MASTER

The Pre-Event Stimulus Ensemble of visual neurons in the corpus geniculatum laterale of the cat : a feature extraction approach

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The Pre-Event Stimulus Ensemble of visual neurons in the Corpus Geniculatum Laterale of the cat.

A feature extraction approach

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This investigation was performed in the period April 1973 - August 1974 in the Laboratory of Medical Physics and Biophysics of the University of Nijmegen as a part of the research of the workgroup Neurophysics, in cooperation with Jacques Sak, under the supervision of Prof.Dr. A.J.H. Vendrik and dr. P.I.M. Johannesma.
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1. Introduction

For the analysis of the relation between stimulus and neural response de Boer and Kuyper (1968) introduced the reverse correlation. Using a complex, unstructured stimulus (Gaussian white noise), they give a first order or linear description by cross correlation between stimulus and response. The 'all or none' character of a spike implies that the cross correlation is equal to the mean value of the stimulus-elements preceding a spike.

The collection of all stimulus-elements preceding a spike, is defined as the Pre-Event Stimulus Ensemble (PESE) (Johannesma, 1972). Characterization of PESE, particularly the differences from the original stimulus ensemble (SE) will contain the information about the stimulus-response relation.

Grashuis (1974) applied this approach to auditory neurons in the Cochlear Nucleus of the cat. He showed, that the first moment of the PESE, based on a SE of stationary white noise, describes the functional properties of neurons with low characteristic frequency and allows a prediction of the response on other stationary, complex stimuli.

Sak (1974) in collaboration with Boezeman started with the analysis of the PESE of visual neurons in the lateral Geniculate Body of the cat. They applied a SE of stationary, spatio-temporal nearly uncorrelated stimuli and found, that neuron characterization by the first moment of PESE was comparable to the more conventional description by scanning the receptive field with single light-pulses.

The present investigation is based on the same exprimental results and makes a further analysis of the visual PESE by extraction of characteristic patterns (features). If a limited system of features should exist, it would allow a compact description of the stimulus-response relation. An optimal feature-description requires that each feature contains new information. The features have to be completely different: conceptually independent.

The mathematical apparatus for the representation is the expansion in an orthogonal system of functions. A well-known extraction method applied in pattern recognition theory, is the Karhunen-Loève expansion (Fu, 1968) which forms an expansion in an orthogonal system of eigenfunctions of the autocorrelation function. The coefficients in that expansion are uncorrelated: effecturally independent.

The resulting set of features is cell-dependent and specific for the investigated PESE. However, the extraction of these features give rise to enormous computer problems and exceeds the computation capacity.

A more sophisticated approach is the construction of an extensive cell-independent feature system suitable to the specifications of the stimulus and analysis equipment. The limitation of the number of features is found by selection from the whole set by the PESE.

Here we introduce the Walsh-functions (Walsh, 1923) which have many applications in pattern recognition (Witz, 1972) and information theory (Harmuth, 1969). Walsh-functions have the following properties

- they match with the digital representation of the stimulus
- they posses a mathematical apparatus
- they are easily in operation in digital computers.

Definitions and further explications are given in chapter 3.

2. Methods

The selection of PESE from SE contains the information about the function of the neuron. This information is limited to the stimuli, present in the SE. As a consequence of this the SE has to possess many characteristics.

The stimulus in this investigation is a series of a fast succession of light-flashes of short duration with a constant intensity. The spatial position of each flash is pseudo-randomly varied on the whole of the receptive field ($20^o * 20^o$). This stimulus, which has the following properties:

- flash duration of 2.7 msec at a rate of 375 flashes/sec resulting in a temporal resolution of 2.7 msec
- spatial resolution, horizontal $\leq 0.16^o$ and vertical $\leq 0.08^o$
- succeeding flashes are spatially nearly uncorrelated

may be interpreted as a stationary, white noise for the neuron.

For a complete description of the physiological experimental conditions we refer to Sak (1974).

Stimulation is performed by a Tektronix 604 display oscilloscope which covers a space field of $20^o * 20^o$. The elicted spike sequence is registrated with glass micropipettes, filled with 3 M.KCL, tipdiameter 1.0 - 1.5μ, resistance 5 - 10 MΩ. In the computer analysis of the stimulus-response relations use was made of a PDP-9 digital computer.

3. Walsh-functions

Walsh-functions may be defined by different but equivalent expressions (Harmuth, 1969); we choose here

$$wal_o(x) = 1 \qquad -\tfrac{1}{2} \leq x < \tfrac{1}{2}$$

$$wal_o(x) = 0 \qquad x < -\tfrac{1}{2},\ x \geq \tfrac{1}{2}$$

$$wal_{2j+p}(x) = (-1)^{\left[\frac{j}{2}\right]+p} wal_j\{2(x+\tfrac{1}{4})\} + (-1)^{\left[\frac{j}{2}\right]+j} wal_j\{2(x-\tfrac{1}{4})\}$$

$p = 0, 1$

$j = 0, 1, 2, \ldots$

$\left[\frac{j}{2}\right] \equiv$ largest integer $\leq \frac{j}{2}$

From this definition 2 properties follow

1 The Walsh-system forms an Abelian group with respect to the multiplying operator and unit-element $wal_o(x)$.

This implies the following relation between Walsh-functions:

$$wal_i(x)\ .\ wal_j(x) = wal_k(x) \qquad k = i \oplus j$$

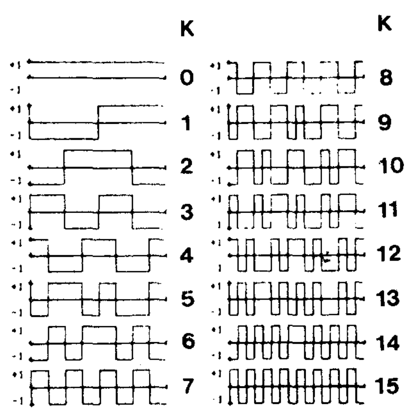
The operation $\oplus$ is defined as 'addition modulo 2' i.e. binary addition without draught.

2 The Walsh-functions are orthonormal.

More dimensional functions are created by multiplication of the one-dimensional functions. Walsh-functions of 3 variables (x, y, t) which we need for the analyses of SE and PESE are defined

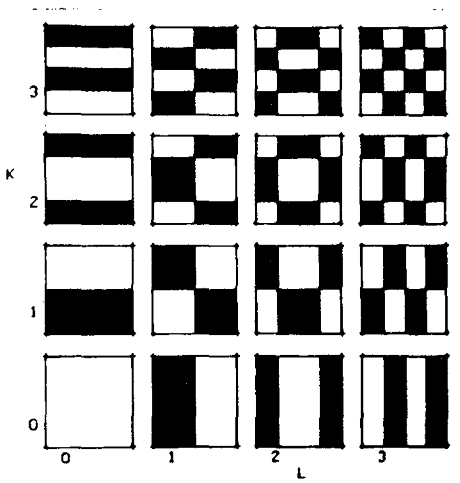
$$wal^3_{ijk}(x,y,t) = wal_i(x)\ .\ wal_j(y)\ .\ wal_k(t)$$

Fig. 1-2 shows a graphical representation of one- and two-dimensional Walsh-functions.



WALSH-FUNCTIONS OF THE ORDER K

fig. 1



2-D. WALSH-FUNCTIONS OF THE ORDER K.L

WHITE INDICATES +1 BLACK INDICATES -1

fig. 2

4. PESE, SE and their Walsh-representation

The stimulus is a series of light-pulses, varied spatio-temporal on the whole of the receptive field. Mathematically it can be denoted as a product of 3 Dirac-functions:

$$S(x,y,t) = S_o \sum_{m=o}^{M} \delta(x-x_m) \cdot \delta(y-y_m) \cdot \delta(t-t_m) \tag{1}$$

The neural activity consists of a sequence of action potentials or spikes

$$z(t) = \sum_{n=o}^{N} \delta(t-t_n) \tag{2}$$

To every spike $\delta(t-t_n)$ belongs a pre-event stimulus $S_n(x,y,\tau)$ with a finite relevant time length T ~ 150 msec before the spike (Sak, 1974).

$$\begin{aligned} S_n(x,y,\tau) &= S(x,y,t_n-\tau) \qquad\qquad 0 \leq \tau \leq T \\ &= S_o \sum_{m=1}^{M} \delta(x-x_m) \cdot \delta(y-y_m) \cdot \delta(t_n-\tau-t_m) \end{aligned} \tag{3}$$

It is the collection of all $S_n(x,y,\tau)$ n = 1, N which forms the PESE.

$$\left\{ \begin{matrix} S_n(x,y,\tau) & 0 \leq \tau \leq T \\ & n = 1, N \end{matrix} \right\} \tag{3a}$$

The presence of the features in each SE-element S(x,y,t) is given by the coefficient c_{ijk} in the expansion of S(x,y,t) in the orthonormal feature system $\{wal^3_{ijk}(x,y,t)\}$

$$S(x,y,t) = \sum_{i,j,k=o}^{I,J,K} c_{ijk} \cdot wal^3_{ijk}(x,y,t) \tag{4a}$$

$$c_{ijk} = \iiint_{SE} dxdydt \cdot S(x,y,t) \cdot wal^3_{ijk}(x,y,t) \tag{4b}$$

in which $\iiint_{SE}$ indicates that the integration-boundaries coincide with the spatio-temporal extent of the stimulus-ensemble.

The number of coefficients necessary I.J.K in eq. (4a) depends on the number of logons of S(x,y,t). The number of logons represents the number of independent aspects and equals with the quotient ($\sim 2.10^6$) of the range and resolution of S(x,y,t).
Equation (4) means that if the feature system is known, S(x,y,t) is represented completely by one to one mapping with the series of coefficients c_{ijk}.

$$S(x,y,t) \rightarrow (c_{111}, \ldots c_{IJK}) \qquad (5)$$

Because of the increasing resolution of the Walsh-set (fig. 1, 2) and the stimulus resolution, which is large with respect to the resolution of the receptive field, the analysis is started with a system of only the first 512 Walsh-features.

$$\{wal^3_{ijk}(x,y,t);\ i,j,k = 0 - 7\} \qquad (6)$$

This system possesses for different neurons a temporal resolution 12.5 - 20.0 msec and a spatial resolution $1.0^\circ - 1.5^\circ$. The system resolution (especially the spatial resolution) is of the order of the size of the receptive fields (Sak, 1974) but computer capacity forms the restrictive factor for a more extensive system.

The orthonormal Walsh-features in (6) span a 512-dimensional space, defined as the Walsh-Feature-Space (WFS). In the WFS each ensemble-element corresponds to a point or vector $\vec{c}$. The whole SE is represented by a cluster of vectors $\vec{c}$, with the frequency-distribution

$$f(c)$$

The PESE forms a subset of this cluster with the frequency-distribution under the condition that each element is followed by a spike z(t) = e

$$f(c|z(t) = e) = f(c|e)$$

By projection on each feature-axis the clusters generate the frequency-distributions

- $f(c_{ijk})$, the a priori distribution of c_{ijk} in SE,
- $f(c_{ijk}|e)$, the conditional or a posteriori distribution of c_{ijk} in PESE.

5. Evaluation of the Walsh-Feature-Space

The significance of a Walsh-feature for the characterization of the neuron function is determined by the degree in which PESE and SE differ with respect to this feature, in other words by the differences of $f(c_{ijk}|e)$ and $f(c_{ijk})$. Two qualitative criteria are devoloped abreast.

- The first measure

$$\Phi_{ijk} = \int d\, c_{ijk} \,\{f(c_{ijk}|e) - f(c_{ijk})\}^2 \tag{7}$$

corresponds with the mean square difference of the a posteriori and a priori distributions of c_{ijk}.

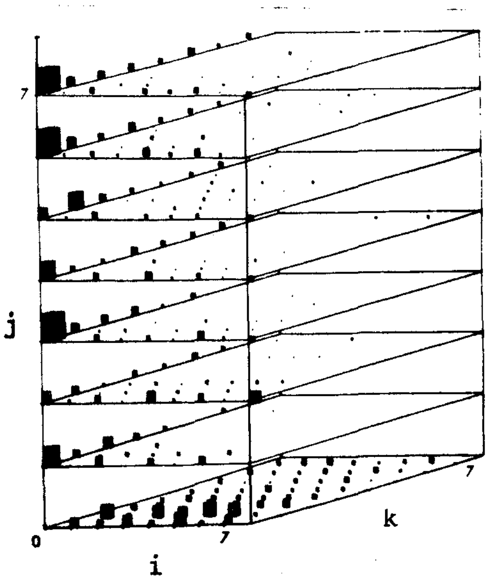
- The second measure

$$\Delta\bar{c}_{ijk} = \overline{c_{ijk}}^{PESE} - \overline{c_{ijk}}^{SE}$$

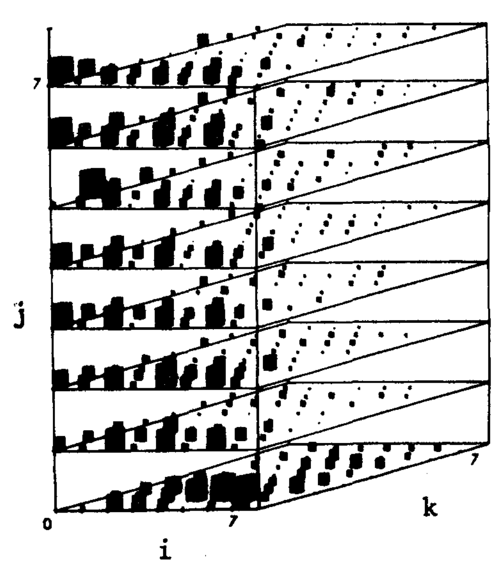
$$= \left| \int d\, c_{ijk} \cdot c_{ijk} \cdot \{f(c_{ijk}|e) - f(c_{ijk})\} \right| \tag{8}$$

corresponding with the absolute difference of the mean value of the arguments in the a posteriori and a priori distributions. This measure agrees with the interpretations of the distributions as probability density functions.

Figure 3A shows for unit 82-1 in a 3-dimensional representation the result of Φ for each (i,j,k)-cominbation. The size of Φ is represented by the volume of a block on the coordinates (i,j,k). Figure 3B shows the results of $\Delta\bar{c}$.



Φ fig. 3A



$\Delta\bar{c}$ fig. 3B

From figure 3A, B the following conclusions can be drawn

- between the different features difference in significance can be shown.
- it appears that low order features are more important than high order features.

This suggests that feature-extraction on the basis of the first 512 Walsh-functions in (6) can be successful.

In the WFS the PESE is represented through a cluster of points. The center of mass of this cluster is given by

$$\vec{\gamma} = \frac{1}{N} \sum_{n=1}^{N} \vec{c}_n \tag{9}$$

The first-order cross correlation between stimulus S(x,y,t) and neural response z(t) is given by

$$\delta(x,y,\tau) = \frac{1}{T_o} \int_o^{T_o} dt\ z(t) \cdot S(x,y,t-\tau) \tag{10}$$

It can easily be shown (Sak, 1974) that a combination of (2) and (10) leads to

$$\begin{aligned} \rho(x,y,\tau) &= \frac{1}{T_o} \sum_{n=1}^{N} S(x,y,t_n-\tau) \\ &= \frac{N}{T_o} \frac{1}{N} \sum_{n=1}^{N} S_n(x,y,\tau) \end{aligned} \tag{11}$$

Equation (11) indicates that the cross correlation equals the product of the average stimulus preceding a neural event and the factor $\frac{N}{T_o}$, interpreted as the average spike activity for the observed SE (Grashuis, 1974). Because of the linearity of eq. (4) it follows from (9-11) that the center of mass $\vec{\gamma}$ equals the Walsh representation of the cross correlation or mean value of the elements in PESE.

6. Prediction of neural responses

A global description of WFS can be found by the analysis of $\vec{\gamma}$ and the scalar product P_n of each $\vec{c}_n$ and $\vec{\gamma}$ (Grashuis, 1974) defined as

$$P_n = (\vec{c}_n . \vec{\gamma}) = \sum_{i,j,k=o}^{7} c_{ijk} \cdot \bar{c}_{ijk} \tag{12}$$

Because each $S_n(x,y,t)$ consists of an equal number (~ 64) of flashes with intensity S_o, the energy E_n and so $|\vec{c}_n| = \sqrt{E_n}$ is constant. It means that the sphere with radius $\sqrt{E_n}$ in WFS is the collection of all stimulus points.

The 2 ensembles PESE and SE leads to different distributions of P_n in WFS. The collection $\vec{c}_n$ generates from the PESE the a posteriori probability density distribution of P_n

$$f(P|e) \tag{13}$$

The original collection $\vec{c}$ of the elements of SE give rise to the a priori distribution

$$f(P) \tag{14}$$

The description may be verified by evaluation of the a posteriori and a priori distributions, resulting in neural prediction. According to the Bayes' probability relation (13) and (14) can be combined to

$$\frac{f(P|e)}{f(P)} = \frac{f(P,e)}{f(P).f(e)} = \frac{f(e|P)}{f(e)} \tag{15}$$

with

$f(P,e)$ = combined probability density distribution.

$f(e|P)$ = conditional probability density distribution with respect to the scalar product P, representing the probability of the occurrence of a neural event following immediately a stimulus with similarity P with $\vec{\gamma}$.

$f(e)$ = unconditional probability density distribution of the generation of a neural event, interpreted as the average spike-activity for the observed SE.

Rearranging of (15) leads to

$$f(e|P) = \frac{f(P|e)}{f(P)} f(e) \qquad (16)$$

Equation (16) predicts that the probability, that a stimulus with similarity P_n with $\vec{\gamma}$ is followed by a spike equals the quotient of probabilities of P_n in PESE and SE respectively, multiplied with scaling factor f(e). Equation (16) is the predictor for spike activity based on 2 stages of analysis

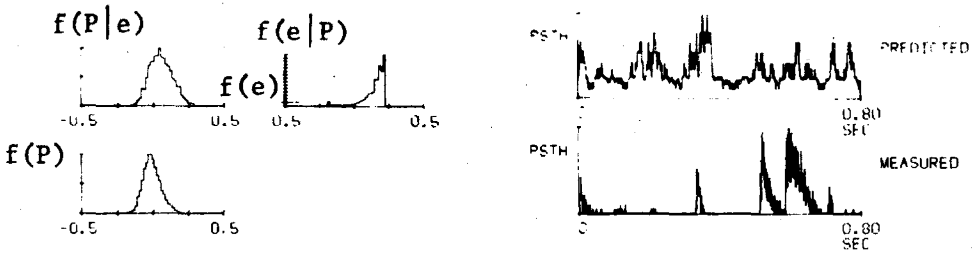
- feature extraction of PESE through the system of 512 lowest order Walsh-functions.
- characterization of WFS by its first moment.

The prediction is verified by comparing it to the experimental measured spike-response probability, the PSTH (averaged spike-response) on repeated stimulus sequences.

Figure 5-7 shows for 3 units the distributions of P in PESE and SE, the predictor $f(e|P)$ and the predicted and measured PSTH on short stimulus sequences.

Figure 5

UNIT 77-2



Number of spikes 5730

Walsh x,y-resolution 2 dgr.

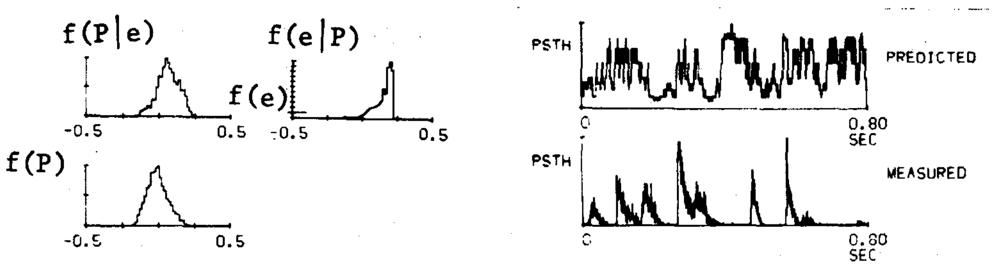
Walsh t-resolution 12,5 msec

t-range PESE 100 msec

x,y-range PESE 16 dgr.

Figure 6

UNIT 80-5B



Number of spikes 4288

Walsh x,y-resolution 1 dgr.

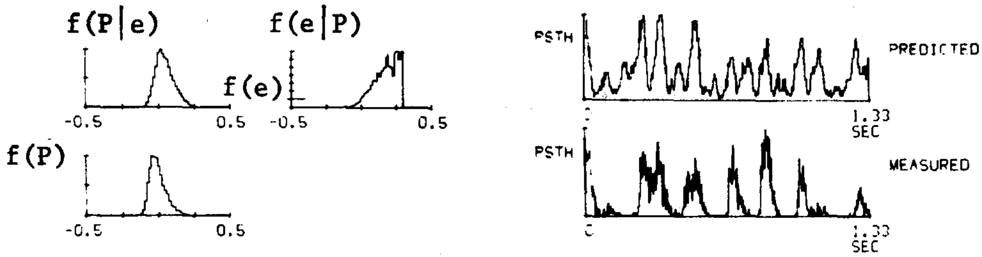
Walsh t-resolution 12,0 msec

t-range PESE 96 msec

x,y-range PESE 8 dgr.

Figure 7

UNIT 82-1



Number of spikes 8998

Walsh x,y-resolution 1 dgr.

Walsh t-resolution 12,5 msec

t-range PESE 100 msec

x,y-range PESE 8 dgr.

7. Discussion

The stimulus-response relation is determined by a system of orthonormal features: the Walsh-functions. The number of independent arguments in the relation is reduced to one: the similarity of the stimulus and the average pre-event stimulus, represented by the feature-system. The experimental verification results in 3 predictions of neural activity. The predictions do not fit very well with the measured neural activity, with the exception of Unit 82-1 (fig. 7). This gives rise to the following remarks;

- The system of Walsh-features is cell-independent and is based on stimulus and analysis arguments. The Karhunen-Loève expansion generates features, which fit best to the investigated neuron (effectually independent).However, their interpretation will be difficult, because different neurons lead to different feature-systems. It seems to be more promissing to extract feature-systems from groups of neurons, which belongs together functionally (morpholocially or histologically).
- Many features in the Walsh-system are less siginifcant as shown in figure 3A, B. The "completeness" of the Walsh-system i.e. the number of missing significant features, cannot be shown in this way.

  An adaptive feature extraction, in which the least significant features are replaced by new high order features seems to be attractive.

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