfactory bulb in three stages, each with six sessions: in Stage I, odors A+ and B−; in Stage II, odors C+ and B−; and in Stage III, odors C+ and A−. Spatial EEG amplitude patterns were measured for multiple control (C), CS+, and CS− EEG bursts in each trial. Data were transformed via factor analysis and expressed by factor scores as spatial patterns specified by factor loadings. In discriminant analysis of the factor scores, we correctly classified the C and CS bursts on the average by 65–80% from all trials for each subject and session and by 75–90% for trials with correct CRs. The latter was confirmed with a stepwise linear discriminant analysis of the original 64-variable data. Factor patterns were relatively invariant within but changed between stages. The results implied that stable spatial patterns of bulbar activity emerged in respect to CSs under reinforcement and persisted until the stimulus–response contingencies were changed.

The aim of three reports—this one, Freeman and Viana Di Prisco's (1986), and Freeman and Baird's (1987)—was to identify odor-specific neural activity patterns in the olfactory bulbar electroencephalogram (EEG). It was hypothesized that for animals trained to discriminate odors, an activity pattern specific to each odor conditioned stimulus (CS) existed in the bulb during its presentation. Furthermore, this neural activity pattern served as a basis for discriminative responding and hence had to occur before the onset of the correct conditioned response (CR). These neural activity patterns were expected to be manifested in the spatial patterns of EEG activity recorded at the bulbar surface.

Goals of this report were threefold: (a) to develop and validate a statistical test for identification and classification of odor-specific bulbar spatial EEG patterns, (b) to demonstrate pattern invariance within training stages with fixed stimulus–response (S–R) contingencies, and (c) to confirm pattern changes observed for changes in S–R contingencies (Viana Di Prisco & Freeman, 1985).

The data base for this report consisted of recordings of EEG bursts from rabbits appetitively (classically) conditioned to respond to one odor (CS+) by licking, with or without sniffing, and to respond by sniffing to another (the CS−) odor. EEG recordings were obtained with chronically implanted 8 × 8 electrode arrays from the olfactory bulbar surface. Recordings were taken during inhalation of background or control (C) air and odor conditioned stimuli (CS+, CS−). Control bursts recorded during CS+ trials were labeled C+ bursts; those during CS− trials were labeled C− bursts. Licking responses were measured as jaw movement, here denoted CR+. Sniffing was measured via on-line detection of changes in respiratory rate, here denoted CR−. Behavioral training was in three stages, each with six sessions. In Stage I the CS+ was n-butanol (A+) and the CS− was benzaldehyde (B−); in Stage II, ethylacetate (C+) was introduced as CS+ and B− continued as the CS−; in Stage III, C+ was continued and n-butanol was reintroduced as CS− (A−). The behavioral results and preliminary EEG measurements have been reported (Viana Di Prisco & Freeman, 1985).

Analysis of the pooled data from Sessions 4–6 in Stage I showed that odor-specific information could be extracted from the bulbar EEG by use of temporal and spatial filtering and deconvolution (see Method section). The information was not localized to a subset of the 64 channels but was distributed over the entire array. The behavioral test for odor specificity was the ability of the EEG-derived information to classify EEG bursts correctly with respect to C, CS+, and CS− stimulus conditions.

Our goals were met through factor analysis of amplitudes of recorded bursts. The test for odor specificity was by the behavioral assay applied to the factor scores with classification of burst with respect to odor CSs. It was validated by discriminant analysis of burst factor scores. Pattern invariance was measured via factorial invariance, which was tested by cross-correlation of factor loadings and by cross-classification of samples between sessions within stages. Changes in patterns with changes in S–R were measured via cross-correlation of factor loadings in each session with the factor loadings from each of the 17 other sessions. The essential finding of odor-specific EEG was confirmed with a stepwise linear discriminant procedure carried out on the original 64-amplitude burst data.

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Table 1
Examples of the First 12 Eigenvalues From Factor Analysis of the Correlation Matrix of Normalized Amplitudes of Selected Electroencephalogram Bursts

	Eigenvalue												
Subject	1	2	3	4	5	6	7	8	9	10	11	12	%
1	23.60	9.56	6.22	4.04	3.28	2.75	2.36	2.03	1.42	1.23	1.20	0.98	90.16
2	36.74	13.82	4.16	2.17	1.48	1.36	0.79	0.66	0.52	0.41	0.33	0.29	93.34
3	48.34	5.72	3.16	2.74	1.02	0.78	0.43	0.36	0.24	0.21	0.18	0.15	96.47
4	27.66	13.38	7.36	3.27	2.75	2.07	1.73	0.89	0.72	0.66	0.57	0.44	90.97
5	32.55	12.47	4.62	4.44	1.76	1.43	1.26	0.94	0.69	0.52	0.48	0.39	91.44

Note. The percentage of the total variance is that included by the sum over factors with eigenvalues exceeding unity (the Kaiser-Guttman rule).

from 90% to 96% across subjects. The modal number of eigenvalues greater than or equal to one across subjects was 7. When only these factors were used (the Kaiser-Guttman Rule), the percentage of variance explained ranged from 88% to 96% ($M = 92\%$).

The orthogonal factor model suggested that each burst amplitude pattern could be expressed as a linear combination of stereotypic factor patterns. Ideally, the pattern of loadings in each column would suggest a stereotypic spatial pattern. With or without rotation, visual inspection failed to reveal uniqueness among columns of the factor-loading matrix. The nature and the significance of the factor patterns therefore remain to be determined.

The optimal number of factors (K_c) and rotation type were determined via the behavioral assay. We reduced the dimensionality of each burst from 64 to K_c by calculating its *PC* or *F* scores. Class centroids for C+, C−, CS+, and CS− classes were calculated in K_c space. Distances were calculated between each burst and the $\overline{C+}$, $\overline{C-}$ centroids for control bursts and $\overline{CS+}$, $\overline{CS-}$ centroids for odor bursts. Each was labeled "correct" if the distance to its "true" centroid was less than the distance to the other paired centroid. The percentage of correct distances for control bursts was subtracted from the percentage of correct distances for odor bursts. Because the C+ and C− bursts were from a common population, random classification was expected. The percentage difference assay measured the departure from random classification of odor bursts. Standard errors for the measure were obtained by Freeman and Baird (1987).

The number of factors, *K*, was varied from 2 to 16 in unit steps. The resultant assay values are shown in Figure 1. The optimal number of factors, K_c, was 4 for two rabbits, 9 for a third, and 11 for a fourth. A fifth subject showed no significant classification of bursts, which was consistent with the lack of behavioral evidence for odor discrimination (Table 2). The assay value at K_c was nearly identical to that obtained with 64 amplitude values: 24.2% (80.0 − 55.8), across subjects. Increasing *K* from 2 to K_c preferentially increased the percentage of correct classifications for odor bursts; increasing *K* to numbers beyond K_c preferentially increased that percentage for control bursts. When the number of factors was selected according to the Kaiser-Guttman rule, the results were nearly identical. Varimax rotation of factors selected according to the Kaiser-Guttman rule yielded K_c values between 3 and 5 for four rabbits. The assay value was 24.8% (78.4 − 53.6) across subjects. Oblique rotation was not evaluated.

Factorial Invariance

Factorial invariance was demonstrated in several ways. Jackknifing, cross-classification of factor scores, correlation of factor loading matrices, and burst amplitude pattern reconstruction yielded convergent results.

With jackknifing (leaving a different burst out of the data set for each calculation), factor analysis with varimax rotation was repeated 40 times for each subject. The behavioral assay was run on the *F* scores for each run, and their means and standard deviations were computed (Table 3). The distribution of the percentage values was normal. The mean was significantly above zero ($p < .01$, *t* test) for each subject. The grand mean standard deviation, 4.1%, confirmed the result obtained by this procedure applied to amplitude values (Freeman & Viana Di Prisco, 1986) and provided another estimate of the 99% confidence interval for the behavioral assay (± 10.1%).

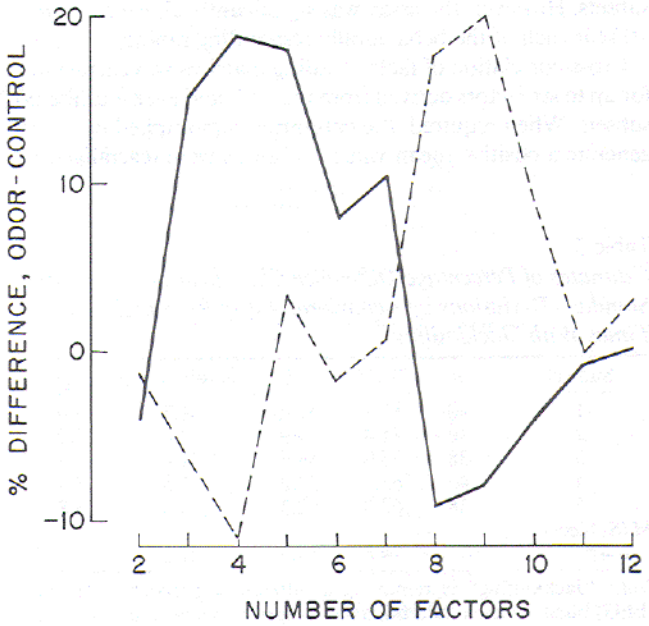

Figure 1. Examples from 2 subjects of the percentage difference behavioral assay of the factor scores (without rotation) as a function of the number of factors entered. (The optimal number was close or equal to that from the Kaiser-Guttman rule for each subject.)

Table 2
Conditioned Response Classification

Subject	Correct: Lick CS+	Correct: Sniff CS−	Incorrect: Sniff CS+	Incorrect: Lick CS−	No response: CS+	No response: CS−
1	19	10	9	3	2	17
2	20	13	5	9	5	9
3	25	10	3	2	2	18
4	25	18	5	2	0	10
5	4	7	23	4	3	19
Mean % (Subjects 1–4)[a]	74	42	18	13	8	45

Note. The rates of correct responding for CR+ (conditioned lick response) and CR− (discriminative control) and of no or incorrect responding are summarized over Sessions 4–6 of Stage I, which served as the test bed for development of the analysis. CS+ = conditioned stimulus odor; CS− = discriminative control odor.
[a] Subject 5 was excluded from the mean because it did not acquire the discriminative CR.

In cross-classification, the data set for the three sessions of fixed S–R contingencies was divided into even- and odd-numbered bursts. Each subset served in turn as a "learning" set and a "validation" set. The percentage difference values were calculated for each subject operating on itself and on its twin. The results (Table 4) showed that the efficacy of cross-subset classification was not significantly different from that of within-subset classification within the estimate of error for the assay.

Similarly, factor loadings were derived from two other subsets. The trials with correct CRs (licking and sniffing) and those with incorrect or no CRs yielded matrices $\mathbf{X}_{\text{correct}}$ and $\mathbf{X}_{\text{incorrect}}$, respectively. Classification of F scores generated with $\mathbf{X}_{\text{incorrect}}$ rather than $\mathbf{X}_{\text{correct}}$ was lower both within and across subsets. However, the assay was significantly above zero ($p < .01$) for each of the behaviorally responding rabbits.

Cross-correlation of factor-loading matrices was carried out for up to six factors derived from the odd- and even-numbered subsets. When required, the column was multiplied by −1 to generate a positive mean value. Columns were rearranged by eigenvalue and placed in such a way that their column number was equal to the row number of the largest loading value in that column. The top half of Table 5 shows the mean values (by Fisher's z transform) of the correlation matrices for the four behaviorally responding subjects. The diagonal elements

Table 3
Estimates of Percentage Difference Classification Values and Standard Deviations by Behavioral Assay Repeated Five Times With "Jackknifing"

Subject	n	% CS	% C	% difference	SD
1	40	87.9	53.6	34.3	4.0
2	39	71.4	53.9	17.6	2.9
3	38	76.0	54.6	21.4	5.3
4	40	63.7	52.2	11.5	3.9
5	38	62.0	62.3	0.3	3.8
M (Subjects 1–4)[a]		74.8	53.6	21.2	4.1

Note. "Jackknifing" is removing a different electroencephalogram (EEG) burst on each determination of group means and cross products. (See Table 4 for the numbers of bursts.) Over 40 runs, one of twenty control or one of ten odor bursts were removed. CS = odor stimulus; C = control (background) air.
[a] Subject 5 was excluded from the mean because it did not acquire the discriminative CR.

Table 4
Testing for Factorial Invariance by Use of "Training" and "Test" Sets

Condition	Subject 1	2	3	4	5	M
No. bursts in a priori groups (Sessions 4–6, Stage I)						
Even (X_e)						
C+	13	6	9	13	17	12
CS+	7	19	19	10	13	14
C−	10	5	12	11	16	11
CS−	13	10	20	12	14	14
Odd (X_o)						
C+	9	9	19	7	8	10
CS+	11	16	10	14	22	15
C−	13	6	14	12	10	11
CS−	10	9	17	13	20	14
Total	86	80	120	92	120	100
% difference classification measure						
Training[a]						
$X_e * X_e$	26.2	−5.2	9.2	15.2	−4.3	11.4
$X_o * X_o$	18.6	18.2	16.1	4.3	−8.8	14.3
Test[b]						
$X_e * X_o$	26.2	−5.2	9.2	19.0	−1.3	12.3
$X_o * X_e$	28.1	26.6	18.1	12.3	−2.7	21.3

Note. See Table 3 for the error of estimate. C+ = control electroencephalogram (EEG) bursts during CS+ (lick-eliciting odor) trials; C− = control EEG bursts during CS− (sniff-eliciting odor) trials.
[a] Same factor loadings were used.
[b] Opposite factor loadings were used.

Table 5
Correlations of Factor Loadings

Factor	I	II	III	IV	V	VI
Derived from odd- and even-numbered electroencephalogram bursts[a]						
I′	.94*	−.23	−.31	.02	−.05	−.07
II′	−.08	.95*	−.29	−.32	−.14	.10
III′	−.31	−.21	.86*	.04	−.11	.02
IV′	−.10	−.37	−.18	.80*	−.09	.02
V′	−.21	−.11	.01	.09	.41	.21
VI′	.06	−.13	−.03	.04	.21	.33
Sessions 4–6[b]						
I′	.86*	−.09	−.28	−.02	.00	.01
II′	−.19	.94*	−.35	−.38	−.19	−.13
III′	−.34	−.20	.79*	−.15	−.17	.04
IV′	.06	−.49	.07	.83*	−.08	−.00
V′	−.17	−.13	.06	.14	.46	.22
VI′	.07	−.14	−.06	.04	.17	.39

[a] Averaged via Fisher's z transform over the 4 behaviorally responding subjects.
[b] Averaged over subjects and sessions pairs.
* $p < .001$.

for the highest four factors averaged 0.90 and off-diagonal elements averaged −0.22, which indicates that the factor patterns extracted from the two subsets were the same. For subsetting by CR, the diagonal elements averaged 0.81 over the first four factors and −0.24 over the off-diagonal elements.

Cross-classification and factor-loading correlation were performed session by session. In order to ensure an adequate sample size, bursts were included from trials irrespective of CR. The even or odd cross-subset classification value of 15.3% (69.5 − 54.2) was within one standard error from the within-subset value of 17.9% (70.5 − 52.6). The correlation matrices again indicated that the same spatial patterns of factor loadings were extracted from all three sessions (Table 5, bottom half). The average of the first four diagonal elements was 0.86.

Burst pattern reconstruction with F scores yielded normalized and nonnormalized displays of spatial amplitude patterns. An example of the patterns is shown in Figure 2 in the form of density plots. The bottom row displays the means of the patterns reconstructed from the factor scores and loadings. The top row shows the means of the nonnormalized amplitudes of bursts by groups (C+, CS+, C−, and CS−, and the disorderly bursts with low or varying frequencies, termed *CHAOS*). The second row shows the standard deviations for each group. The third row shows the means for the pooled C+ and C− groups, the CS+ group, and CS− group, separated into those correctly and incorrectly classified by discriminant analysis (see the next section). These plots showed that spatial pattern differences were visualized between groups of normalized amplitudes and that they were expressed in the weighted sums of factor patterns. In contrast, the nonnormalized patterns conformed in the main to the signature pattern for each subject; differences between groups were virtually impossible to detect by visual inspection (Viana Di Prisco & Freeman, 1985).

Reconstruction errors were lowest for correctly classified bursts irrespective of class (C, CS+, CS−, Table 6). Those that were incorrectly classified had larger errors. The subject that showed no significant classification had the largest error in

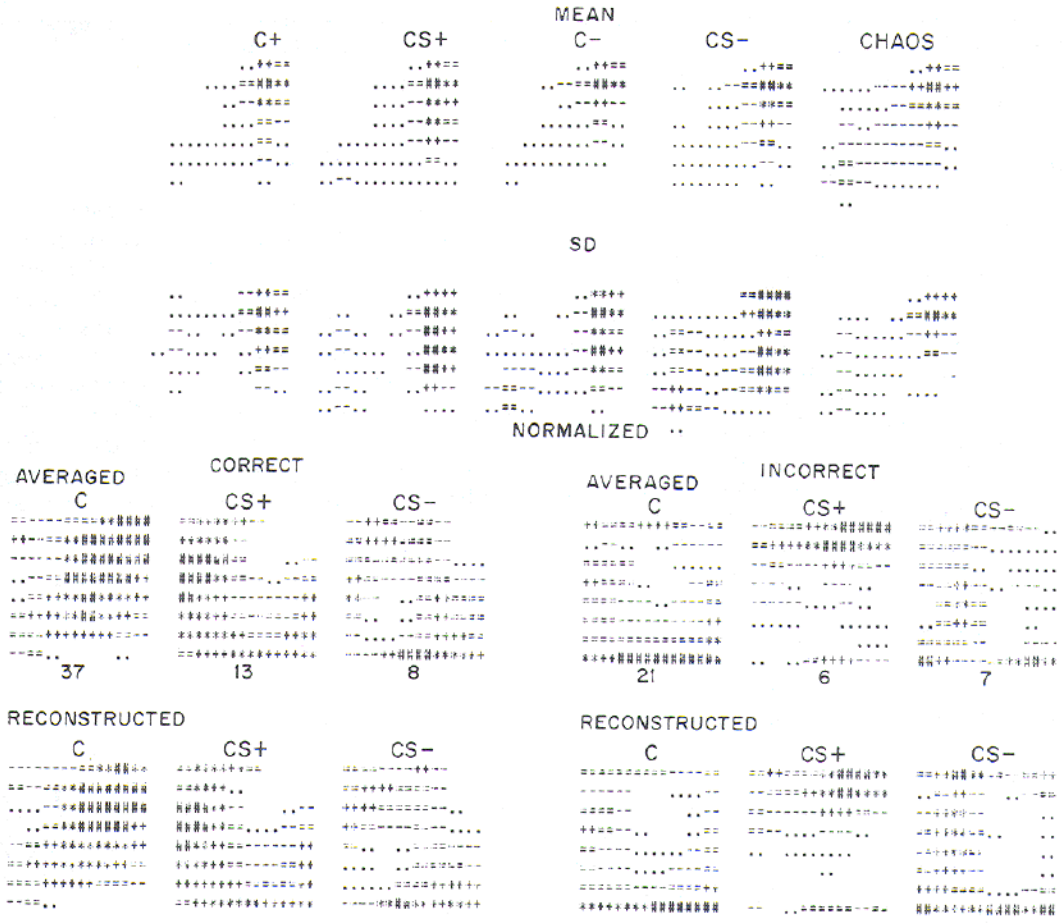

Figure 2. Density ploys (seven levels in descending order of amplitude: #, *, =, +, −, •, "blank space") from Subject 4. [Upper frames: Means and standard deviations of amplitudes (CHAOS refers to the disorderly bursts not subject to classification in respect to odors). Lower frames: Amplitudes normalized by channel and by group, with those correctly classified at left and those incorrectly classified by discriminant analysis (see bottom half of Table 7) at right. Bottom row: Patterns reconstructed from factor scores and loadings.]

Table 6
Differences Between Observed Patterns of Amplitude and Those Reconstructed From Sums of Factor Loadings

Subject	Stimulus			Response	
	C	CS+	CS−	Incorrect	No CR
1	0.60	0.46	11.93	14.08	6.23
2	2.56	5.92	3.78	11.61	10.20
3	2.67	5.32	5.48	18.14	12.60
4	5.19	3.66	8.22	12.05	7.59
5	17.49	10.01	10.05	20.81	14.27
M (Subjects 1–4)[a]	2.76	3.84	9.80	13.97	9.16

Note. Factor loadings were weighted by *F* scores, expressed as the percentage of residual variance. The smallest differences (for control C and odor CS+ electroencephalogram bursts) were associated with the highest rates of correct classification and of correct CRs. C = control (background) air; CS+ = lick-eliciting odor; CS− = sniff-eliciting odor; CR = conditioned response.
[a] Subject 5 was excluded from the mean because it did not acquire the discriminative CR.

reconstruction, which indicates that the factor analysis was of questionable value for its data. Comparable error values were found in a separate analysis of trials in which no or incorrect responses occurred. The average error (8%) was traced to their specific factor matrix, E.

Factor Patterns Over Sessions and Stages

Viana Di Prisco and Freeman (1985, Figure 7) demonstrated changes in spatial patterning with changes in S–R contingency. A multidimensional scaling technique (Sammon, 1969) was used to cluster control-burst amplitude patterns by stage. Cross-correlation of factor loadings within subjects across sessions and stages confirmed this result.

For each session i ($i = 1, \ldots, 18$), we performed a factor analysis in which we selected those six factor loadings with highest eigenvalue. Sign reversal and switching of columns in the matrix were designed to ensure analysis of compatible loadings. Cross-correlation of the resulting pair of six factors of each Session i with every other Session j yielded a 6×6 correlation matrix that was Fisher z transformed. The averaged value of the six diagonal elements was entered into position (i, j) of an 18×18 table maintained for each subject. Each position (i, j) in the table was a measure of the average correlation of factor loadings derived from Session i with those derived from Session j. The tables were averaged across subjects and are shown in Figure 3. Unit correlations on the diagonal were suppressed in plotting.

The within-stage loading correlation was higher than that between stages for each subject (Figure 4). This implied that the factor patterns were stable within stages, as suggested by the cross-classification results of Tables 2 and 3 for Sessions 4–6 in Stage I.

Changes in the factor patterns occurred between stages. The amount of difference was small. The within-stage values of the 18×18 table for each subject averaged 0.703, in comparison with 0.645 for between stages. The shared fraction of variance differed by 0.079 (0.495 − 0.416).

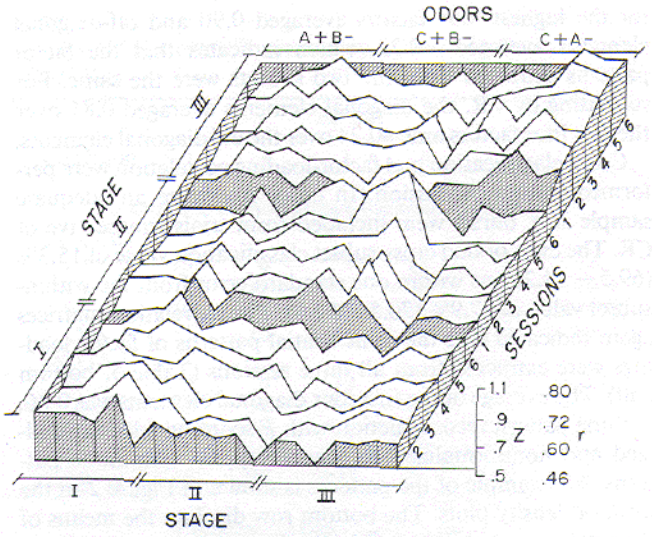

Figure 3. Comparison of factor loadings from each session with those from the other 17 sessions. [Each point is the average correlation expressed by Fisher's z over the first six factors (the diagonals in the bottom half of Table 5) and averaged over the 5 subjects. Each trace shows the mean correlation of the session designated at the left with the session shown on the abscissa.]

Discriminant Analysis

Validation of the results of the behavioral assay was done by linear discriminant analysis of the factor scores (Sessions 4–6 of Stage I). Various combinations of classes, discriminant functions, and normalization methods demonstrated that odor-specific bulbar spatial EEG patterns could be expressed and classified through factor analysis. We validated the behavioral assay that was based on Euclidean distances by classifying *F* scores of four classes (C+, CS+, C−, CS−) with three discriminant functions. The levels of classification achieved (Table 7, top half) were comparable with those from the behavioral assay (Tables 3 and 4). The order of ranking

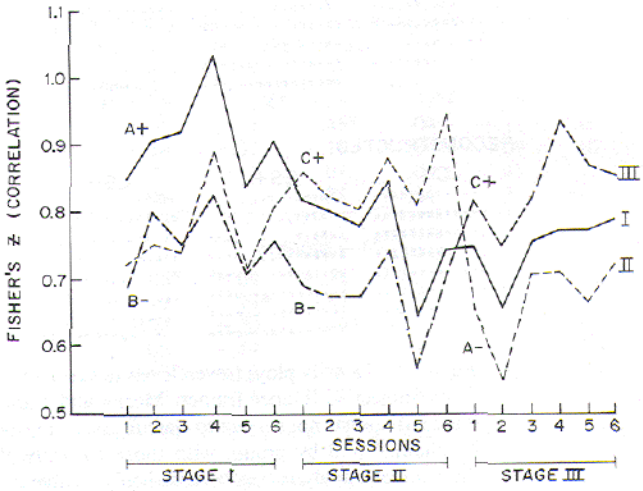

Figure 4. The data in Figure 5 averaged over the three stages.

Table 7
Classification by Discriminant Analysis of F Scores Into Groups

Trials	Subject 1 (n = 68)	2 (n = 88)	3 (n = 101)	4 (n = 103)	5 (n = 36)	M (Subjects 1–4)[a]
Four-group classification[b]						
C						52.8
No. correct bursts	21	20	23	13	3	
No. total bursts	28	35	47	37	7	
CS+						77.8
No. correct bursts	15	14	20	15	2	
No. total bursts	15	19	26	21	5	
C−						46.0
No. correct bursts	11	12	3	7	9	
No. total bursts	17	22	19	28	13	
CS−						67.4
No. correct bursts	7	10	5	9	9	
No. total bursts	8	12	9	17	11	
CS	93.8	78.5	66.2	62.2	61.0	72.6
C	69.9	55.8	32.4	30.1	56.1	49.4
% difference	23.9	22.7	33.9	32.1	4.9	23.2
Three-group classification[c]						
C						80.7
No. correct bursts	45	46	55	42	19	
No. total bursts	45	57	66	65	20	
CS+						86.1
No. correct bursts	15	17	19	17	4	
No. total bursts	15	19	26	19	5	
CS−						73.9
No. correct bursts	8	10	7	9	7	
No. total bursts	8	12	9	17	11	
% trials						
CS+	100.0	100.0	80.8	86.1	86.1	91.7
C	100.0	85.7	77.8	62.4	63.6	81.9
% correct	100.0	83.0	80.2	66.7	83.3	82.5

Note. C+ = control electroencephalogram (EEG) bursts during CS+ (lick-eliciting odor) trials; C− = control EEG bursts during CS− (sniff-eliciting odor) trials; CS = odor stimulus; C = control (background air) bursts including C+ and C−.
[a] Subject 5 was excluded from the mean because it did not acquire the discriminative CR.
[b] Classification to confirm the validity of the Euclidean distance behavioral assay.
[c] Classification to estimate the efficacy of classification into control and odor groups. Proportion (%) of trials with correct CRs are those on which at least one test EEG burst was correctly classified. n = total number of the bursts in Sessions 4–6 for each subject that were determined to be classifiable (Freeman & Viana Di Prisco, 1986).

of the subjects was not the same. Again, for the subject that failed behaviorally to discriminate CS odors, classification was near zero.

In pooling the C+ and C− groups, we used two discriminant functions to classify three groups. On the average, 82.5% of bursts were correctly classified (Table 7, bottom half) with roughly equal proportions of correct classification in the three groups. The procedure was repeated with a different set of two of the three control bursts, and the step of group normalization was omitted (Table 8, top half). In this case the percentage correct control bursts was not significantly affected, but the percentage correct fell to 74% for CS+ bursts and to 65% for CS− bursts. In an example in Figure 5, we compared the two sets of results for Subject 1. Without group normalization (left), the variance of the control group was greater than those of the CS groups because the amplitude of control bursts exceeded that of the odor bursts by up to threefold, by burst amplitude suppression upon odor presentation (Viana Di Prisco & Freeman, 1985). The wider scatter of the control bursts without group normalization decreased the resolution among bursts. This result showed that burst amplitude suppression on odor presentation did not contribute to odor discrimination.

Discriminant analysis without group normalization was done both on sets of trials with correct CRs and with no or incorrect CRs. The factor loadings from each trial set were used as "learning" and "test" sets to generate F scores by linear regression. The percentage of correct classification (Table 8, bottom half) for trials without correct CRs was lower than that for trials with correct CRs but still far above chance levels. The results from cross-classification showed that the same factors were present in both trial sets, although they were more clearly expressed in the trial set with correct CRs.

Last, discriminant analysis was done without group normalization on bursts from all trials and all 5 subjects in each session through all 18 sessions (Figure 6). Overall 73% of

Table 8
Classification of Electroencephalogram (EEG) Bursts by Discriminant Analysis of F Scores

EEG bursts	Subject 1	2	3	4	% correct
Correct CRs					
Control					
n	43	55	64	58	
Training	32	53	53	35	78.6
Test	30	51	55	34	77.3
CS+					
n	15	19	26	19	
Training	12	16	19	14	77.2
Test	11	15	16	11	67.1
CS−					
n	8	12	9	17	
Training	5	7	5	12	63.0
Test	5	3	5	11	52.2
Incorrect or no CRs					
Control					
n	28	21	13	14	
Training	16	21	32	3	67.9
Test	22	19	31	10	77.4
CS+					
n	2	6	4	3	
Training	2	5	3	0	66.7
Test	1	4	3	0	53.3
CS−					
n	14	5	28	6	
Training	11	4	17	4	67.9
Test	18	4	16	2	75.5

Note. CR = conditioned response; CS+ = lick-eliciting odor; CS− = sniff-eliciting odor. In training sets, the same factor loadings were used: in test sets, different factor loadings were used.

bursts were correctly classified. The highest rate was 80.1 ± 9.1% for control bursts; CS+ and CS− bursts were correctly classified 66.2 ± 8.2% and 64.8 ± 9.0%, respectively.

These odor-burst correct classification rates were higher than the rates previously determined (Viana Di Prisco & Freeman, 1985, Figure 2) for CR+ (jaw movement) and CR− (respiratory rate), which were 45.2 ± 9.6% and 57.0 ± 11.3%, respectively. A noteworthy feature of these graphs was downward trends over sessions for both the percentage correct CS+ rate and the percentage correct CR+ rate. The correlation between these rates (averaged via Fisher's z over subjects) was .54 ($p < .01$). The percentage correct CR− rate similarly declined, but the percentage correct CS− rate did not (r = .16, *ns*). Apart from the inferior performance of Subject 5 after Session 3 in both CS and CR classification rates, there was no significant relation among subjects in respect to these rates. The fifth subject did consistently respond to both odors with sniffing, and the control bursts were distinguished from odor bursts by discriminant analysis, but the CS+ and CS− odor bursts were not distinguished from one another.

Stepwise Linear Discriminant Analysis

To verify independently the finding of odor-specific EEG patterns, the 64-amplitude dominant component data were subjected to linear stepwise discrimination. The three classes (C+ and C− combined, CS+, and CS−) were pooled and normalized by channel to remove the signature pattern (Stage I, Sessions 4–6). Each burst was then normalized to zero mean and unit standard deviation to standardize group variance.

Data and jackknifed total classification rates showed a characteristic function of the number of variables used. When the best single variable was used, these rates differed by 1% or less and ranged from 49.2% to 72.4% for the subjects showing discriminative responding. For the remaining subject, the data and jackknifed rates were 70.3% and 61.9%, respectively. For all subjects, the best single variable typically pulled control bursts apart from odor bursts, with random CS+ and CS− (combined) classification. When the number of variables increased (up to 16), the data rate increased steadily, but with diminishing increments. A plateau was typically reached by the 10th variable entered. The jackknifed rate behaved similarly but reached its plateau near the optimal number of variables. Across subjects with discriminative responding, the percentage increase in data and jackknifed classification rates with the optimal set of variables with respect to the single best was 15.68 ± 6.6% and 11.74 ± 8.1%, respectively. For the remaining subject, the increases were 19.35% and 28.79% for data and jackknifed rates. Inspection revealed that the high rates for this subject were misleading because the CS− bursts were classified at rates expected of random classification (i.e., 33% correct). This finding motivated the criterion for optimal variable selection that correct classification for every group exceed 50%.

For these data sets, the optimal number of variables was between 3 and 7, across subjects. Data classification rates for the subjects showing odor discrimination were 71.8 ± 14.0% for control bursts, 79.7 ± 14.0% for CS+ bursts, and 64.2 ± 6.0% for CS− bursts. Jackknifed classification rates were 69.4 ± 12.0%, 73.0 ± 14.0%, and 61.6 ± 8.0%, respectively (Table 9). The subject that did not show discriminative responding had data rates of 88.5% (C), 73.9% (CS+), and 62.5% (CS−). Jackknifed rates showed that CS− classification was nearly random at 37.5%, whereas C and CS+ classification remained high (86.2% and 70.0%, respectively). The variables selected for each subject were distributed across the entire array. For one of the "discriminating" subjects, two pairs of the seven optimal variables had adjacent positions on the array; the remaining three were widely scattered. These results were consistent with those obtained with factor analysis showing that EEG information for odor-pattern discrimination was distributed across the entire array.

The data sets used in the stepwise analysis were similar, but not identical to those used for factor analysis. They differed in the number of bursts per group; all information extraction and normalization procedures were identical. Factor analysis with these sets gave results similar to those in Table 8 (bottom half). A comparative study of several parametric and nonparametric techniques applied to our data appears elsewhere (Grajski et al., 1986); the results and conclusions conformed to those reported here.

Discussion

Findings and Limitations

The main finding in this study is the existence of stable and reproducible spatial patterns in the EEG that relate to the

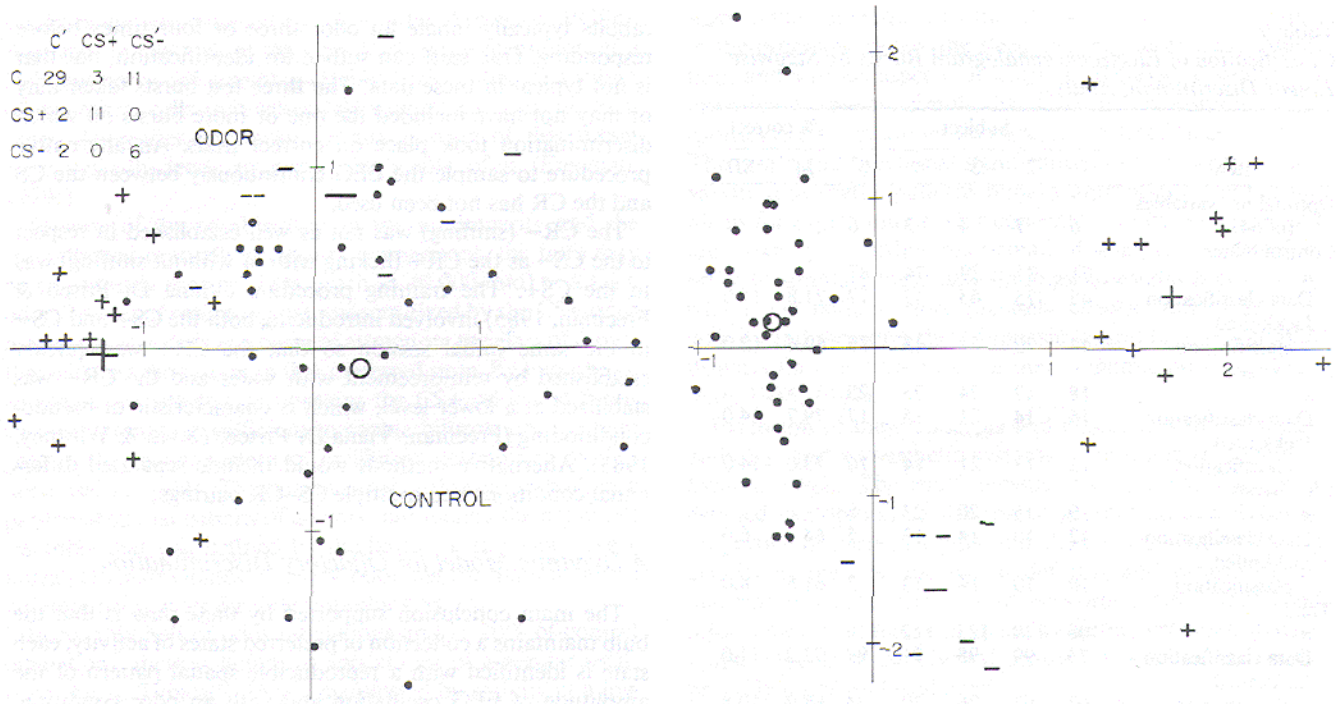

Figure 5. Results of discriminant analysis of factor scores from Subject 1 with two discriminant functions for three groups, without (left) and with (right) group normalization.

three odor conditions established by conditioning with odor CSs. These patterns were reformulated by factor analysis of the amplitudes of oscillatory EEG segments recorded from electrode arrays. The loadings of a small number of factors were essentially invariant over sessions in which S–R contingencies were fixed, and they changed when a new behavioral response pattern was introduced. These patterns were evident in all CS trials. Resolution was higher on trials with correct CRs than on trials with incorrect CRs, as quantified by the behavioral assay and discriminant analysis.

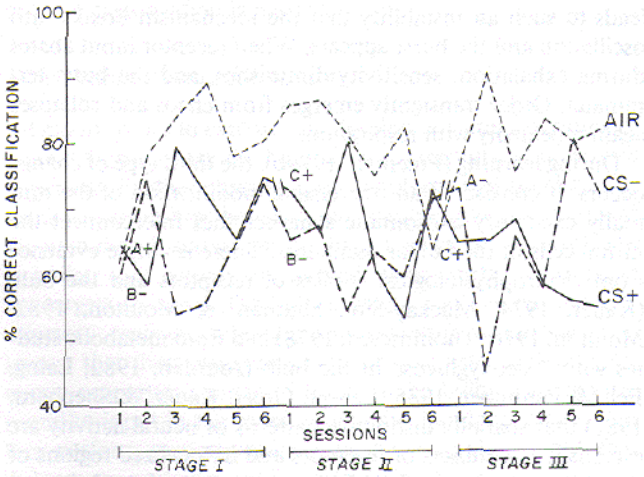

Figure 6. Percentage of correct classification by groups (control C or air, odor CS+, and odor CS– bursts) within sessions averaged over 5 subjects. [For comparison with CR+ (jaw movement) and CR– (respiratory) rates of responding, see Viana Di Prisco & Freeman, 1985, Figure 2. The symbols A+, A–, B–, and C+ refer to the three odors and reinforcement conditions.]

The factor patterns extended over the entire array. By inference, the neural activity patterns extend over the entire main bulb. In themselves the factors appear to have no physiological meaning in our data; there was no apparent relationship between each factor and each odor state. The mean factor scores were positive and negative in varying combinations, which suggests that the loadings serve to express sets of invariant spatial patterns statistically but that they have not converged onto functional entities. The spatial patterns corresponding to the neural activity distributions of odor states appeared only in the weighted sums of the loadings when multiplied by the factor scores. The factor scores served to classify correctly 65–80% of the EEG segments that were used to derive the factor loadings.

As an independent check, a stepwise linear discrimination procedure was performed on 64-amplitude dominant component data. From three to seven variables sufficed to correctly classify (jackknifed rate) 62–73% of bursts by group. This is an improvement of nearly 100% in comparison with random class assignment (33% correct), and it lies within one standard error of classification with factor scores. The scattered locations of channels selected confirmed that odor-specific information in the EEG is distributed across the entire array.

These performance ranges reflect, in part, limitations imposed by the recorded data and behavioral training. The surface area of the rabbit olfactory bulb is on the order of 100 mm^2, whereas the arrays cover from 12 mm^2 to 16 mm^2. If

Table 9
Classification of Electroencephalogram Bursts by Stepwise Linear Discriminant Analysis

Item	Subject 1	2	3	4	5	% correct *M*	*SD*
Optimal no. variables (of 64)	6	7	4	3	6		
Control bursts							
n	71	87	79	74	87		
Data classification	45	75	63	43	77	71.8	14.0
Jackknifed classification	44	70	61	43	75	69.4	12.0
CS+ bursts							
n	18	17	24	25	23		
Data classification	16	14	21	15	17	79.7	14.0
Jackknifed classification	13	13	21	14	16	73.0	14.0
CS− bursts							
n	19	15	20	23	8		
Data classification	12	10	14	13	5	64.2	6.0
Jackknifed classification	10	10	14	13	3	61.6	8.0
Total							
n	108	119	123	122	118		
Data classification	73	99	98	71	99	72.2	11.0
Jackknifed classification	67	93	96	70	94	68.9	10.8

Note. CS+ = lick-eliciting odor; CS− = sniff-eliciting odor. The jackknifed rates are obtained by means of successively leaving out single bursts in the calculation of group means and variances; it serves to cross-validate the data classification rate. The *M* and *SD* are for Subjects 1–4.

odor-specific activity patterns cover the entire main bulb, then the sample derived from the array incorporates only one sixth to one eighth of the whole.

Furthermore, the spatial grain of the array (spacings between electrodes) is 0.5–0.6 mm. The glomerular layer imposes a spatial grain of 0.25 mm on bulbar inputs from the primary olfactory nerve (PON). Therefore, after spatial deconvolution, each electrode measures activity of a neighborhood of four to eight bulbar "columns." Fine pattern differences cannot be resolved. Volume conduction properties of the granule cell generator result in smoothing of high spatial frequencies in activity patterns. There is tenfold attenuation with each increment of 0.5 c/mm. At the spatial frequency of the glomeruli (2 cycles/mm), the attenuation is 10^{-4}. Much of the detail in neural activity patterns is irretrievably lost in the EEG by smoothing. It is quite unlikely that any components above 0.6–1.0 cycles/mm can be recovered from the bulbar EEG.

The oscillatory burst may be as brief as 60 ms or may last several hundred milliseconds, depending on respiratory rate. A fixed segment duration of 76 ms was imposed here mainly for convenience in data processing. This may have been inappropriate for some bursts because it may have been improperly centered with respect to information content. However, this brevity provides an advantage in respect to sampling during each trial. The time interval between odor onset and licking (the CR+) varies between 0.25 s and over 2 s with a mean of 0.88 s. At respiratory rates of 4–5 s, the rabbits typically inhale an odor three or four times before responding. One sniff can suffice for identification, but that is not typical in these data. The three test bursts taken may or may not have included the one or more bursts on which discrimination took place on correct trials. An alternative procedure to sample the EEG continuously between the CS and the CR has not been used.

The CR− (sniffing) was not as well established in respect to the CS− as the CR+ (licking with or without sniffing) was to the CS+. The training procedure (Viana Di Prisco & Freeman, 1985) involved introducing both the CS+ and CS− in the same initial session so that the CR+ was quickly established by reinforcement with water and the CR− was stabilized at a lower level, which is characteristic of pseudoconditioning (Freeman, Viana Di Prisco, Davis, & Whitney, 1983). Alternative methods would include separated differential conditions and multiple CS–CR pairings.

A Dynamic Model for Olfactory Discrimination

The main conclusion supported by these data is that the bulb maintains a collection of preferred states of activity; each state is identified with a reproducible spatial pattern of the amplitude of EEG oscillation and with an odor condition. The bifurcation or switching of the bulb from one preferred state to another requires a change within the neural system, not merely in the input. Three types of change are of paramount importance for bulbar function. One is an increase in the basal level of activity of the bulb that is analogous to an increase in the temperature of a physical or chemical system. This aspect is under centrifugal control by pathways effecting changes relating to increasing arousal and motivation (Freeman, 1975). The second is an increase in the sensitivity of the bulbar neurons; it is caused by any excitatory input to the bulb from receptors. This coupling renders the bulbar dynamics nonlinear (Freeman, 1979a); with each inhalation, the bulb is excited and sensitized. The increased feedback gain leads to such an instability that the mechanism breaks into oscillation and the burst appears. When receptor input abates during exhalation, sensitivity diminishes, and the burst terminates. Order transiently emerges from chaos and collapses again repeatedly with respiration.

During learning (Freeman, 1979b), the third type of change occurs. It consists of an irreversible modification of the mutually excitatory axosomatic synapses that interconnect the mitral cells of the bulbar oscillators. There is ample evidence from electrophysiological studies of receptors and the bulb (Kauer, 1974; Mackay-Sim, Shaman, & Moulton, 1982; Moulton, 1976; Thommesen, 1978) and from metabolic studies with 2-deoxyglucose in the bulb (Jourdan, 1982; Laing, Bell, & Panhuber, 1985; Lancet, Greer, Kauer, & Shepherd, 1982) that spatially distinctive patterns of neural activity are established in subsets of receptors and in localized regions of the glomerular layer of the bulb by exposure of nonbehaving animals to selected odors. By hypothesis, during presentation of a CS+ odor there is coactivation of numerous and overlapping pairs of mitral cells by selectively responsive receptors. Under reinforcement that involves the release of norepinephrine into the bulb (Gray, Freeman, & Skinner, 1986), these

synapses are strengthened by up to 40% (Freeman, 1979b). Repeated inhalations of the CS+ lead to the formation of a Hebbian nerve cell assembly (Hebb, 1949)—that is, a subset of the mitral cells that selectively excite and re-excite each other. Thereafter, excitation of any portion of this subset stereotypically tends to excite the whole of it (Freeman, 1979c).

Because of the combination of the nonlinearity and the strengthened mutually excitatory connections, the bulb may be enormously sensitized (as much as 40,000-fold) to a CS+ odor. The set of receptors that was sensitized by the CS+ odor during training defines a basin of attraction: the class of inputs that will lead the system to that preferred state. By hypothesis, whenever the inhaled air contains the CS+ odor and motivational strength is sufficient to enable bifurcation, the bulb goes to the spatial pattern of oscillation determined by that nerve cell assembly. The output involves the entire bulb in a particular spatial pattern of activity, not merely the nerve cell assembly that was defined by the basin. In this view, every mitral cell participates in every odor discrimination but at different firing rates for different odor CSs.

In roughly half of odor inhalations and in 20% of control inhalations, there is failure of appearance of a regular oscillatory burst. Typically, this is manifested by activity at a low frequency with strong modulation or at multiple frequencies, as though masses of oscillators in the bulb had failed to converge to a common mode, and competing modes of oscillation were engaged in an erratic tug of war with a low average frequency. Almost invariably this pattern appears on presentation of a novel odor that leads to an orienting response. Therefore the disorderly or chaotic bursts may serve the role of reporting failures of convergence, leading to retesting by sniffing and thereafter to habituation or formation of a new preferred pattern or updating of an existing one, depending on the absence or presence of reinforcement. However, the 50% failure rate during CS odor testing seems intuitively to be excessive, and so further study of the criteria of burst classification is needed.

New Problems and Directions

Opportunities to explore and develop our understanding of brain dynamics with the help of these concepts lie in several directions. Further physiological and pharmacological studies on the relationships between the spatiotemporal patterns of the granule cell activity in the EEG and those of mitral cells in bulbar unit activity are needed, as are further studies on the targets to which the bulb projects, such as the anterior olfactory nucleus, tubercle, and prepyriform cortex. It is known that these structures have neural, structural, and dynamic properties similar to those of the bulb, that they respond to input in the manner of active bandpass filters, that they perform spatiotemporal integration on their input, that they are connected by feedback to each other and to the bulb, and that they undergo changes in activity patterns with learning that are comparable with those changes in the bulb (Freeman, 1975; Bressler, 1984, 1987a, 1987b). Their physiological and behavioral functions are largely undefined (Freeman, 1987). The mechanisms of the several centrifugal pathways to the bulb require further study, particularly in relation to the processes underlying sleep, arousal, motivation, attention, and various aspects of learning. Behavioral studies on orienting to novel stimuli, habituation, acquisition of responses to odor mixtures, and selective extinction are needed. The origin and functional significance of the between-session variation in spatial patterns remain unresolved. The mechanisms for expression of odor concentration by bulbar output are unknown. Further mathematical analysis is needed in order to simulate these new findings, to establish criteria by which one defines more precisely chaotic and limit cycle activity and measures their dimensions, and to devise graphic displays for comprehension of their dynamic portraits (Freeman, 1986, 1987).

Extension of these concepts and procedures to the visual, auditory, and somesthetic systems is desirable (Freeman & Skarda, 1985). The most pressing requirement for this is detailed exploration of the spatial geometries and dynamic properties of cortical EEGs and their correlative multiunit activity as the best means for defining and measuring the macroscopic state variables of neocortex. Until that solid information base has been made available, proposed macroscopic models of neocortical sensory processing cannot be properly tested and evaluated.

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