SPATIAL ORGANIZATION OF EEGS FROM OLFACTORY BULB AND CORTEX

STEVEN L. BRESSLER

Department of Physiology-Anatomy, University of California, Berkeley, CA 94720 (U.S.A.)

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The concept of 'wave packet' has been advanced by Freeman (1975, 1981) to mean a 'coherent pattern of neural activity' in the olfactory bulb. Implicit in this definition is the idea that olfactory EEGs display a high level of wave form similarity across the spatial extent of the bulb. Limited focal regions have been studied in the bulb within which EEG activity is spatially distributed as a common wave form with differences in amplitude and phase depending on location (Freeman 1978a). This study presents evidence that EEGs sampled from the entire rabbit olfactory bulb are highly similar, as are EEGs from a large portion of the prepyriform cortex.

Neural activity in the olfactory bulb is detected as a 35–85 c/sec sinusoidal burst in the EEG (Adrian 1950). Bulbar activity is transmitted to the prepyriform cortex by pulse activity in mitral cells, whose axons leave the bulb to form the lateral olfactory tract (LOT) which terminates in the cortex. Pulse activity on axons in the LOT is synchronized with the bulbar EEG. The density of pulses in the LOT provides oscillatory input to the cortex at the same frequency as the bulbar burst (Freeman 1975). During states of behavioral arousal, bulbar burst amplitude is greatest, and similar bursts appear concurrently in the cortex (Fig. 1).

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1 Supported by Grant MH06686 from the National Institute of Mental Health to Walter J. Freeman.
2 Present address: EEG Systems Laboratory, 1855 Folsom Street, San Francisco, CA 94103, U.S.A.

Fig. 1. Concurrent EEG records from 2 bulbar and 2 cortical electrode sites, demonstrating the effect of arousal as increased burst amplitude. Here arousal was brought about by odor stimulation, but the effect can also be produced through other sensory modalities.

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This report presents findings on the similarity among EEGs recorded from a spatial distribution of sites in the bulb, among EEGs from another such distribution in the cortex, and between bulbar and cortical EEGs. The results indicate that: (a) EEGs from spatially distributed sites in the olfactory bulb display a high level of concomitant variation with an overall uniformity in frequency composition, (b) cortical EEGs are also highly correlated and show uniform frequency, and (c) bulbar and cortical EEGs have two common frequency components.

Methods

(1) Procedures

Electrodes were chronically implanted at multiple sites of the bulb and cortex of 4 rabbits. The goal in the arrangement of electrodes was a representative sampling of activity from bulb and from cortex.

Placement of 9 tungsten microelectrodes in the depth of the bulb was guided by the antidromic evoked potential response to electrical stimulation of the LOT. Maximizing the amplitude of the initially positive peak assured that the electrode tip passed the zero-isopotential plane, which is approximately at the mitral cell body layer (Freeman 1975). Electrodes were situated 2 mm apart at a depth of 2–5 mm from the dorsal surface (6–8 mm total depth).

The spatial distribution of activity in the cortex, which has a sheet-like structure, was sampled with a surface electrode array. Cortical EEGs were recorded from 60 electrodes in an array (4.0 mm × 7.2 mm) on the epidural surface, covering approximately three-quarters of the frontal olfactory cortex (Fig. 3). The necessity of adequately sampling cortical activity, using such an array, required removal of the orbital contents under deep pentobarbital anesthesia (protocol approved by Committee for Animal Protection, University of California, Berkeley). This was followed by resection of the medial wall of the orbit with a drill (Freeman 1978a). A 10 × 6 rectangular array of electrodes (300 μm stainless steel wires embedded in dental acrylic at 0.8 mm spacing) was placed epidurally on the surface of the cortex. Following implantation of the array, the orbital tissue was tightly closed around the dental cement holding the array, sealing the wound to prevent infection. Animals were kept in a stable, healthy condition for long periods after surgery (some for longer than 2 years).

Recording began 5–10 days postoperatively and continued weekly for 6–8 weeks. Animals were held in a restraining harness in a quiet room. A cone placed over the muzzle delivered a constant filtered air supply. EEGs were amplified and filtered with pre-amplifiers set at a 10–300 Hz bandwidth. They were multiplexed and digitized sequentially across channels with a 10 μsec delay between channels for each time bin. The digitizing interval (dt) between time bins was 1.0 msec.

All EEG records were examined off-line on a visual display monitor connected to an Interdata 7/16 computer. High amplitude bursts, 75–200 msec long, were selected for processing on a CDC 6400 computer. For ease of computation in later processing, the amplitude of each burst was normalized to zero mean and unit standard deviation by performing the following operation:

\[
f(t) = \left( f(t) - \mu_T \right) / \sigma_T;
\]

for \( t = 0, T - 1 \)

where \( f(t) \) was the unnormalized amplitude value, \( T \) was the burst duration, \( \mu_T \) and \( \sigma_T \) were the mean and standard deviation of amplitude over \( T \) and \( f(t) \) was the normalized amplitude value.

The term ‘burst’ will be used to describe the oscillatory waveform recorded at a single olfactory site. The term ‘burst ensemble’ will designate the collection of bursts recorded during the same period from the spatial distribution of sites in either the bulb or cortex.

(2) Measurement of cross-correlation

Two methods, cross-correlation and spectral analysis, were used to determine the degree of spatial variation of the burst ensemble within the bulb and within the cortex. The first method is discussed in this section and the second method will be presented in the next section.

The product moment correlation coefficient (PMCC), which was the value of the cross-correla-
tion function at zero lag, was employed as a linear estimate of concomitant variation of activity among the bursts of an ensemble (Marmarelis and Marmarelis 1978). First, the average burst of the ensemble was calculated as:

$$E(t_j) = \left(\frac{1}{N}\right) \sum_{i=0}^{N-1} f_i(t_j) \text{ for } j = 0, \ldots, T - 1$$

(2)

where $E(t)$ was the average burst of the ensemble, $f_i(t)$ (i = 1, N) were the N individual normalized bursts, and T was the burst duration.

Then each burst in the ensemble was cross-correlated with the ensemble average at zero lag to give a value of PMCC for that burst. (This procedure avoided having to compute the PMCC for each of the 36 bulbar or 1770 cortical pairs of bursts.) The PMCC between each channel, i, and the ensemble average was computed as:

$$C_i(0) = \left(\frac{1}{T}\right) \sum_{j=0}^{T-1} f_i(t_j) E(t_j) \Delta t, \quad -1 < C_i(0) < 1$$

(3)

where $\Delta t$ was the digitizing interval. PMCC values were Fisher z-transformed to normalize their distribution. All PMCC means and standard deviations reported here were re-transformed to a range of −1 to 1. The mean of the set of PMCCs corresponding to a burst ensemble measured the degree of concomitant variation exhibited by the bursts in the ensemble.

(3) Measurement of power spectra

The second method employed to analyze the extent of spatial variation in the burst ensemble was spectral analysis. Autospectra of bulbar and cortical bursts were obtained from the Fourier transform of their autocorrelation function. Burst frequency was defined as the frequency at the peak of the autospectrum. The equation for the autospectrum was:

$$S_e(\omega) = \frac{2A(\tau_m)}{\Delta\tau} \left[ A(0) + \sum_{i} \cos(\omega \tau_i) \right]$$

$$+ A(\tau_m) \cos(\omega \tau_m)$$

(4)

where $A(\tau)$ was the autocorrelation function, $\omega$ was frequency, $\Delta\tau$ was the lag interval used in computation of $A(\tau)$, $m$ was the maximum number of lags used, and $\tau_m$ was the maximum lag used. A ‘Hamming’ window was employed to reduce side lobes (Blackman and Tukey 1959).

An example is shown (Fig. 2, smooth line) of an autospectrum produced from a representative burst (100 msec long, 1 msec dt). Superimposed (Fig. 2, dashed line) is the autospectrum of a sinusoidal wave form (also 100 msec long, 1 msec dt) with the same frequency (56 c/sec) as the peak of the burst autospectrum. Both spectra are characteristic of broad due to the limited sample duration. The close similarity between the two autospectra shows the highly sinusoidal nature of the olfactory burst.

The similarity of bursts to pure sinusoids was further substantiated by determining the peak frequency of a burst spectrum, and then cross-correlating the burst with a pure sinusoid of frequency equal to that peak frequency. The maximum value of the cross-correlation function measured the similarity of the two wave forms. The re-transformed sample mean of 200 Fisher z-transformed maximum cross-correlation values was 0.91 (+ 0.05, −0.10), larger than that obtained from two pure sinusoids differing by only 3 c/sec at any frequency from 35 to 85 c/sec. Thus, on the average, olfactory bursts were closely similar to pure sinusoids.
Fig. 3. Concomitant EEGs of a burst ensemble, recorded in a waking rabbit from a 6 × 10 electrode array placed over the left olfactory cortex. The array dimensions were 40 mm × 7.2 mm, with interelectrode spacing of 0.8 mm. Left side is anterior, top is dorsal. Duration of record: 75 msec. Vertical calibration: 1 mm equals 50 μV.

Results

1) Intrabulbar relations

Mean Fisher z-transformed PMCCs were calculated for each of a sample of 160 burst ensembles from 4 rabbits. After re-transformation, the grand mean for the sample was 0.85 ± 0.03. The peak autospectral frequency of each burst in the burst ensemble was measured to determine the degree of spatial variation of burst frequency (frequency divergence) in the bulb. Peak frequencies were measured at 9 sites for a sample of 120 burst ensembles from 4 rabbits. For each burst ensemble, the mean and standard deviation of peak frequency across sites were calculated. The grand sample mean of the ensemble mean frequencies was 63 ± 10 c/sec. The grand sample mean of the ensemble standard deviations (i.e., the mean spatial standard deviation) was 3 ± 2 c/sec. Therefore the mean standard deviation over space (3 c/sec) was 30% of the standard deviation across the sample (10 c/sec).

From a sample of 125 burst ensembles, 43% of the ensemble showed, in addition to the 35–85 c/sec peak, a peak in the 15–35 c/sec range on at least one electrode out of 9. (In this sample only two bursts had spectra showing a 15–35 c/sec peak without a concomitant 35–85 c/sec peak, and then only at one electrode site.) The mean peak frequency ratio of the 15–35 c/sec to the 35–85 c/sec peak from a sample of 100 autospectra which clearly showed both components was 0.35 ± 0.05.

2) Intracortical relations

As in the bulb, the spatial variability of the cortical burst pattern was examined in two ways. The first method was by cross-correlation of each of the 60 individual bursts with the ensemble average. Re-transformed PMCCs for most bursts were greater than 0.9 at all sites, indicating a high degree of uniformity across the array. Careful examination of the wave forms which gave low PMCCs failed to show oscillations at different frequencies. Low PMCC values were primarily due to the absence of burst activity at sites at the edges
of the array which were not on the cortex. The mean PMCC was computed for each of a sample of 160 burst ensembles from 4 rabbits. The retransformed grand sample mean was $0.94 \pm 0.02$.

The second method, spectral analysis, was employed to test the apparent wave form uniformity over the array. Burst ensembles with mean frequencies (calculated across electrode sites) throughout the 35–85 c/sec range were examined. Spectral analysis was performed for all 60 electrode sites on 85 burst ensembles sampled from 4 rabbits. The grand sample mean of the ensemble mean frequencies was $56 \pm 6$ c/sec. The grand sample mean of the ensemble standard deviations was $2 \pm 2$ c/sec. As in the bulb, the standard deviation over space (2 c/sec) was roughly one-third of the sample standard deviation (6 c/sec).

The 15–35 c/sec component was more prevalent in the cortical EEG than the bulb. Autospectra at all 60 electrode sites were determined for a sample of 60 cortical burst ensembles from 4 rabbits. 90% of the burst ensembles had 15–35 c/sec activity at one or more sites. The mean ratio of 15–35 c/sec to 35–85 c/sec frequencies was $0.38 \pm 0.10$. Unlike the bulb, 9 burst ensembles out of the 60 had at least one site which showed the 15–35 c/sec component without a 35–85 c/sec component.

(3) Relations between olfactory bulb and cortex

A sample of 50 bulbar and cortical concurrent burst ensembles was taken from 4 rabbits. The largest amplitude burst from the bulbar burst ensemble and from the cortical one was selected for spectral analysis. The mean peak frequency of the bulbar autospectra was $61 \pm 11$ c/sec, and of the cortical autospectra $58 \pm 11$ c/sec. On the average the cortical frequency was lower than the bulbar by $3.0 \pm 6.8$ c/sec.

Autospectra of concomitant bursts in bulb and cortex were sampled to determine the relative occurrence of the 15–35 c/sec component in the two structures. There was no apparent relation between the number of sites showing 15–35 c/sec activity in the bulb and cortex. For a sample of 42 burst ensembles from 4 rabbits, there were 29 cases in which a 15–35 c/sec peak appeared in the cortical spectrum and not in the bulb (Fig. 4). However, no cases were observed of 15–35 c/sec activity in the bulb without any in the cortex.

Discussion

The spatial characteristics of the burst ensemble in the bulb have been described for a region comprising roughly 15% of the total surface area in the rabbit (Freeman 1978a), with electrode spacings (0.5 mm) at the limit of resolution of bulbar EEG spatial frequency (1 c/mm) (Freeman 1978b). In the present study, EEGs were recorded from a set of depth electrodes distributed so as to give a sample from the entire bulb at lower spatial resolution (2 mm separation). The results of this study indicated a high level of concomitant variation and a uniformity of frequency for electrode sites distributed throughout the bulb. This finding is consistent with the concept of 'wave packet' as proposed by Freeman (1975, 1981). Minimum interelectrode separations of 2 mm were employed. This ensured that volume conduction from one electrode site to its neighbor could be ruled out as a source of this uniformity since the point spread function undergoes a sharp falloff at around 0.5 mm (Freeman 1978b). Frequency variation between sampled burst ensembles was approximately 3 times greater than the mean frequency diver-
gence over the spatial extent of the bulb. Thus there was a greater spatial similarity across a single burst ensemble than between ensembles at different times.

In the cortex, too, the burst was found to behave as a spatially coordinated event, consistent with the ‘wave packet’ concept. Contour maps of the PMCC revealed a high degree of similarity among traces from the array. Spectral analysis demonstrated a uniformity in frequency across the array for the individual burst ensemble. As in the bulb, there was greater frequency variation between ensembles in a sample than within ensembles over space.

The greater extent of the bulbar sampling region may have been responsible for the bulb having lower mean PMCC and larger frequency divergence than the cortex. (Bulbar bursts, recorded from the depth rather than the surface, were of greater amplitude than cortical bursts. Therefore this result was not due to a greater error of measurement for the bulb.) These findings are consistent with the report of Livianov (1977) that spatial synchronization of electrical activity between two recording electrodes in the rabbit neocortex decreases with increasing interelectrode distance.

The existence of the 15–35 c/sec secondary component in the cortical EEG of cats has been previously reported (Freeman 1960). The ratio of frequencies of the dominant to the secondary component was 0.38 in the present study, whereas in the report of Boudreau and Freeman (1963) for the cat, the secondary peak was consistently found to be 0.55 (10% greater than the calculated half-harmonic of the dominant peak).

There is prior evidence that the 15–35 c/sec rhythm is generated in the cortex. Becker and Freeman (1968) reported that cortical 15–35 c/sec activity persisted after, bulb and cortex having been undercut from the rest of the brain, the bulb was subsequently removed. Freeman (1975) thereafter proposed that the 15–35 c/sec oscillation represents the output of the cortex to other forebrain structures. The present study has confirmed that this component is present in the cortical signal of the rabbit, and has also established its presence in the bulb. Furthermore, its presence has been detected in the cortex while not in the bulb, but not in the bulb without also being present in the cortex. Several authors have described an anatomical feedback pathway, passing deep to the LOT, by which the cortex projects to the bulb (Broadwell and Jacobowitz 1976; Dennis and Kerr 1976; and De Olmos et al. 1978). I therefore propose that the cortex generates the 15–35 c/sec rhythm which is transmitted to the bulb by this feedback pathway. Further testing of this hypothesis could be accomplished by measuring the change in frequency composition of the bulbar and cortical spectra following lesion of the feedback pathway to the bulb, leaving the LOT intact.

Summary

This report presents evidence for the concept of ‘wave packet’ (Freeman 1975) in the olfactory system. EEG bursts recorded from electrodes chronically implanted at multiple sites in the olfactory bulb and cortex in awake rabbits were spatially coherent, iso-frequency events. Both bulbar and cortical bursts were composed of a major oscillation in the 35–85 c/sec range. The dominant cortical frequency was within 5% of that of the bulb. A secondary oscillation in the 15–35 c/sec range was found in both bulb and cortex. This was thought to represent a feedback signal of the cortex to the bulb.

Résumé

Organisation spatiale de l’EEG du bulbe olfactif et du cortex

Cette étude présente une preuve du concept ‘de paquets d’ondes’ (Freeman 1975) dans le système olfactif. Des décharges EEG enregistrées à partir d’électrodes implantées chroniquement dans de multiples sites du bulbe olfactif et du cortex de lapins éveillés ont constitué des événements spatialement cohérents et iso-fréquentiels. Tout à la fois les décharges provenant du bulbe et celles venues du cortex étaient composées d’une oscillation majeure dans la bande 35–85 c/sec. La fré-
quence corticale dominante se situait dans une marge de 5% de celle du bulbe. Une oscillation secondaire vers 15–35 c/sec était recueillie dans le bulbe et sur le cortex. On peut penser qu'elle représente un signal en feedback du cortex vers le bulbe.

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References