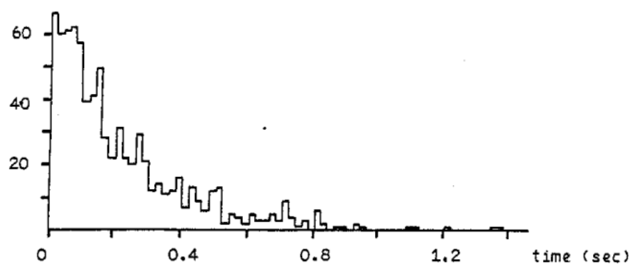


**Figure 3.5** A histogram of waiting times between spontaneously occurring small voltage changes in a muscle cell due to activity in a neighbouring nerve cell. From Fatt and Katz (1952).

between such events. According to the Poisson assumption, the waiting time should have an exponential density which is seen to be a good approximation to the observed data. This may also be rendered more precise with a $\chi^2$ goodness of fit test. For further details see Van der Kloot *et al.* (1975).

## 3.6 POISSON POINT PROCESSES IN TWO DIMENSIONS

Instead of considering random points on the line we may consider random points in the plane $\mathbb{R}^2 = \{(x, y) | -\infty < x < \infty, -\infty < y < \infty\}$, or subsets thereof.

**Definition** **A point process $N$ is an homogeneous Poisson point process in the plane with intensity $\lambda$ if:**

**(i) for any subset $A$ of $\mathbb{R}^2$, the number of points $N(A)$ occurring in $A$ is a Poisson random variable with parameter $\lambda|A|$, where $|A|$ is the area of $A$;**
**(ii) for any collection of disjoint subsets of $\mathbb{R}^2$, $A_1, A_2, \ldots, A_n$, the random variables $\{N(A_k), k = 1, 2, \ldots, n\}$ are mutually independent.**

Note that the number of points in $[0, x] \times [0, y]$ is a Poisson random variable with parameter $\lambda xy$. Putting $x = y = 1$ we find that the number of points in the unit square is Poisson with parameter $\lambda$. Hence $\lambda$ is the expected number of points per unit area.

### Application to ecological patterns

Ecologists are interested in the spatial distributions of plants and animals (see for example MacArthur and Connell, 1966). Three of the situations of interest are:



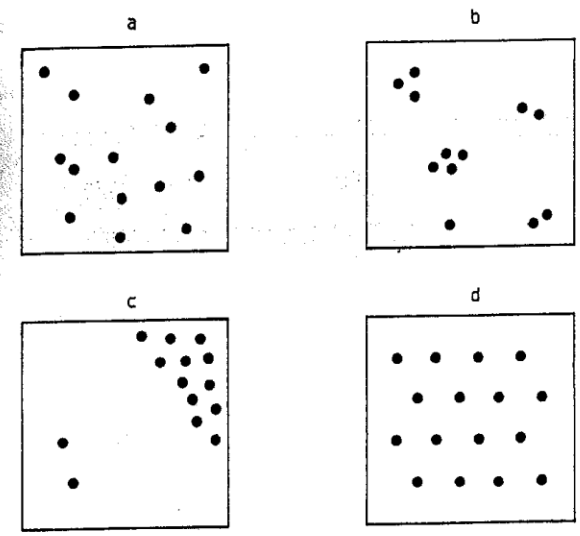


**Figure 3.6** Some representative spatial patterns of organisms: (a) random, (b) clumping in groups, (c) preferred location, (d) regular.

(i) the organisms are distributed randomly;
(ii) the organisms have preferred locations in the sense that they tend to occur in groups (i.e. are clustered or clumped) or in some regions more frequently than others;
(iii) the organisms are distributed in a regular fashion in the sense that the distances between them and their nearest neighbours tend to be constant.

These situations are illustrated in Fig. 3.6. We note that clumping indicates cooperation between organisms. The kind of spacing shown in Fig. 3.6(d) indicates competition as the organisms tend to maintain a certain distance between themselves and their neighbours.

An important reason for analysing the underlying pattern is that if it is known, the total population may be estimated from a study of the numbers in a small region. This is of particular importance in the forest industry.

The hypothesis of randomness leads naturally, by the same kind of argument as in Section 3.5, to a Poisson point process in the plane. Ecologists refer to this as a **Poisson forest**. Under the assumption of a Poisson forest we may derive the probability density function of the distance from one organism (e.g. tree) to its nearest neighbour. We may use this density to test the hypothesis of randomness. We first note the following result.

**Theorem 3.6 In a Poisson forest, the distance $R_1$ from an arbitrary fixed point to the nearest event has the probability density**

$$\boxed{f_{R_1}(r) = 2\lambda\pi r e^{-\lambda\pi r^2}}, \qquad r > 0. \tag{3.11}$$

*Proof* We will have $R_1 > r$ if and only if there are no events in the circle of radius $r$ with centre at the fixed point under consideration. Such a circle has area $\pi r^2$, so from the definition of a Poisson point process in the plane, the number of events inside the circle is a Poisson random variable with mean $\lambda\pi r^2$. This gives

$$\Pr\{R_1 > r\} = e^{-\lambda\pi r^2}.$$

We must then have

$$f_{R_1}(r) = \frac{d}{dr}(1 - e^{-\lambda\pi r^2})$$

which leads to (3.11) as required.

We may also prove that the distance from an event to its nearest neighbour in a Poisson forest has the density given by (3.11). It is left as an exercise to prove the following result.

**Theorem 3.7 In a Poisson forest the distance $R_k$ to the $k$th nearest event has the density**

$$\boxed{f_{R_k}(r) = \frac{2\pi\lambda r(\lambda\pi r^2)^{k-1}e^{-\lambda\pi r^2}}{(k-1)!}}, \qquad r > 0, \qquad k = 1, 2, \ldots.$$

### Estimating the number of trees in a forest

If one is going to estimate the number of trees in a forest, it must first be ensured that the assumed probability model is valid. The obvious hypothesis to begin with is that one is dealing with a Poisson process in the plane. A few methods of testing this hypothesis and a method of estimating $\lambda$ are now outlined. For some further references see Patil *et al.* (1971) and Heltshe and Ritchey (1984). An actual data set is shown in Fig. 3.7.

*Method 1 – Distance measurements*

Under the assumption of a Poisson forest the point–nearest tree or tree–nearest tree distance has the density $f_{R_1}$ given in (3.11). The actual measure-



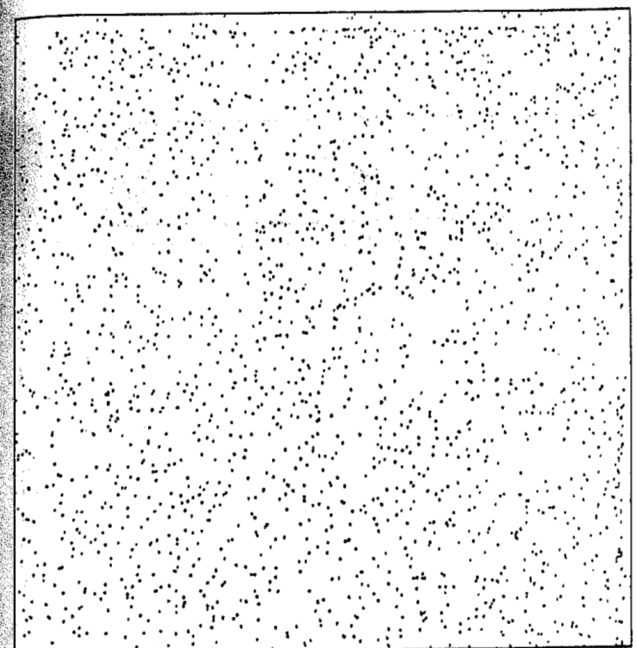

**Figure 3.7** Locations of trees in Lansing Woods. Smaller dots represent oaks, larger dots represent hickories and maples. The data are analysed in Exercise 22. Reproduced with permission from Clayton (1984).

ments of such distances may be collected into a histogram or empirical distribution function. A goodness of fit test such as $\chi^2$ (see Chapter 1) or Kolmogorov–Smirnov (see for example Hoel, 1971; or Afifi and Azen, 1979) can be carried out. Note that **edge effects** must be minimized since the density of $R_1$ was obtained on the basis of an infinite forest.

Assuming a Poisson forest the parameter $\lambda$ may be estimated as follows. Let $\{X_i, i = 1, 2, \ldots, n\}$ be a random sample for the random variable with the density (3.11). Then it is shown in Exercise 21 that an **unbiased estimator** (see

Exercise 6) of $1/\lambda$ is

$$\hat{\Lambda}^{-1} = \frac{\pi}{n} \sum_{i=1}^{n} X_i^2.$$

An estimate of $\lambda$ is thus made and hence, if the total area $A$ is known, the total number of trees may be estimated as $\lambda A$. For further details see Diggle (1975, 1983), Ripley (1981) and Upton and Fingleton (1985).

*Method 2–Counting*

Another method of testing the hypothesis of a Poisson forest is to subdivide the area of interest into $N$ equal smaller areas called cells. The numbers $N_k$ of cells containing $k$ plants can be compared using a $\chi^2$-test with the expected numbers under the Poisson assumption using (3.10), with $\bar{n}$ = the mean number of plants per cell.

**Extensions to three and four dimensions**

Suppose objects are randomly distributed throughout a 3-dimensional region. The above concepts may be extended by defining a Poisson point process in $\mathbb{R}^3$. Here, if $A$ is a subset of $\mathbb{R}^3$, the number of objects in $A$ is a Poisson random variable with parameter $\lambda|A|$, where $\lambda$ is the mean number of objects per unit volume and $|A|$ is the volume of $A$. Such a point process will be useful in describing distributions of organisms in the ocean or the earth's atmosphere, distributions of certain rocks in the earth's crust and of objects in space. Similarly, a Poisson point process may be defined on subsets of $\mathbb{R}^4$ with a view to describing random events in space–time.

## 3.7 COMPOUND POISSON RANDOM VARIABLES

Let $X_k, k = 1, 2, \ldots$ be independent identically distributed random variables and let $N$ be a non-negative integer-valued random variable, independent of the $X_k$. Then we may form the following sum:

$$S_N = X_1 + X_2 + \cdots + X_N, \tag{3.12}$$

where the number of terms is determined by the value of $N$. Thus $S_N$ is a **random sum of random variables**: we take $S_N$ to be zero if $N = 0$. If $N$ is a Poisson random variable, $S_N$ is called a **compound Poisson random variable.** The mean and variance of $S_N$ are then as follows.

**Theorem 3.8 Let $E(X_1) = \mu$ and $\mathrm{Var}(X_1) = \sigma^2$, $|\mu| < \infty, \sigma < \infty$. If $N$ is Poisson with parameter $\lambda$, then $S_N$ defined by (3.12) has mean and variance**

$$E(S_N) = \lambda\mu$$
$$\mathrm{Var}(S_N) = \lambda(\mu^2 + \sigma^2).$$

*Proof* The law of total probability applied to expectations (see p. 8) gives

$$E(S_N) = \sum_{k=0}^{\infty} E(S_N | N = k) \Pr\{N = k\}.$$

But conditioned on $N = k$, there are $k$ terms in (3.12) so $E(S_N | N = k) = k\mu$. Thus

$$\begin{aligned} E(S_N) &= \sum_{k=0}^{\infty} \mu k \Pr\{N = k\} \\ &= \mu E(N) \\ &= \lambda\mu. \end{aligned}$$

Similarly,

$$\begin{aligned} E(S_N^2) &= \sum_{k=0}^{\infty} E(S_N^2 | N = k) \Pr\{N = k\} \\ &= \sum_{k=0}^{\infty} [\mathrm{Var}(S_N | N = k) + E^2(S_N | N = k)] \Pr\{N = k\} \\ &= \sum_{k=0}^{\infty} (k\sigma^2 + k^2\mu^2) \Pr\{N = k\} \\ &= \sigma^2 E(N) + \mu^2 E(N^2) \\ &= \sigma^2\lambda + \mu^2[\mathrm{Var}(N) + E^2(N)] \\ &= \sigma^2\lambda + \mu^2(\lambda + \lambda^2). \end{aligned}$$

The result follows since $\mathrm{Var}(S_N) = E(S_N^2) - \lambda^2\mu^2$.

**Example** The number of seeds ($N$) produced by a certain kind of plant has a Poisson distribution with parameter $\lambda$. Each seed, independently of how many there are, has probability $p$ of forming into a developed plant. Find the mean and variance of the number of developed plants (ignoring the parent).

*Solution* Let $X_k = 1$ if the $k$th seed develops into a plant and let $X_k = 0$ if it doesn't. Then the $X_k$ are i.i.d. Bernoulli random variables with

$$\Pr\{X_1 = 1\} = p = 1 - \Pr\{X_1 = 0\}$$

and

$$E(X_1) = p$$
$$\mathrm{Var}(X_1) = p(1 - p).$$

The number of developed plants is

$$S_N = X_1 + X_2 + \cdots + X_N$$

which is therefore a compound Poisson random variable. By Theorem 3.8, with $\mu = p$ and $\sigma^2 = p(1-p)$ we find

$$\begin{aligned} E(S_N) &= \lambda p \\ \mathrm{Var}(S_N) &= \lambda(p^2 + p(1-p)) \\ &= \lambda p. \end{aligned}$$

As might be suspected from these results, in this example $S_N$ is itself a Poisson random variable with parameter $\lambda p$. This can be readily shown using generating functions – see Section 10.4.

## 3.8 THE DELTA FUNCTION

We will consider an interesting neurophysiological application of compound Poisson random variables in the next section. Before doing so we find it convenient to introduce the delta function. This was first employed in quantum mechanics by the celebrated theoretical physicist P.A.M. Dirac, but has since found application in many areas.

Let $X_\varepsilon$ be a random variable which is uniformly distributed on $(x_0 - \varepsilon/2, x_0 + \varepsilon/2)$. Then its distribution function is

$$F_{X_\varepsilon}(x) = \Pr\{X_\varepsilon \leqslant x\} = \begin{cases} 0, & x \leqslant x_0 - \varepsilon/2, \\ \frac{1}{\varepsilon}[x - (x_0 - \varepsilon/2)], & |x - x_0| < \varepsilon/2, \\ 1, & x \geqslant x_0 + \varepsilon/2 \end{cases}$$
$$\doteq H_\varepsilon(x - x_0).$$

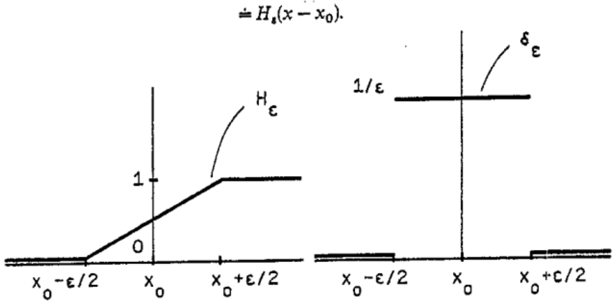


Figure 3.8



The density of $X_\varepsilon$ is

$$f_{X_\varepsilon}(x) = \frac{dF_{X_\varepsilon}}{dx} = \begin{cases} 1/\varepsilon, & |x - x_0| < \varepsilon/2, \\ 0, & \text{otherwise.} \end{cases}$$
$$\doteq \delta_\varepsilon(x - x_0).$$

The functions $H_\varepsilon$ and $\delta_\varepsilon$ are sketched in Fig. 3.8.

As $\varepsilon \to 0$, $H_\varepsilon(x - x_0)$ approaches the unit step function, $H(x - x_0)$ and $\delta_\varepsilon(x - x_0)$ approaches what is called a delta function, $\delta(x - x_0)$. In the limit as $\varepsilon \to 0$, $\delta_\varepsilon$ becomes 'infinitely large on an infinitesimally small interval' and zero everywhere else. We always have for all $\varepsilon > 0$,

$$\int_{-\infty}^{\infty} \delta_\varepsilon(x - x_0)\,dx = 1.$$

We say that the limiting object $\delta(x - x_0)$ is a **delta function** or a **unit mass** concentrated at $x_0$.

**Substitution property**

Let $f$ be an arbitrary function which is continuous on $(x_0 - \varepsilon/2, x_0 + \varepsilon/2)$. Consider the integrals

$$I_\varepsilon = \int_{-\infty}^{\infty} f(x)\delta_\varepsilon(x - x_0)\,dx = \frac{1}{\varepsilon}\int_{x_0-\varepsilon/2}^{x_0+\varepsilon/2} f(x)\,dx.$$

When $\varepsilon$ is very small,

$$I_\varepsilon \simeq \frac{1}{\varepsilon}\varepsilon f(x_0) = f(x_0).$$

We thus obtain the **substitution property** of the delta function:

$$\int_{-\infty}^{\infty} f(x)\delta(x - x_0)\,dx = f(x_0). \tag{3.13}$$

Technically this relation is used to define the delta function in the theory of **generalized functions** (see for example Griffel, 1985). With $f(x) = 1$, (3.13) becomes

$$\int_{-\infty}^{\infty} \delta(x - x_0)\,dx = 1.$$

Furthermore, since $\delta(x) = 0$ for $x \neq 0$,

$$\int_{-\infty}^{x} \delta(x' - x_0)\,dx' = H(x - x_0) = \begin{cases} 0, & x < x_0, \\ 1, & x \geqslant x_0. \end{cases}$$

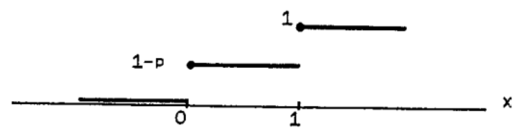


Figure 3.9

Thus we may informally regard $\delta(x - x_0)$ as the derivative of the unit step function $H(x - x_0)$. Thus it may be viewed as the density of the constant $x_0$.

**Probability density of discrete random variables**

Let $X$ be a discrete random variable with $\Pr(X = 1) = 1 - \Pr(X = 0) = p$. Then the probability density of $X$ is written

$$f_X(x) = (1 - p)\delta(x) + p\delta(x - 1).$$

This gives the correct distribution function for $X$ because

$$F_X(x) = \Pr(X \leqslant x) = \int_{-\infty}^{x} f_X(x')\,dx' = (1 - p)H(x) + pH(x - 1)$$

$$= \begin{cases} 0, & x < 0, \\ 1 - p, & 0 \leqslant x < 1, \\ 1, & x \geqslant 1, \end{cases}$$

as is sketched in Fig. 3.9.

Similarly, the probability density of a Poisson random variable with parameter $\lambda$ is given by

$$f_X(x) = e^{-\lambda} \sum_{k=0}^{\infty} \frac{\lambda^k}{k!} \delta(x - k).$$

## 3.9 AN APPLICATION IN NEUROBIOLOGY

In Section 3.5 we mentioned the small voltage changes which occur spontaneously at nerve–muscle junctions. Their **arrival times** were found to be well described by a Poisson point process in time. Here we are concerned with their **magnitudes**. Figure 3.10 depicts the anatomical arrangement at the nerve–muscle junction. Each cross represents a potentially active site.

The small **spontaneous** voltage changes have amplitudes whose histogram is fitted to a normal density – see Fig. 3.11. When a **nerve impulse**, having travelled out from the spinal cord, enters the junction it elicits a much bigger

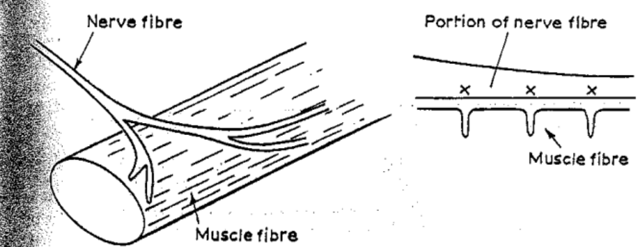


Figure 3.10 The arrangement at a nerve–muscle junction.

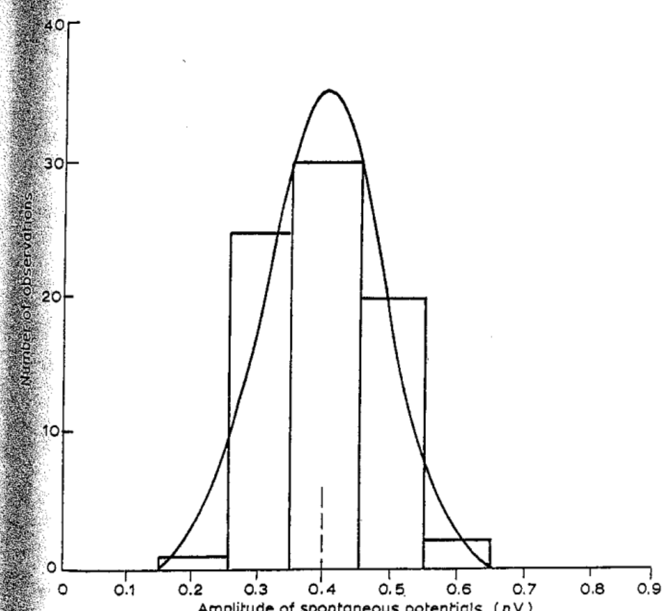


Figure 3.11 Histogram of small spontaneous voltage changes and fitted normal density. From Martin (1977). Figures 3.11–3.13 reproduced with permission of the American Physiological Society and the author.

response whose amplitude we will call $V$. It was hypothesized that the large response was composed of many unit responses, the latter corresponding to the spontaneous activity.

We assume that the unit responses are $X_1, X_2, \ldots$ and that these are normal with mean $\mu$ and variance $\sigma^2$. A large response consists of a random number $N$ of the unit responses. If $N = 0$, there is no response at all. Thus

$$V = X_1 + X_2 + \cdots + X_N,$$

which is a random sum of random variables. A natural choice for $N$ is a binomial random variable with parameters $n$ and $p$ where $n$ is the number of potentially active sites and $p$ is the probability that any site is activated. However, the assumption is usually made that $N$ is Poisson. This is based on the Poisson approximation to the binomial and the fact that a Poisson distribution is characterized by a single parameter. Hence $V$ is a compound Poisson random variable. The probability density of $V$ is then found as follows:

$$\Pr\{V \in (v, v + dv)\} = \sum_{k=0}^{\infty} \Pr\{V \in (v, v + dv) \mid N = k\} \Pr\{N = k\}$$

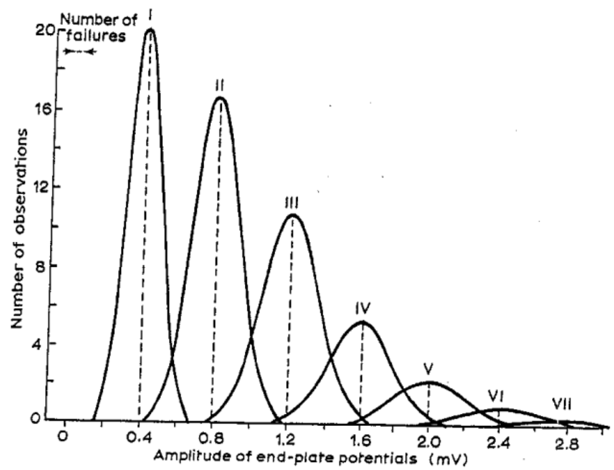


**Figure 3.12** Decomposition of the compound Poisson distribution. The curve marked I corresponds to $p_1$, the curve marked II to $p_2$, etc., in (3.14).



$$= e^{-\lambda} \Pr\{V \in (v, v + dv) \mid N = 0\}$$
$$+ \sum_{k=1}^{\infty} \frac{e^{-\lambda}\lambda^k}{k!} \Pr\{V \in (v, v + dv) \mid N = k\}$$
$$= \left[ e^{-\lambda}\delta(v) + e^{-\lambda} \sum_{k=1}^{\infty} \frac{\lambda^k}{k!} \frac{1}{\sqrt{2\pi k\sigma^2}} \exp\left( \frac{-(v - k\mu)^2}{2k\sigma^2} \right) \right] dv$$
$$\doteq \left[ e^{-\lambda}\delta(v) + \sum_{k=1}^{\infty} p_k(v) \right] dv,$$

where $\delta(v)$ is a delta function concentrated at the origin. Hence the required density is

$$\boxed{f_V(v) = e^{-\lambda}\delta(v) + \sum_{k=1}^{\infty} p_k(v)}. \qquad (3.14)$$

The terms in the expansion of the density of $V$ are shown in Fig. 3.12. The density of $V$ is shown in Fig. 3.13 along with the empirical distribution. Excellent agreement is found between theory and experiment, providing a validation of the 'quantum hypothesis'. For further details see Martin (1977).

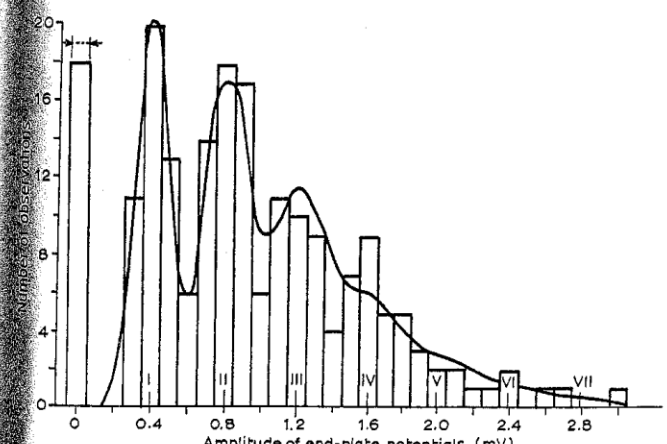


**Figure 3.13** Histogram of responses. The curve is the density for the compound Poisson distribution, the column at 0 corresponding to the delta function in (3.14).