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DOES THE BRAIN HAVE SYMMETRY?

I. Vision

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GERHARD MACK



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Center For Theoretical Studies
 University of Miami / Coral Gables, Florida 33124

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DOES THE BRAIN HAVE SYMMETRY?

I. Vision*

Gerhard Mack**
Center for Theoretical Studies
University of Miami, Coral Gables, Florida 33124

ABSTRACT

The present paper is concerned with vision and pattern recognition. It will be demonstrated how related problems can be reformulated by using group theoretical methods, in particular harmonic analysis, in such a way that they become accessible to methods of control theory and systems analysis. Topics discussed include: A control mechanism which we believe to be mainly responsible for the fact that a "constant" world is seen despite the many voluntary and involuntary movements of head and eye balls. Recognition of symmetrical forms. Receptive fields.

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** Present Address: Sektion Physik der Universität München, Germany.

I. Introduction

Symmetries and the mathematical methods to exploit them have played an important role in the exact sciences. A prominent example is atomic physics, which builds the theoretical foundation of chemistry. It has recently become clear that one may, from symmetry considerations alone, deduce the complete hydrogen spectrum and therefore the classification of atomic levels which is summarized in the periodic table of elements (Malkin and Manko, 1966). Already powerful in themselves, group theoretical methods acquire additional usefulness by providing a framework in which dynamical theories can be formulated and analysed. In biological organisms, dynamics enters in particular through the action of a multitude of control circuits. In the present paper we are concerned with vision and pattern recognition. It will be demonstrated how related problems can be reformulated by using group theoretical methods, in particular harmonic analysis, in such a way that they become accessible to methods of control theory and systems analysis. As an example we describe (in Sec. 6) a control mechanism which we believe to be mainly responsible for the fact that a "constant" world is seen despite the many voluntary and involuntary movements of head and eye balls.

Application of symmetry considerations and group theoretical methods in the neurosciences is not new, and in fact the present work has been much stimulated by an early paper of McCulloch and Pitts (1947): "How we perceive universals ...". These authors have first formulated the idea that neural nets (e.g. of the cortex) may be considered as manifolds on which realizations of certain transformation groups act. One can think of various such groups with fundamentally different psychological significance, and we hope to come back to some of these in the future.

Conceptually the simplest ones are of a geometrical nature. That is they are groups of transformations of the 3-dimensional space in which we live. They are relevant for pattern recognition. As has been recognized for a long time, the very concept of form or figure has little meaning without reference to its invariance under certain transformations of location, size and even certain changes in shape itself. Mathematically one might define patterns as equivalence classes of visually perceived objects, two objects being called equivalent if they can be transformed into each other by a specified group of transformations of 3-dimensional space. This group of "symmetry transformations" as we will call them may in general be different for different species of animals and would have to be experimentally determined for each. Linear transformations of space will usually correspond to changes in size and orientation, while nonlinear ones will involve changes in shape itself.

These invariance properties of patterns should not mislead one to believe though that only invariants are visually perceived. There is ample experimental evidence pointing to the contrary (Hake, 1966). One knows for instance that recognition accuracy depends upon orientation of forms (Gibson and Robinson, 1935). That patterns can be recognized as such means only that the brain is able to compensate for the effect of symmetry transformations. The ease, reliability and time necessary for such adaptation may very well depend on the transformation, the initial state, and possibly even the object viewed.

In the present paper we propose a model which is designed to describe the first few steps of the processing of information along the visual pathways. The number of neurons needed for its implementation suggests that a significant part of this activity (in particular the harmonic

analysis, s. below) may already be carried out in the retina, at least in the frog.

Our central hypothesis is that the first few orders of neurons carry out a harmonic analysis over the group of symmetry transformations. Harmonic analysis is a process similar to holography (s. Sec. 2). Even though it involves a summation process over extended areas of the retina, it has the important property that no information (including orientation etc.) is lost. However, there results a simple and well defined change in neuronal activity (firing rates) when the visual field is subject to a symmetry transformation. Such changes could be compensated by a well defined change in certain neuronal "amplification factors" (Sec. 5). Neurons with controllable amplification factors will be called "mixer neurons", in analogy with the terminology in electronics. The occurrence in nature of mixer neurons can be considered established by the experimental work of Reichardt (1961).

In Sec. 6 we show how the brain can compute the compensating change of neuronal amplification factors for symmetry transformations induced by continuous rotations of the eyeball. The computation is carried out by a control circuit based on the principle of feedback. It involves a nonlinear dynamical system; nevertheless one can show that it works because of certain compactness properties of the state space. This is the control mechanism mentioned above which makes one see a "constant" world.

In Sec. 7 we investigate the question how the brain can recognize exact and partial symmetries of patterns. Examples would be a circle O which is invariant under all rotations around its centre, or a symbol "+" which has a 4-fold symmetry axis, while an angle "L" has only a partial symmetry under rotations by 90° . The main problem here is that one wants

the symmetry to be recognized irrespective of where in the visual field the object is located. We propose a solution which, again, involves setting up a suitable smooth dynamical system.

In the present model the activity in any given neuron will in general be a weighted average of the excitation ($\sim$ light intensity) in an extended receptive field on the retina (cf. Barlow, 1953), and the inhibitory and excitatory subregions of this receptive field will form geometrical patterns characteristic of the group. These patterns will be determined in Sec. 8 for the lowest order neurons. It will also be explained there why diffuse illumination of the retina will lead to little or no response of most neurons, while sharp boundaries of light-dark will evoke enhanced activity. Finally, the question will be investigated how information from different receptive fields should be added.

A word about notation: Nowhere in this paper did we adopt the summation convention over repeated indices. All sums are indicated explicitly.

II. Preliminaries

In the present section we will recall some features of the ordinary Fourier transform. This will facilitate the readers understanding of harmonic analysis over a general transformation group as presented in Sec. 4 - by way of example. The reader may first skip this section and refer back while reading Sec. 4 if necessary.

Consider points x on the real line R . A translation of this line, $x \rightarrow x + a$, will be denoted by t_a . Obviously a translation t_{a_1} followed by a second translation t_{a_2} is another translation $t_{a_1} \cdot t_{a_2} = t_{a_1+a_2}$.

They form a group. Let us now define for every t_a the quantities

$$D^p(t_a) = e^{ipa} \quad (2.1)$$

Obviously,

$$D^p(t_{a_1}) D^p(t_{a_2}) = D^p(t_{a_1} \cdot t_{a_2}) \quad (2.2)$$

It will be helpful later to think of $D^p(t_a)$ as 1×1 matrices. The matrices $D^p(t_a)$ are said to form the irreducible representation (p) of the translation group, and (2.2) is called the group representation law (cf. Sec. 4 for general definitions). Consider now a square integrable function $f(x)$ defined on R . The Fourier theorem says that it may be expanded according to

$$f(x) = \int_{-\infty}^{+\infty} dp A(p) e^{ipx} \quad (2.3)$$

We can imagine f as defined as a function on the translation group by $f(t_x) \equiv f(x)$. By definition (2.1) we may rewrite expansion (2.3) as

$$f(t_x) = \int_{-\infty}^{+\infty} dp \operatorname{tr}(A(p) D^p(t_x)) \quad (2.4)$$

Here we consider $A(p)$ as a 1×1 matrix; tr stands for the trace.

Eq. (2.4) is said to provide an expansion of a function f on the translation group in terms of the irreducible representations of this group. The translations form a commutative but noncompact group. Later we will have to consider noncommutative but finite or compact groups. The analogue of p (called μ in Sec. 4) will then only take discrete values, but the matrices will no longer be 1×1 .

The Fourier transform has found many technical applications. We mention in particular that holography, or at least one version of it

known as Fourier-holography, amounts essentially to storing a function $f(x)$ in the form of its Fourier transform $A(p)$ (DeVelis and Reynolds, 1967).

There is one more fact about Fourier transform which must be mentioned. This is the behavior of $A(p)$ for large p as an indication of the smoothness of the function f . If $f(x)$ is an infinitely differentiable function of compact support (i.e. $f(x) = 0$ outside some finite interval) then $A(p)$ decreases faster than any power of $1/|p|$ for large $|p|$. If, on the other hand, $f(x)$ has a jump somewhere, then $A(p)$ decreases only like $|p|^{-1}$.

III. Symmetry transformations

Let us denote by x points in the 3-dimensional space in which we live. By the well known laws of geometrical optics, a point x in space will be mapped into a point z on the retina; see Fig. 1.

Observation shows that patterns, say a letter A , can be recognized irrespective of whether it is large or small, rotated or distorted in many other ways. Such changes can in general be induced by a 1-1 mapping (transformation) $\hat{g}$ of the underlying space of points x into itself:

$$x \rightarrow x' = \hat{g}x \quad (3.1)$$

Note that we do not require the mapping $\hat{g}$ to be linear. The reader may think of a rubber sheet with a letter A painted on it. Such a rubber sheet is a 2-dimensional space. Pulling the rubber sheet in some arbitrary way amounts to a transformation of this space, the points on it will be transformed according to some rule (3.1), and the letter A will appear distorted.

Given two transformations $\hat{g}_1$ and $\hat{g}_2$, we can define their product

$\hat{g}_1\hat{g}_2$ as the transformation effected by first carrying out transformation $\hat{g}_1$ and subsequently $\hat{g}_2$. There is also an identity transformation $\hat{e}$, defined as "no transformation at all". We will only consider transformations $\hat{g}$ which have an inverse $\hat{g}^{-1}$ so that $\hat{g}\hat{g}^{-1} = \hat{e}$.

We are interested in transformations of 3-dimensional space whose effects the viewers brain can compensate for. [The retina is also a part of the brain (diencephalon), as is known from embryology.] To give them a name, we will call them "symmetry transformations". We will assume that with any two such transformations $\hat{g}_1$ and $\hat{g}_2$ the product $\hat{g}_1\hat{g}_2$ is also of this kind, as well as the inverse transformation $\hat{g}_1^{-1}$. This is definitely an assumption, but one which would appear accessible to experimental test. The time necessary for adaption may depend on the transformation $\hat{g}$. As a consequence of the stated assumptions, the symmetry transformations form a group $\hat{G}$.

As a space point x is transformed by g into x' , its image z on the retina will be mapped into z' . Under certain conditions this provides a correspondence between transformations $\hat{g}$ in x -space and transformations g of the retina such that

$$z \rightarrow z' = gz \quad (3.2)$$

and these transformations form a group G . The condition for this to be true comes from the fact that one cannot in general see through solid objects. The restriction is that for any solid object any point on the surface which "can be seen", i.e. has an image on the retina, before the transformation should do so also after any transformation $\hat{g}$ in $\hat{G}$. A rotation around the dashed-dotted line in Fig. 1 (rotation in the frontal plane) satisfies this criterion. A rotation around an arbitrary

axis perpendicular to it will not however, because the eye may see the front of the object before the rotation and its back afterwards. We will only be interested in transformations of the first kind, so that there exists a group G acting on the retina⁺). That we can recognize a person whether we see his front, side or back has to be explained by a different mechanism which will have to involve the association networks of the cortex. The present model can be extended to include this, at the cost of introducing some additional hypotheses, but we will not go into this here.

IV. Harmonic Analysis

Before we can proceed with developing the theory we must first review some mathematical results slightly beyond standard group theory, as these will probably be unfamiliar to most readers. We assume that the reader is familiar with the elements of linear algebra, including matrix multiplication.

Let us first recall the definition of a group. A group G is a collection of objects g , called its "elements": $g \in G$, for which an associative multiplication law is defined such that for any two elements $g_1, g_2 \in G$ the product $g_1 g_2$ is also an element of G . Moreover, G contains a unit element $e \in G$ such that $ge = eg = g$ for all $g \in G$, and to every g there is an inverse g^{-1} so that $gg^{-1} = g^{-1}g = e$. Multiplication need not be

⁺) Mathematically, the groups G and $\hat{G}$ are related by a homomorphism $G \cong \hat{G}/P$. If we introduce a coordinate system in x -space with origin in the lens (see Fig. 1) then P consists of dilatations $x_i \rightarrow x_i \rho$, $i = 1, 2, 3$, where ρ is any positive real number. One eye cannot detect the effect of such a dilatation, for which size and distance of all objects change in proportion. The restriction on $\hat{G}$ stated in the text amounts to requiring that P is an invariant subgroup of $\hat{G}$.

commutative, i.e. $g_1 g_2 \neq g_2 g_1$ in general. We will be concerned mainly with finite groups, that is groups with a finite number of elements.

A (linear) representation of the group G is a collection of matrices $D(g)$ such that to every $g \in G$ a square matrix is assigned, and these matrices satisfy the group multiplication law

$$D(g_1)D(g_2) = D(g_1 g_2) \quad \text{and} \quad D(g^{-1}) = [D(g)]^{-1} \quad . \quad (4.1)$$

Two representations D and D' are called equivalent if there exists a nonsingular matrix S such that

$$S D(g) S^{-1} = D'(g) \quad \text{for all } g \in G \quad ; \quad (4.2)$$

otherwise they are called inequivalent. A representation D is called reducible if it is equivalent to a representation D' for which all the matrices $D'(g)$ have block-diagonal form (with ≥ 2 blocks); see Fig. 2. Otherwise it is called irreducible. We will in the following distinguish inequivalent irreducible representations by a superscript μ . The entries of a matrix $D(g)$ are in general complex numbers and will be denoted by $D_{ij}(g)$. The representation is said to have dimension n_μ if the indices i, j can take n_μ values each, that is the matrices have n_μ^2 entries. Equivalent representations have the same dimension. A finite group is known to have only a finite number of inequivalent irreducible representations, and their dimensions satisfy (Hamermesh, 1962)

$$\sum_{\mu} n_{\mu}^2 = n_G \quad . \quad (4.3)$$

n_G is the number of elements in the group.

A special irreducible representation is the trivial 1-dimensional

representation, for which

$$D(g) = 1 \quad \text{for all } g \in G \quad . \quad (4.4)$$

It will be labelled by $\mu = 0$ in the following.

Let us now assume that we have in some way selected one particular representation out of each class (μ) of equivalent irreducible representations. This selection will be referred to as a "choice of basis".⁺) The entries of the corresponding matrices will in the following be denoted by $D_{ij}^{\mu}(g)$. For any fixed triple of values of the indices ($\mu; i, j$), $D_{ij}^{\mu}(g)$ is a function on the group G . That is, it assigns a complex number to every element g of the group. Since i, j can take n_{μ} values each for every μ there are $\sum_{\mu} n_{\mu}^2 = n_G$ such functions, i.e. just as many as there are elements in the group, cf. Eq. (4.3).

The fundamental theorem of harmonic analysis states that these form a complete orthogonal set of functions on the group.

Orthogonality reads

$$\sum_g D_{ij}^{\mu}(g) D_{ml}^{\nu}(g^{-1}) = (n_G/n_{\mu}) \delta_{\mu\nu} \delta_{il} \delta_{jm} \quad . \quad (4.5)$$

The summation over g runs over all elements of the group. The Kronecker δ is defined by

$$\delta_{\mu\nu} = \begin{cases} 1 & \text{if } \mu = \nu \\ 0 & \text{otherwise} \end{cases} \quad \text{etc.}$$

⁺) Matrices can be viewed as operators in a vector space. Under a change of basis in this vector space they transform according to Eq. (4.2).

To explain the meaning of completeness, consider an arbitrary function f on the group. As was mentioned already, a function on the group is a rule which assigns a complex number $f(g)$ to every element g of the group. Completeness means that every such function f can be expanded in terms of the (complete) set of functions $D_{ij}^\mu(g)$, with suitable complex coefficients a_{ji}^μ

$$f(g) = \sum_{\mu} \sum_{i,j} a_{ji}^\mu D_{ij}^\mu(g) \quad . \quad (4.6)$$

The coefficients can be determined in terms of $f(g)$ by using the orthogonality relation (4.5). To do this one multiplies both sides of Eq. (4.6) with $D_{m\ell}^\nu(g^{-1})$ and sums over g . From (3.4) one obtains

$$a_{m\ell}^\nu = (n_\nu/n_G) \sum_g f(g) D_{m\ell}^\nu(g^{-1}) \quad (4.7)$$

where the summation runs over all elements g of the group G . We see that the coefficients a_{ji}^μ are weighted averages of f over the group.

In the applications we have in mind here, the group G is the group of symmetry transformations on the retina which was defined in Sec. 3. The function to be considered is the excitation $i(z)$ at the point z on the retina. We will now explain how this function can be interpreted as a function on the group.

Let us assume that the group G acts transitively on the manifold $M = \{z\}$ of points z (on the retina). That is, having chosen once and for all some arbitrary fixed point $\hat{z}$, one can find for every point z a suitable group element g_z such that

$$z = g_z \hat{z} \quad . \quad (4.8)$$

In the applications to be considered, transitivity will be satisfied.

We may now consider $i(z)$ as a function on the group by considering

$$f(g) \equiv i(g\hat{z}) = i(z) \quad \text{for } z = g\hat{z} \quad . \quad (4.9)$$

As g runs all over the group, each point z will be covered at least once, by transitivity. We may now expand $f(g)$ according to Eq. (4.6). For later convenience we redefine the coefficients a_{ji}^μ by a factor n_μ^{-1} , the new coefficients will be called A_{ji}^μ . One obtains

$$i(z) = \sum_{\mu} \sum_{i,j} n_\mu A_{ji}^\mu D_{ij}^\mu(g_z) \quad (4.10)$$

where g_z satisfies Eq. (4.8). In general g_z is not uniquely determined by the requirement (4.8). The r.h.s. of (4.10) must be the same for any choice of g_z satisfying (4.8). This is a consequence of definition (4.9). This leads to restrictions on the coefficients A_{ji}^μ as will be explained below. The coefficients are given by [cf. Eq. (4.7)]

$$A_{ji}^\mu = n_G^{-1} \sum_g i(g\hat{z}) D_{ji}^\mu(g^{-1}) \quad . \quad (4.11)$$

This expression can be simplified by carrying out a partial summation, cf. Eq. (4.13) below.

The coefficients A_{ji}^μ will turn out to be real. They will later be identified with activities of neurons; these neurons will be labelled by $(\mu; j, i)$. To know how many neurons are needed we have to determine how many nonvanishing coefficients A_{ij}^μ there are. A priori there can be n_G terms in the expansion (4.10) as was stated after Eq. (4.4). On the other hand, if there are n_M points on the retina then there are only n_M linearly independent functions $i(z)$. Consequently only n_M of the

coefficients A_{ji}^μ can be linearly independent. Indeed it is possible to show (see below) that one can, by a suitable choice of basis, make all but n_M of the coefficients A_{ji}^μ vanish identically for all excitations $i(\cdot)$. Thus there are only n_M nonvanishing terms in the expansion (4.10), (4.11), i.e. as many as there are receptors on the retina (see below for the definition of a suitable idealized "retina"). This is a crucial observation which will allow us to improve on McCulloch and Pitts (1947) theory and avoid their problem of too many neurons needed. Because of transitivity $n_G \geq n_M$, and in general n_G is very much larger than n_M . It follows from transitivity that $n_M = n_G/n_H$, where n_H is the number of elements of the "little group" to be defined presently.

Let us consider the subgroup H_S of G consisting of all elements h which satisfy

$$h\hat{z} = \hat{z} \quad . \quad (4.12)$$

This is called the "subgroup of stability" of $\hat{z}$, or sometimes the "little group". Every element g of G may be uniquely decomposed in the form

$$g = g_z h \quad , \quad h \text{ in } H_S \quad ,$$

where $z = g\hat{z}$, and g_z is the standard boost defined before. Eq. (4.11) may therefore be rewritten as

$$A_{ji}^\mu = n_G^{-1} \sum_z \sum_h i(z) D_{ji}^\mu(h^{-1} g_z^{-1}) = n_M^{-1} \sum_k (E^\mu)_{jk} \sum_z i(z) D_{ki}^\mu(g_z^{-1})$$

where
$$E^\mu = n_H^{-1} \sum_{h \in H_S} D^\mu(h) \quad \text{and} \quad n_M = n_G/n_H \quad .$$

Note that with h^{-1} taking every value in H_g once, the same is true of h . E^μ are projection operators (for a proof see Sec. 7, Eq. (7.4) and f.). Therefore E^μ can be diagonalized and have only eigenvalues 0 and 1. A suitable basis is now one in which E^μ are diagonal. Then $A_{ji}^\mu = 0$ unless j is such that $(E^\mu)_{jj} = 1$. The nonvanishing coefficients are given by

$$A_{ji}^\mu = n_M^{-1} \sum_z i(z) D_{ji}^\mu(g_z^{-1}) \quad (4.13)$$

Note that the summation now runs over only n_M terms.

Frequently the condition $(E^\mu)_{jj} = 1$ is satisfied for at most one value of j for each μ . This is in particular true if the group G is exhausted by the rotation group (cf. Sec. 8). A sufficient condition for the general case was given by Wigner (1968).

Up to here we have assumed that G is a finite group. The above considerations can be extended to continuous groups. The technical intricacies involved in this would appear biologically irrelevant because the retina has only finitely many receptors anyway and there are only a finite number of permutations of these.

It is nevertheless sometimes convenient to consider continuous groups. This is because of the important role which continuity plays in the mathematical control theory. In Sec. 6 we shall have occasion to study the group $O(3)$ of all rigid rotations around the point 0 in Fig. 1. This is a compact Lie group; such groups have properties very similar to finite groups. A rigid rotation is a coordinate transformation (see Fig. 1)

$$x'_a = \sum_b R_{ab} x_b \quad (a, b = 1, 2, 3) \quad (4.14)$$

where R is a real orthogonal 3×3 matrix with $\det R = 1$. It is convenient

to take the manifold M as a surface of a unit sphere. Of course neither the receptive fields of certain individual neurons (Barlow (1953), Hubel and Wiesel (1962)) nor the whole sensitive area of the retina cover the whole surface of a sphere. This may be taken into account by putting the excitation $i(z) = 0$ for points $z \in M$ outside. It may be helpful to recall at this time that the contribution to the activities A_{ji}^μ defined by (4.13) from disjoint subsets of M is simply additive, because of linearity of the summation process (4.13).

A point z on M may be characterized by a real unit vector $\underline{z} = (z_1, z_2, z_3)$ and the effect of a rotation (4.14) on the image z of x on the retina M is then given by

$$z'_a = \sum_b R_{ab} z_b \quad . \quad (4.15)$$

Here R is the same matrix as in (4.14). The inequivalent irreducible representations of $O(3)$ are well known (Hamermesh, 1962); they have arbitrary odd dimension $2\mu + 1$, $\mu = 0, 1, 2, \dots$. There are infinitely many of them, but it can be shown that there is no loss of resolution if one restricts oneself to consideration of representations of dimension $\leq 2(n_M)^{1/2}$. There are then again only n_M nonvanishing activities A_{ji}^μ . Harmonic analysis over the rotation group $O(3)$ is known in physics as "partial wave analysis" and has found many applications. The formulae of this section may be carried over to this case by replacing sums by integrals throughout. Eq. (4.13) can be kept as it stands as the appropriate approximation to such an integral, provided the density of receptors on the retina is uniform. If it is not, the r.h.s. of Eq. (4.13) has to be divided by the local density of receptors.

We remark that the rotations act transitively on M . Therefore the

standard boosts g_z may always be chosen as rotations. The representation matrices $D^\mu(R)$ are real orthogonal (for an admissible choice of basis) simultaneously for all R in $O(3)$. Therefore the activities A_{ji}^μ defined by Eq. (4.13) will be real. A real orthogonal matrix is *a posteriori* unitary. Throughout the sequel of this paper all matrices $D^\mu(g)$ will be assumed unitary.

Finally we will state some well known basic facts and definitions from the theory of angular momentum.

A rotation R may be parametrized in terms of a 3-vector $\underline{\theta} = (\theta_1, \theta_2, \theta_3)$. The direction of $\underline{\theta}$ gives the axis of rotation and its length $|\underline{\theta}|$ indicates the angle of rotation. The matrix R itself is given in terms of $\underline{\theta}$ by

$$R(\underline{\theta}) = \exp \left(\sum_a \theta_a X_a \right) \quad . \quad (4.16)$$

The exponential is defined by its power series expansion, and X_a are 3×3 matrices with entries $(X_a)_{bc} = \epsilon_{abc}$, where ϵ_{abc} is the completely antisymmetric tensor in 3 dimensions with $\epsilon_{123} = 1$. The indices a, b, c can take the values 1, 2, 3. The three matrices X_a are said to form the "Lie algebra" of $O(3)$. They do not commute, rather

$$[X_a, X_b]_- \equiv X_a X_b - X_b X_a = \sum_c \epsilon_{abc} X_c \quad . \quad (4.17)$$

From Eq. (4.17) one has

$$X_a = \frac{\partial}{\partial \theta_a} R(\underline{\theta}) \Big|_{\underline{\theta} = 0} \quad . \quad (4.18)$$

One also defines the representation matrices X_a^μ of the Lie algebra by

$$X_a^\mu = \frac{\partial}{\partial \theta_a} D^\mu(R(\underline{\theta})) \Big|_{\underline{\theta} = 0} \quad . \quad (4.19)$$

They are of course $n_\mu \times n_\mu$ matrices. They also satisfy commutation relations (4.17). Since D^μ are unitary, X_a^μ will be antihermitian.

It is convenient to use vector notation $\underline{a} \cdot \underline{b} = a_1 b_1 + a_2 b_2 + a_3 b_3$. We will use this notation also for the vector $\underline{X}^\mu = (X_1^\mu, X_2^\mu, X_3^\mu)$ whose components are matrices, etc.

The following lemma is basic:

Lemma. For continuous $\underline{\omega}(t)$ the differential equation

$$\frac{d}{dt} R(t) - R(t) \underline{X} \cdot \underline{\omega}(t) = 0 \quad (4.20)$$

has a unique solution $R(t)$ in $O(3)$ for any given initial $R(0)$ in $O(3)$. Conversely, if $R(t)$ is a rotation matrix which depends continuously and differentiably on t , then there is a unique continuous $\underline{\omega}(t)$ such that $(d/dt) R(t)$ is given by Eq. (4.20). Furthermore it follows from Eq. (4.20) that for any representation μ

$$\frac{d}{dt} D^\mu(R(t)) = D^\mu(R(t)) \underline{X}^\mu \cdot \underline{\omega}(t) \quad (4.21)$$

If t is time then $\underline{\omega}(t)$ has the geometrical meaning of an angular velocity vector at time t . We should also mention that the representation matrices X_a^μ transform as 3-vectors in the sense that for R in $O(3)$

$$D^\mu(R) X_a^\mu D^\mu(R^{-1}) = \sum_b X_b^\mu R_{ba} \quad (4.22)$$

Since R depends on 3 real parameters θ_a , Eqs. (4.20) are a system of 3 nonlinear differential equations for these 3 parameters. It can, in general, not be solved in closed form. Although we will not use it, it may be helpful for the reader if we remark that there is a formal or

power series solution (Feynman, 1951). To exhibit it, define the matrix

$$V(t) = \underline{X} \cdot \underline{\omega}(t)$$

and the time ordered product ("T-product")

$$T \{V(t_1) V(t_2)\} = \begin{cases} V(t_1) V(t_2) & t_1 \leq t_2 \\ V(t_2) V(t_1) & t_2 \leq t_1 \end{cases}$$

The time ordered product of N factors is defined analogously, the matrix with the latest time argument stands the farthest to the right, etc.

The solution of eqs. (4.20) with $S(0) = 1$ is then

$$\begin{aligned} S(t) &= T \exp \int_0^t dt' V(t') \\ &\equiv 1 + \int_0^t dt_1 V(t_1) + \frac{1}{2} \int_0^t \int_0^t dt_1 dt_2 T \{V(t_1) V(t_2)\} + \dots \end{aligned}$$

The time ordering operation is necessary because of the noncommutativity of matrices X_a , and therefore of $V(t)$ at different times. Using definition (4.18) the reader will find it easy to verify that (4.23) is indeed a solution of Eqs. (4.20).

V. Neuronal implementation

It has been known for a long time that there is a mechanism in the visual pathways for summing excitatory effects from neighbouring areas of the retina. Adrian and Mathews (1927a, b; 1928) and Hartline (1940) showed already that summation occurred if a discharge of impulses in the optic nerve was taken as the index of activity instead of the subjective sensation of light. This suggests that one has to do with a linear process.

Experimentally the quantity which is summated seems to be approximately proportional to the light intensity (in the frog) [Barlow, 1953]. The excitation at a point z of the retina, (taken as approximately proportional to the intensity of light at this point), will be denoted by $i(z)$.

We propose that the first step in the processing along the visual pathways of the information contained in $i(z)$ involves a harmonic analysis over the group G of symmetry transformations defined in Sec. 3. That is, weighted averages of the excitation (over the retina) are computed according to Eq. (4.13), viz.

$$A_{ji}^{\mu} = n_M^{-1} \sum_z i(z) D_{ji}^{\mu}(g_z^{-1}) \quad . \quad (4.13)$$

Presumably in nature the summation is performed in several steps such that summation is first taken over smaller receptive fields $M_{\alpha} \subset M$. (see Sec. 8). Note that the connection between A^{μ} and i is linear.

The neurons of a certain order may now be classified into bundles labelled by μ , with fibres within bundles labelled by (j,i) . Often j will only take one value, and $i = 1, 2, \dots, n_{\mu}$ (see Sec. 4). A_{ji}^{μ} is a measure of the activity in fibre (j,i) of bundle μ ; it may be related to a firing rate, or to the amplitude of modulation of noise if one wants to follow a proposal of Harth et al. (1970). In any case, probabilistic neurons (or receptors) appear necessary to carry out a summation process such as (4.13) (Barlow, 1953). Any probabilistic neurons will do, however, for which the activity (firing rate) is a continuously differentiable function of the excitation, because any such function looks linear locally. This is well known to every electronics engineer: He can use any transistor or vacuum tube he wishes for linear amplification, if

only he makes the amplitude of the input small enough.

In Fig. 3, the neural network implementing our model is shown schematically. Summation (4.13) is carried out by the neurons indicated. The rest of the figure will be explained later on.

Let us now determine the change in the activities A_{ji}^μ if the objects viewed are subject to a symmetry transformation. As was explained in detail in Sec. 3. This is equivalent to a transformation $g_1 \in G$ on the retina:

$$z \rightarrow z' = g_1 z \quad . \quad (5.1)$$

After the transformation the excitation i at the new point z' will be the same as the excitation before the transformation at the old point $z = g_1^{-1} z'$:

$$i(z') \rightarrow i(g_1^{-1} z') \quad \text{for all } z' \in M. \quad (5.2)$$

Hence by Eq. (4.11)

$$\begin{aligned} A_{ji}^\mu &\rightarrow A'_{ji}^\mu = (1/n_G) \sum_g i(g_1^{-1} g z) D_{ji}^\mu(g^{-1}) \\ &= (1/n_G) \sum_{g'} i(g' z) D_{ji}^\mu(g'^{-1} g_1^{-1}) \\ &= (1/n_G) \sum_g i(g z) D_{jk}^\mu(g^{-1}) D_{ki}^\mu(g_1^{-1}) \\ A'_{ji}^\mu &= \sum_k A_{jk}^\mu D_{ki}^\mu(g_1^{-1}) \end{aligned} \quad (5.3)$$

In the second line we introduced $g' = g_1^{-1} g$ and make use of the fact that with g assuming each value in the group once the same is true of g' ; therefore $\sum_g = \sum_{g'}$. In the third line we used the group representation

law (4.1)

From (5.3) we see that the new activities are linear combinations of the old activities in the same bundle μ . This is the crucial observation which allows us to consider each bundle by itself when we try to construct a mechanism of adaptation which can compensate the effect of a symmetry transformation on the activities A_{ji}^μ .

Eq. (5.3) can be inverted by using Eqs. (4.1). This gives

$$A_{ji}^\mu = \sum_k A_{jk}'^\mu D_{ki}^\mu(g_1) \quad . \quad (5.4)$$

Thus the old activities can be recovered from the new ones if the group element g_1 is known. To make use of this observation we propose a second step in the processing of information along the visual pathways. It involves computation of new activities B_{ji}^μ according to

$$B_{ji}^\mu = \sum_k A_{jk}^\mu C_{ki}^\mu \quad (5.5)$$

where the C_{ki}^μ are variable neuronal amplification factors, and are of the general form

$$C_{ki}^\mu = D_{ki}^\mu(g) \quad \text{for suitable } g \in G \text{ indep. of } \mu, k, i. \quad (5.6)$$

Obviously if $A_{jk}^\mu \equiv 0$ for (μ, j) and all k then the same is true of B_{jk}^μ ; therefore there are as many not identically vanishing activities B_{jk}^μ as there are $A_{jk}^\mu \neq 0$.

The computation (5.5) will be carried out by the neurons marked "mixer n", in Fig. 3. We call them "mixer neurons" because they have variable amplification factors. These amplification factors will be functions of the input reaching the neurons through the extra synapses

marked by * in Fig. 3. We propose that these neurons perform a function analogous to those of multi-grid vacuum tubes which are used as multiplicative mixers in electronics. (There the amplification factor with respect to the 1st control grid depends on the input voltage at the 2nd control grid). We will sometimes refer to the C^μ as "synaptical coupling matrices", even though this may be somewhat misleading.

Now the effect on the activities of a symmetry transformation g_1 can be compensated by a corresponding change

$$C_{ki}^\mu \rightarrow \sum_m D_{km}^\mu(g) C_{mi}^\mu \quad (5.7)$$

of the neuronal amplification factors. Such a change is consistent with relation (5.6) because of the group representation law (4.1). We have then from Eq. (5.3) that

$$\begin{aligned} B^\mu &\rightarrow A^\mu D^\mu(g_1^{-1}) D^\mu(g_1) C^\mu = A^\mu C^\mu \\ &= B^\mu \end{aligned} \quad (5.8)$$

so that the activities B_{ji}^μ remain unchanged. Here and in the following we use matrix notation; A^μ , B^μ , C^μ and $D^\mu(g)$ are considered as $n_\mu \times n_\mu$ matrices, etc.

In order to carry out the appropriate adaptation according to (5.7) the group element g_1 which specifies the symmetry transformation on the retina (cf. (5.1)) must be known to the brain, or be computed from available input data. There are several mechanisms which presumably contribute to this - including trial and error, calibration with the help of gravity to specify "down", sensory-motor interaction etc. Here we will be content with describing in some detail one such mechanism which is believed to be mainly responsible that we see a "constant" world despite

the many voluntary and involuntary movements of head and eyeballs. This will be the subject of the next section.

VI. Control

Observation shows that for humans rigid rotations $R \in O(3)$ of the outside world are elements of the symmetry group. That is $O(3) \subset G$. Suppose now for a moment that the observer sees a constant world, and that the only change of the image on his retina is due to a time dependent rotation of the eyeball. Such a rotation is equivalent to the inverse rotation of the outside world (x-space) around the eye. To every time interval $[t_1, t_2)$ there is then a rotation matrix $R_{[t_1 t_2)}$ which rotates a coordinate system in x-space from its orientation at time t_1 to its orientation at time t_2 . These matrices satisfy the law of concatenation:

$$R_{[t_1 t_3)} = R_{[t_1 t_2)} R_{[t_2 t_3)} \quad . \quad (6.1)$$

The time dependence of the neuronal activities A_{ji}^μ follows from Eq. (5.3) as

$$A_{ji}^\mu(t) = \sum_k A_{jk}^\mu(0) D_{ki}^\mu(R_{[0t)}) \quad . \quad (6.2)$$

We will in the present section only deal with continuous rotations such that the entries of the matrix $R_{[0t)}$ are continuously differentiable functions of time t . Then the lemma stated at the end of Sec. 4 may be used to differentiate Eq. (6.2) with respect to time:

$$\dot{A}^\mu(t) = - A^\mu(t) \underline{x}^\mu \cdot \underline{\rho}(t) \quad . \quad (6.3)$$

An overdot stands for time differentiation. $\underline{\rho}(t)$ indicates the angular velocity vector of the eyeball at time t . Throughout the sequel of this paper capital letters will denote matrices.

At time t the brain knows $A^\mu(t)$ and $\dot{A}^\mu(t)$, since their entries are activities of neurons and their time derivatives. The problem is to compute from these the appropriate time development of the coupling matrices $C^\mu(t)$ occurring in Eq. (5.5) in such a way that $B^\mu = A^\mu(t)C^\mu(t)$ are time independent. This is not difficult to do. One considers Eqs. (6.3) for all μ as a highly overdetermined system of linear equations for the 3 quantities $\underline{\omega} = (\omega_1, \omega_2, \omega_3)$. We know that it has at least one solution, namely $\underline{\omega}(t) = \underline{\rho}(t)$, where $\underline{\rho}$ is the angular velocity of the eyeball introduced above. We know from Sec. 5 that we should look for $C^\mu(t)$ of the form

$$C^\mu(t) = D^\mu(S^{-1}(t))C^\mu(0) \quad (6.4)$$

where $S(t)$ is a time dependent rotation matrix. Let us now impose on S the dynamics

$$\dot{S}(t) - S(t) \underline{X} \cdot \underline{\omega}(t) = 0 \quad (6.5)$$

with initial condition $S(0) = 1$. We know from the lemma of Sec. 4 that (6.5) has a unique solution. By the last statement of the lemma we obtain $\frac{d}{dt} D^\mu(S) = D^\mu(S) \underline{X} \cdot \underline{\omega}$. Taking the hermitian conjugate of this and inserting into Eq. (6.4) gives

$$\dot{C}^\mu(t) - \underline{\omega}(t) \underline{X}^\mu C^\mu(t) = 0 \quad (6.6)$$

We used unitarity, $D^\mu(S^{-1}) = [D^\mu(S)]^+$, and antihermiticity of X_a^μ .

Since by definition $\underline{\omega}(t)$ is a solution of differential equations (6.3) it follows finally that

$$\dot{B}^\mu = \dot{A}^\mu C^\mu + A^\mu \dot{C}^\mu = (\dot{A}^\mu + A^\mu \underline{\omega} \cdot \underline{X}^\mu) C^\mu = 0$$

as desired.

This solves the problem; nevertheless no biologist will be happy with such a solution. This is because one believes that the fundamental biological control problems are solved in nature by use of the principle of feedback, for reasons of stability. We can use feedback if we are willing to introduce a time constant τ into the problem, and take as control not $\underline{\omega}$ appearing in Eq. (6.6), but its time derivative $\dot{\underline{\omega}}$. This is a standard trick (Kalman, 1968). We then propose to set up a smooth dynamical system with states $(\underline{\omega}, S)$, control $(\underline{u})$, and output $(B^\mu, \dot{B}^\mu, \underline{Y}^\mu)$. S is a rotation matrix.

$$\text{state development:} \quad \dot{\underline{\omega}}(t) = \frac{1}{\tau} \underline{u}(t) \quad (\Sigma 1)$$

$$\dot{S} - S \underline{X} \cdot \underline{\omega} = 0 \quad (\Sigma 2)$$

$$\text{output map:} \quad \underline{Y}^\mu = (C^\mu)^{-1} \underline{X}^\mu C^\mu \quad (\Sigma 3)$$

$$B^\mu = A^\mu C^\mu \quad (M1)$$

$$\dot{B}^\mu = \dot{A}^\mu C^\mu + A^\mu \underline{\omega} \cdot \underline{X}^\mu C^\mu \quad (M2)$$

$$\text{where } C^\mu(t) = D^\mu(S^{-1}(t))C^\mu(0) \quad (M3)$$

$$\text{regulator:} \quad \underline{u} = \text{solution of } B^\mu \underline{Y}^\mu \cdot \underline{u} = -\dot{B}^\mu \text{ for all } \mu \cdot (R)$$

We pointed out previously that Eqs. ($\Sigma 2$) and ($M3$) imply that $\underline{\omega} \cdot \underline{X}^\mu C^\mu = \dot{C}^\mu$, so that it is indeed true that $\dot{B}^\mu$ defined by Eq. ($M2$) is equal to $\frac{d}{dt} B^\mu$.

The regulator computes the control from the output, therefore the principle of feedback is satisfied. The activities A^μ and $\dot{A}^\mu$ are

supplied by nature (see above), and are to be considered as part of the specifications of the machine.

These equations have been set up from intuition, and we will now have to prove that the whole control circuit works for sufficiently smooth input activities $A^\mu(t)$. In fact it must even be shown that it is consistent, because (R) is a highly overdetermined system of linear inhomogeneous equations for $\underline{u}$.

Our dynamical system is nonlinear, because the manifold $O(3)$ of state projections $\{S\}$ has no linear structures but is a curved space. However, it is compact, and this compactness is the deep reason why the following analysis succeeds.

Given initial $\underline{\omega}(0)$, Eq. (E1) is trivial to solve and its solution satisfies the hypothesis of the lemma of Sec. 4 for nonpathological $\underline{u}$. Hence (E2) has a unique solution. Let us then substitute the equations defining the output map into the regulator equation. The result is the following system of equations equivalent to (R), which determines the control from the state

$$A^\mu \underline{X}^\mu \cdot \underline{u} = -\dot{A}^\mu + A^\mu \underline{X}^\mu \cdot \underline{\omega} \quad . \quad (6.8)$$

By our working hypothesis that all time dependence comes from a rotation of the eyeball we know that $\dot{A}^\mu$ satisfy Eq. (6.3) for some $\underline{\rho}$. Therefore the highly overdetermined regulator equation (6.8) has a solution

$$\underline{u}(t) = \underline{\rho}(t) + \underline{\omega}(t) \quad . \quad (6.9)$$

Actually this solution will be unique except in special circumstances (when the outside world looks invariant under some continuous one parameter subgroup of $O(3)$). Substituting (6.9) into (E1) gives 3 linear

differential equations for the 3 quantities $\omega_a(t)$,

$$\tau \dot{\omega}(t) + \omega(t) = -\underline{\rho}(t) \quad (6.10)$$

with general solution

$$\omega(t) = -\underline{\rho}(t) + [\omega(0) + \underline{\rho}(0)]e^{-t/\tau} + \int_0^t d\sigma e^{-(t-\sigma)/\tau} \dot{\underline{\rho}}(\sigma) \quad (6.11)$$

Finally, substituting (6.10) back into (R) gives

$$\dot{B}^\mu = -B^\mu \underline{Y}^\mu (\underline{\rho} + \omega) \quad (6.12)$$

Note that there is still a dependence on $S(t)$ in this through the matrices Y_a^μ , cf. (Σ3) and (M3). To get an explicit solution of our system of equations (Σ1)...(R) we would therefore have to solve Eq. (Σ2) with ω from (6.11), compute $\underline{Y}^\mu$ from (Σ3) and (M3), substitute them into Eqs. (6.12) and solve this latter system of differential equations for $B^\mu(t)$, with initial condition $B^\mu(0) = A^\mu(0)C^\mu(0)$. However, because of the noncommutativity of matrices X_a , Eq. (Σ2) cannot be solved in closed form (cf. end of sec. 4), and neither can (6.12). Fortunately one can derive from (6.12) a good estimate of $\dot{B}^\mu$ without knowing S .

We will first show that $\dot{B}^\mu(t) \rightarrow 0$ if $\omega(t) \rightarrow -\underline{\rho}(t)$. Under what circumstances this latter condition is satisfied can be investigated from the explicit form (6.11) of $\omega(t)$.

We start by recalling the following properties of the norm of a matrix.

$$\|A B\| \leq \|A\| \|B\|, \quad \|C^{-1} A C\| = \|A\|.$$

If U is unitary, that is $U^{-1} = U^+$, then

$$\| U A \| = \| A U \| = \| A \| \quad .$$

Finally, and most important

$$\| A \| = 0 \text{ implies } A = 0 \quad . \quad (6.13)$$

By our standing assumption all $D^\mu(R)$ are unitary for R in $O(3)$. That this is a consistent assumption ultimately traces back to the fact that $O(3)$ is compact. Using Eqs. (M3) and (6.2) we find that $B^\mu(t) = A^\mu(0) D^\mu(R_{[0t]}) S^{-1}(t) C^\mu(0)$. Hence

$$\| B^\mu(t) \| \leq \| A^\mu(0) \| \| C^\mu(0) \|\quad$$

and, consequently, from (6.12)

$$\| \dot{B}^\mu(t) \| \leq | \underline{\rho}(t) + \underline{\omega}(t) | \| A^\mu(0) \| \| C^\mu(0) \| \max_{|\underline{e}|=1} \| \underline{e} \underline{X}^\mu \| ,$$

where the maximum is taken with respect to all unit vectors $\underline{e}$. From the well known representation theory of the rotation group (Hamermesh, 1962) one obtains that

$$\| \underline{e} \underline{X}^\mu \| \leq \frac{1}{2} (n_\mu - 1) \quad \text{independent of } \underline{e} \quad .$$

where as usual n_μ is the dimension of the representation (μ) of the full symmetry group G . Hence finally

$$\| \dot{B}^\mu \| \leq K_\mu | \underline{\rho}(t) + \underline{\omega}(t) | \quad (6.14)$$

where $K_\mu = \frac{1}{2} (n_\mu - 1) \| A^\mu(0) \| \| C^\mu(0) \|$ are finite numbers independent of t . Therefore $\dot{B}^\mu(0) \rightarrow 0$ if $\underline{\omega}(t) \rightarrow -\underline{\rho}(t)$.

Next we observe that we may obtain from the explicit expression (6.11) for $\underline{\omega}(t)$ an inequality

$$| \underline{\omega}(t) + \underline{\rho}(t) | \leq \tau \sup_{t' < t} | \dot{\underline{\rho}}(t') | \quad . \quad (6.15)$$

Recall that $\underline{\rho}(t)$ is the angular velocity vector of the eyeball at time t . Let us now assume that the rotations $R_{[0t]}$ of the eyeball are sufficiently smooth as functions of time so that the sup in (6.15) is finite. From Eq. (6.14) we get then our final estimate

$$\| \dot{B}^\mu \| \leq \tau K_\mu \sup_{t' < t} | \dot{\underline{\rho}}(t') | \quad . \quad (6.16)$$

From Estimate (6.16) we see in particular that the temporal change $\dot{B}_{ji}^\mu$ of activities B_{ji}^μ becomes very small if

$$| \dot{\underline{\rho}}(t') | \ll \frac{1}{\tau} \quad \text{for all } t' < t \quad , \quad (6.17)$$

that is, if the time constant τ is sufficiently small.*) In particular $\dot{B}_{ji}^\mu \rightarrow 0$ if $\tau \rightarrow 0$. In the idealized case of an arbitrarily small time constant τ we thus recover the ideal response $\dot{B}^\mu = 0$.

The whole control circuit is included in schematic form in Fig. 3. It is assumed that the mixer neurons are calibrated in such a way that they compute output activities B^μ from input activities according to Eq. (M1), with $C^\mu(t)$ from (M3). In drawing the control circuit in Fig. 3 we have taken as output variable $S(t)$ in place of $Y_a^\mu(t)$. This is possible since we may define time independent triples of matrices $\underline{z}^\mu = (z_1^\mu, z_2^\mu, z_3^\mu)$ by $\underline{z}^\mu = [C^\mu(0)]^{-1} \underline{x}^\mu C^\mu(0)$. Then

* If control fails because condition (6.17) is not satisfied, then the subject will get dizzy.

$$y_a^\mu(t) = D^\mu(S(t)) z_a^\mu D^\mu(S^{-1}(t)) = \sum_b z_b^\mu S_{ba}(t); \quad (6.18)$$

cf. Eq. (4.22).

The reader may wonder why we used Eqs. (R) or, equivalently, (6.8) as regulator equations. Since they are highly overdetermined systems of equations for only 3 quantities $\underline{u} = (u_1, u_2, u_3)$ one might think of selecting a subgroup of 3 independent equations to determine $\underline{u}$. This, however, is not a sensible thing to do:

Until now we have assumed that the eye sees a "constant" world, so that the only change of the image on the retina is due to the rotation of the eyeball. As a consequence the temporal change of the activities $A^\mu(t)$ was of the form (6.2). This is an idealization which does not correspond to reality; in general the eye will see a changing world. This will result in fluctuations of the activities A^μ around values of the form (6.2). These fluctuations can be treated as noise. As a consequence, B^μ as given by Eq. (M1) will also be affected by noise. Therefore the regulator equation (R) is now a system of linear inhomogeneous equations with noisy coefficients. From it $\underline{u}$ must be determined in such a way that the effect of this noise is minimized. This is a problem in information theory which will not be attacked here. It is however clear that an optimal solution will require the use of all the equations (R). (cf. Winograd and Cowan, 1963).

VII. Perception of symmetrical objects.

Imagine that our "good old eye" is located at the centre of a hollow sphere whose surface is formed by a spherical white wall. Imagine further that a small circle is painted somewhere on this wall. Such a circle is a very symmetrical object: it remains invariant under the

action of any rotation around the axis formed by the straight line joining the centre of the painted circle to the centre of the eye's lens. We want the eye to recognize the symmetry of such a circle, and of other symmetrical objects, irrespective of where in the visual field they are located. We will obtain a solution to this problem in the present section.

Mathematically the problem may be formulated as follows: Let there be given a subgroup H of our group G of symmetry transformations. We want a criterion expressed in terms of the neuronal activities B_{ji}^μ which is satisfied if and only if there exists a rotation R in $O(3)$ such that the excitation $i(z)$ on the retina M satisfies

$$i(z) = i(h'z) \quad \text{for all } h' \text{ in } H' = RHR^{-1}, \quad (7.1)$$

and for all z on M . The group H' consists of all those elements of G which are of the form $h' = RhR^{-1}$, h in H . We will say that H' is "rotationally conjugate" to H . In the above example H is the continuous 1-parameter group of all rotations around some fixed axis, and R is the rotation which takes this fixed axis into the line joining the circle's centre to the eye (s. above). The group elements act on the retina in the way explained in detail in Sec. 3; it is convenient to idealize the retina as a surface of a sphere. There are of course other subgroups H which are relevant in practise, for instance discrete rotations by multiples of $2\pi/n$. The following discussion will be valid for an arbitrary subgroup H of G .

We shall first formulate our criterion in terms of the primary activities A_{ji}^μ ; it can afterwards be rewritten in terms of B_{ji}^μ by virtue of relation (5.5), viz. $A^\mu = B^\mu (C^\mu)^{-1}$.

Let us first define, as a measure of the total illumination of the retina, the quantity

$$i_{\text{tot}}^2 = n_M^{-1} \sum_z [i(z)]^2 \quad . \quad (7.2)$$

The basis of our analysis will be the following relation, which is known as "Plancherel's theorem":

$$\sum_{\mu} n_{\mu} \left(\sum_{j,i} |A_{ji}^{\mu}|^2 \right) \equiv \sum_{\mu} n_{\mu} \text{tr}(A^{\mu} A^{\mu+}) = i_{\text{tot}}^2 \quad . \quad (7.3)$$

A^+ stands for the hermitian conjugate of a matrix A , and tr denotes the trace. Plancherel's theorem follows from the completeness properties explained in Sec. 4, and is one of the fundamental theorems in harmonic analysis.

To start with, let us consider some fixed subgroup H' of G , with n_H elements. (We use discrete notation throughout, but all results are equally valid for continuous subgroups if sums are replaced by integrals in the obvious way). Let us define the matrices

$$E_{H'}^{\mu} = n_H^{-1} \sum_{h'} D^{\mu}(h') \quad , \quad (7.4)$$

where summation is over all elements h' of H' . These matrices are projection operators, that is

$$(a) E^2 = E \quad , \quad \text{and} \quad (b) E^+ = E \quad . \quad (7.5)$$

Furthermore a matrix A^{μ} satisfies

$$A^{\mu} D^{\mu}(h') = A^{\mu} \quad , \quad \text{for all } h' \text{ in } H' \quad , \quad \text{if and only if} \quad A^{\mu} = A^{\mu} E_{H'}^{\mu} \quad (7.6)$$

[Proofs: Lemma (7.6): " " is obvious. " ": Let $A^\mu = A^\mu E_{H'}^\mu$; then $A^\mu D^\mu(h') = \sum_{h''} A^\mu D^\mu(h'') D^\mu(h') = \sum_{h''} A^\mu D^\mu(h''h') = \sum_{h'''} A^\mu D^\mu(h''') = A^\mu E_{H'}^\mu$. Here we used the fact that with h'' assuming every value in the group H' exactly once, the same is true of $h''' = h'' h'$.

By the same argument one finds that $E_{H'}^\mu = E_{H'}^\mu D^\mu(h')$ for all h' in H' . Eq. (7.5a) follows then from (7.6). Finally, (7.5b) is proven by using unitarity of D , viz. $[D^\mu(h')]^\dagger = D^\mu(h'^{-1})$.]

Finally we recall an elementary lemma from linear algebra which says that for any projection operator E and arbitrary matrix A

$$\text{tr}(AEA^\dagger) \leq \text{tr}(AA^\dagger) \quad (7.7)$$

and the equality sign holds if and only if $A = AE$.

Noting that every term in the sum (7.3) is positive we can apply these results to obtain

$$(i_{\text{tot}}^2)^{-1} \sum_{\mu} n_{\mu} \text{tr}(A^\mu E_{H'}^\mu A^{\mu\dagger}) \leq 1 \quad (7.8)$$

where the equality holds if and only if

$$A^\mu = A^\mu D^\mu(h') \quad \text{for all } h' \text{ in } H', \text{ and for all } \mu. \quad (7.9)$$

Comparing this condition with the transformation law (5.3) of the neuronal activities A_{ji}^μ under a symmetry transformation (5.2) we see that (7.9) is just the condition that the excitation $i(z)$ on the retina is invariant under H' .

Now let $H' = RHR^{-1}$. From definition (7.4) of $E_{H'}^\mu$, and the group representation law (4.1) one finds that

$$E_{H'}^\mu = D^\mu(R) E_H^\mu D^\mu(R^{-1}) \quad (7.10)$$

Let us define the function $\alpha(R)$ on the 3-dimensional manifold $O(3)$ of all rigid rotations R by

$$\alpha(R) = (i_{\text{tot}}^2)^{-1} \sum_{\mu} n_{\mu} \text{tr}(A^{\mu} D^{\mu}(R) E_H^{\mu} D^{\mu}(R^{-1}) A^{\mu+}) \quad (7.11)$$

Since a rotation R is characterized by 3 real variables $\underline{\theta} = (\theta_1, \theta_2, \theta_3)$ according to Eq. (4.16), α is a function of 3 real variables. By our previous considerations $\alpha(R) \leq 1$, and $=1$ if and only if the excitation $i(z)$ is invariant under $H' = RHR^{-1}$. Hence we finally find that the invariance property (7.1) is satisfied for a suitable R if and only if

$$\max_R \alpha(R) = 1 \quad (7.12)$$

This is the desired criterion. The maximum is with respect to all rotations R in $O(3)$. It can be shown that $\alpha(R)$ is continuous and continuously differentiable, because of the finite resolution of the eye (cf. end of Sec. 4), hence $\alpha(R)$ attains its maximum since $O(3)$ is compact. If the invariance of $i(z)$ is only approximate then $\max \alpha(R) = 1 - \delta$, where $\delta > 0$ is a quantitative measure of how badly the invariance is violated.

The criterion (7.12) could be more easily used if one could derive an expression for the rotation R for which the maximum is attained. We will now present a partial solution to this problem.

Differentiability of $\alpha(R)$ implies that it attains its maximum for a value of R such that

$$\delta \alpha(R) = 0 \quad (7.13)$$

for infinitesimal variations of R , viz. $R \rightarrow RR_{\epsilon}$, where R_{ϵ} differs infinitesimally from the unit matrix 1 . Let us now define the functions ("vector field") $\underline{\beta}(R) = (\beta_1, \beta_2, \beta_3)$ by

$$\underline{\beta}(R) = (i_{\text{tot}}^2)^{-1} \sum_{\mu} n_{\mu} \text{tr}(A^{\mu} D^{\mu}(R) [X^{\mu}, E_H^{\mu}] D^{\mu}(R^{-1}) A^{\mu+}) \quad . \quad (7.14)$$

According to the group representation law (4.1) and definition (6.6) of X^{μ} one has $D^{\mu}(RR_{\epsilon}) = D^{\mu}(R)D^{\mu}(R_{\epsilon}) = D^{\mu}(R)(1 + \epsilon X^{\mu})$, where $\epsilon = (\epsilon_1, \epsilon_2, \epsilon_3)$ are infinitesimal parameters. Inserting this into definition (7.11) of α we find that the condition $\delta \alpha(R) = 0$ is equivalent to

$$\underline{\beta}(R) = 0 \quad . \quad (7.15)$$

This is a system of 3 transcendental equations for the 3 real parameters θ characterizing R . A solution of these equations corresponds to a local extremum of $\alpha(R)$.

One can set up a smooth dynamical system to compute such external values of α . To this end let us consider a time dependent rotation matrix $R(t)$. We impose on $R(t)$ a time development as follows

$$\tau \dot{R} - R \underline{X} \cdot \underline{\beta}(R) = 0 \quad (7.16)$$

where τ is some time constant. A dot stands for differentiation with respect to t . The solutions of (7.16) with initial $R(0)$ in $O(3)$ are rotation matrices (Helgason, 1962. See also lemma (4.20) of Sec. 4). By differentiating definition (7.1) of $\alpha(R(t))$ with respect to time t one finds after some algebra (which should by now be familiar to the reader) that

$$\frac{d}{dt} \alpha(R(t)) = |\underline{\beta}(R(t))|^2 \geq 0 \quad . \quad (7.17)$$

Thus $\alpha(R(t))$ is monotonically increasing with t . Since it is also bounded by 1 it has a limit

$$\lim_{t \rightarrow \infty} \alpha(R(t)) = \alpha_{\infty} \quad .$$

Consequently $\beta(R(t)) \rightarrow 0$ as $t \rightarrow \infty$, by (7.17). Therefore α_∞ is an extremum. This is true whatever the initial value $R(0)$ chosen for solving the differential equation (7.16) for $R(t)$. Using this result we get a useful sufficient condition that (7.1) will be satisfied for a suitable R :

Let $R(t)$ be a solution of differential equations (7.16) and let R_∞ be a limit point of $R(t)$ as $t \rightarrow \infty$. If $\alpha(R_\infty) = 1$ then the excitation $i(z)$ is invariant under a subgroup H' rotationally conjugate to H .

Note that a limit point of $R(t)$ always exists because the manifold of $O(3)$ is compact. Results from global analysis (Smale, 1967) indicate that the extremum $\alpha(R_\infty)$ will "almost always" be at least a local maximum, rather than a minimum or saddle point. (Almost always means except for initial values $R(0)$ in a set of Haar measure zero.) The just derived sufficient condition would therefore also be a necessary one, at least in a statistical sense, if every local maximum of α were guaranteed to be also a global maximum. Unfortunately this cannot be expected to be always satisfied. It seems nevertheless quite possible that the brain makes use only of the sufficient condition (7.18) rather than the more complicated necessary and sufficient condition (7.12). After all it is certainly conceivable that the brain sometimes fails to recognize an invariance.

We should also remark that, although the transition from a system of ordinary transcendental equations (7.15) to nonlinear differential equations (7.16) might hardly seem progress from a mathematical point of view, it is otherwise from a biological point of view. This is because neuronal implementations of (smooth) dynamical systems is presumably what the brain is composed of.

In the above deliberations, the activities A_{ji}^μ were treated as independent of t . If t is to be identified with physical time, this means that we assumed that these activities stay approximately constant over time intervals of length τ . This assumption can be relaxed by going over to the activities B_{ji}^μ ; these are approximately time independent as a result of the working of the control mechanism described in Sec. 6.

In the simplest case that the rotation group $O(3)$ exhausts the whole group G of symmetry transformations one has $C^\mu = D^\mu(S)$ for some S in $O(3)$, so that $D^\mu(R)C^\mu = D^\mu(RS)$. We may then define new functions

$$\alpha(R) = (i_{\text{tot}}^2)^{-1} \sum_{\mu} n_{\mu} \text{tr}(B^\mu D^\mu(R) E_H^\mu D^\mu(R^{-1}) B^{\mu+}) \quad , \quad (7.19)$$

$$\underline{\beta}(R) = (i_{\text{tot}}^2)^{-1} \sum_{\mu} n_{\mu} \text{tr}(B^\mu D^\mu(R) [\underline{X}^\mu, E_H^\mu]_- D^\mu(R^{-1}) B^{\mu+}) \quad .$$

In terms of these new functions α and $\underline{\beta}$ the necessary and sufficient criterion (7.12) and the sufficient condition (7.18) with (7.16) remain valid literally as they stand.

VIII. Local response function of individual neurons.

Let us consider the response of an individual neuron to an excitation i at a point z of the retina. The set of all points z whose excitation can influence the activity of the given neuron is called the "receptive field" of this neuron. Suppose we increase the excitation at a point z in the receptive field by an amount $\delta i(z) > 0$. Then z is said to lie in an excitatory region of the receptive field if this change results in an increase in activity of the given neuron. If instead a decrease results then z is said to lie in an inhibitory region of the receptive field. Experimentally the excitatory and inhibitory regions of a receptive field often form geometrical patterns which show

a certain amount of symmetry (Barlow (1953), Hubel and Wiesel (1962)). Such a geometrical pattern will be called the "characteristic pattern" of the neuron considered. We wish to investigate how their symmetry properties can come about in the present model. In comparing with experimental data it must of course be remembered that the present model is only designed to describe the first few steps in the processing of visual information, including in particular those carried out in the retina. It is not meant to give a description of the certainly much more complex action of the association networks of the visual cortex of a cat, for instance.

Let us consider low order neurons whose activities are assumed to be given by Eq. (4.13). For points z outside the receptive field one has to put $i(z) = 0$. The quantity

$$I_{jm}^{\mu}(z) = D_{jm}^{\mu}(g_z^{-1}) \quad (8.1)$$

will be called the "local response function" of neuron $(\mu; j, m)$. From Eq. (4.13) we see that it is positive on excitatory regions and negative on inhibitory regions of the receptive field. Its magnitude indicates the strength of the excitation or inhibition.

The characteristic pattern of neuron $(\mu; j, m)$ will be invariant under a symmetry transformation which takes

$$z \rightarrow hz$$

if

$$I_{jm}^{\mu}(z) = I_{jm}^{\mu}(h^{-1}z) \quad (8.2)$$

for all z in the receptive field.

Let us now assume for simplicity that the rotation group $O(3)$ exhausts the whole group G of symmetry transformations. Since one may in any case take the standard boosts g_z as rotations, generalization to larger symmetry groups would bring nothing essentially new. The representation matrices $D^\mu(R)$ of irreducible representations (μ) of the rotation group can be found in any standard text book, e.g. Hamermesh (1962), Sec. 9-3. The choice of basis is essentially fixed by the requirements listed under Eq. (4.13) of Sec. 4. There is still the freedom of choosing the standard point $\hat{z}$ (see Sec. 4). It will turn out that $\hat{z}$ will be the centre of symmetry of many characteristic patterns. Experimental evidence cited above suggests that it should be chosen in the centre of the receptive field. Let (θ, ψ) be polar coordinates of a point z on the idealized retina (unit sphere) M with north pole $\hat{z}$:

$$z = (\sin \theta \cos \psi, \sin \theta \sin \psi, \cos \theta) ; \hat{z} = (0, 0, 1) .$$

From the well known representation theory of the rotation group and the requirements stated under Eq. (4.13) of Sec. 4 we find that j takes only one value $j = 0$, so that all neurons are labelled $(\mu; 0, m)$. The local response functions are given by

$$I_{0m}^\mu(z) = \begin{cases} \sqrt{2} P_\mu^m(\cos \theta) \cos m\psi & m > 0 \\ P_\mu^0(\cos \theta) & m = 0 \\ \sqrt{2} P_\mu^{-m}(\cos \theta) \sin m\psi & m < 0 \end{cases} \quad (8.3)$$

$$m = \pm 1, \pm 2, \dots, \pm \mu .$$

The functions P_μ^m and $P_\mu = P_\mu^0$ are spherical harmonics (associated Legendre functions). Some of the characteristic patterns determined by

Eq. (8.3) are shown in Fig. 4.

From Eq. (8.4) we can read off symmetries of the characteristic patterns. Evidently the characteristic pattern of neuron $(\mu; 0, m)$ will be invariant under rotations by multiples of $2\pi/n$ around $\hat{z}$:

$$\psi \rightarrow \psi + k \frac{2\pi}{n} , \quad k = 0, 1, 2, \dots ,$$

if and only if m is divisible by n . Therefore approximately 50% of the neurons will have characteristic patterns with a 2-fold symmetry axis, ~ 33% with a 3-fold axis, and ~25% with a 4-fold axis, etc. A few neurons - those with $m = 0$ - will have a characteristic pattern with complete circular symmetry.

We also wish to point out that a large majority of neurons will not respond to illumination of the retina with diffuse light, assuming that the numbers of receptors in the receptive fields are large and that their boundaries are not sharp. According to the statements under Eq. (4.15) of Sec. 4, μ must then take all integer values up to a large number. Since m can take $2\mu + 1$ values for each μ , most neurons will be labelled by large μ , and often large $|m|$ in addition. If μ is large, the local response function $I_{Om}^{\mu}(z)$ will be a rapidly oscillating function of z . The activity A_{Om}^{μ} given by Eq. (4.13) will accordingly be very small if $i(z)$ is a smooth function of z as corresponds to diffuse illumination. The activity will be much larger if $i(z)$ has a discontinuity such as a sharp light-dark boundary. These features are analogous to those of the ordinary Fourier transform which were mentioned at the end of Sec. 2 (at least qualitatively).

Finally we wish to make some remarks on the addition of information from different receptive fields.

Consider a set of receptive fields M_α , $\alpha: 1, 2, \dots$, and let $\hat{z}_\alpha$ the standard point (symmetry axis, see above) be in the centre of M_α . The standard boosts will be denoted by g_z^α ; by definition they satisfy

$$z = g_z^\alpha \hat{z}_\alpha \quad \text{for } z \text{ in } M_\alpha \quad . \quad (8.4)$$

Let us now assume that activities $A_{ji}^\mu(\alpha)$ are computed according to Eq. (4.13) from the excitation $i(z)$ (z in M_α) on the receptive field M_α , viz

$$A_{ji}^\mu(\alpha) = \sum_{z \in M_\alpha} i(z) D_{ji}^{\mu\alpha} ((g_z^\alpha)^{-1}) \quad . \quad (8.5)$$

Here we dropped an inessential proportionality factor. The index α on matrices $D^{\mu\alpha}$ serves to remind us that in general a different choice of basis for the representation matrices D^μ will be necessary for different α . According to the requirements stated in Sec. 4 after Eq. (4.12), the basis must be chosen in such a way that the projection operators

$$E^{\mu\alpha} = n_H^{-1} \sum_{h \in H_\alpha} D^{\mu\alpha}(h) \quad (8.6)$$

are diagonal. H_α consists of all elements h for which $h\hat{z}_\alpha = \hat{z}_\alpha$, thus it clearly depends on α . n_H is the number of elements in H_α . It does not depend on α because the groups H_α are conjugate.

Let us assume for simplicity that the receptive fields M_α are disjoint, that is $M_\alpha \cap M_\beta = \emptyset$ for $\alpha \neq \beta$. The question is how the activities $A_{ji}^\mu(\alpha)$ should be added so that the excitation $i(z)$ on the larger manifold $M = \bigcup_\alpha M_\alpha$ can be recovered from the new activities. The answer will be given in Eq. (8.12) below.

To derive it let us select in some arbitrary way a new standard $\hat{z}$, and choose g_α in G such that

$$\hat{z}_\alpha = g_\alpha \hat{z} \quad . \quad (8.7)$$

To every z on M we may then define a new standard boost g_z by

$$g_z = g_z^\alpha g_\alpha \quad \text{if } z \in M_\alpha \quad . \quad (8.8)$$

(There is no sum over α , neither here nor anywhere, except when explicitly indicated). Obviously

$$z = g_z \hat{z} \quad \text{for all } z \text{ in } M = \bigcup_\alpha M_\alpha \quad . \quad (8.9)$$

Let H be the subgroup of stability of z , and let E^μ be the associated projection operators. Let D^μ be the representation matrices in a basis where E^μ are diagonal. Since D^μ and the various $D^{\mu\alpha}$ differ only by a choice of basis there are matrices $S^{\mu\alpha}$ such that (see Eq. (4.2))

$$D^{\mu\alpha}(g) = (S^{\mu\alpha})^{-1} D^\mu(g) S^{\mu\alpha} \quad \text{for all } g \text{ in } G \quad . \quad (8.10)$$

It is a matter of straightforward algebra to verify that $D^{\mu\alpha}$ satisfy the above stated requirements if

$$S^{\mu\alpha} = D^\mu(g_\alpha) \quad . \quad (8.11)$$

Let us now define the new activities

$$A_{ji}^\mu = \sum_\alpha \left(\sum_k A_{jk}^\mu(\alpha) D_{ki}^\mu(g_\alpha^{-1}) \right) \quad . \quad (8.12)$$

Note that only activities with the same index μ are added. Inserting Eqs. (8.5) with $D^{\mu\alpha}$ given by Eqs. (8.10) and (8.11) we find

$$A^\mu = \sum_{z \in M} i(z) D^\mu(g_z^{-1}) \quad . \quad (8.13)$$

Here we used the group representation law (4.1) and expression (8.8) for the standard boost g_z . According to Eq. (4.10) we can invert Eq. (8.13) to recover $i(z)$

$$i(z) \propto \sum_{\mu} n_{\mu} \operatorname{tr}(A^{\mu} D^{\mu}(g_z)) \quad \text{for all } z \text{ in } M = \bigcup_{\alpha} M_{\alpha}.$$

This proves that Eq. (8.12) specifies a correct way of adding information from disjoint receptive fields M_{α} .

Generalization to overlapping receptive fields is straightforward. Let there be given a "partition of unity", i.e. a set of functions $e_{\alpha}(z)$ such that $\sum_{\alpha} e_{\alpha}(z) = 1$ for all z in M , and $e_{\alpha}(z) = 0$ for z outside M_{α} . Then partial activities $A_{ji}^{\mu}(\alpha)$ may be computed from the excitation $i(z)$ (z in M_{α}) on the receptive fields M_{α} according to

$$A_{ji}^{\mu}(\alpha) = \sum_z i(z) e_{\alpha}(z) D_{ji}^{\mu\alpha}((g_z^{\alpha})^{-1}) \quad . \quad (8.14)$$

A correct way of adding these is again given by Eq. (8.12).

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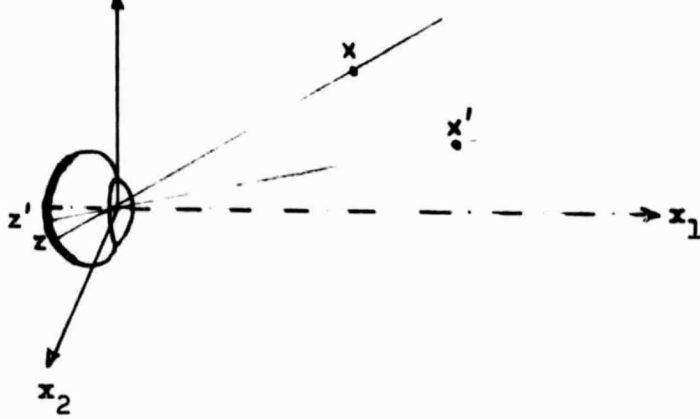


Fig.1. Image on the retina (see Sec.3)

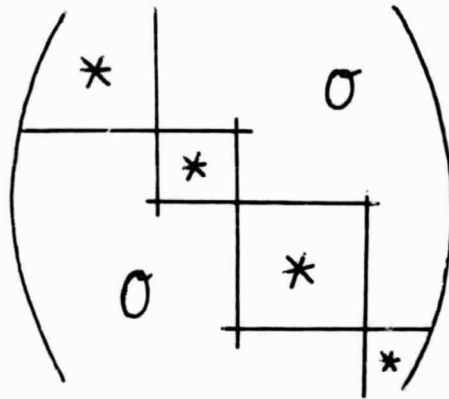


Fig.2. Block diagonal matrix (see Sec.4)

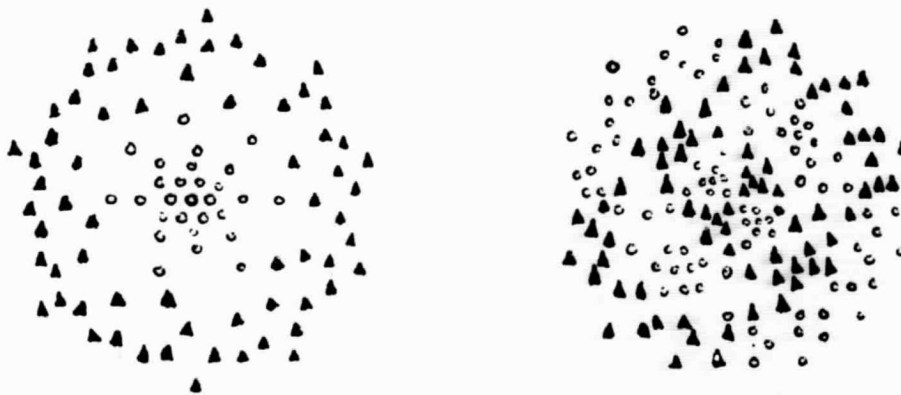


Fig.4. Examples of receptive fields (see Sec.8)

o = excitatory region , Δ = inhibitory region (or vice versa)

The density of symbols is meant as a rough indication of the strength of excitation or inhibition

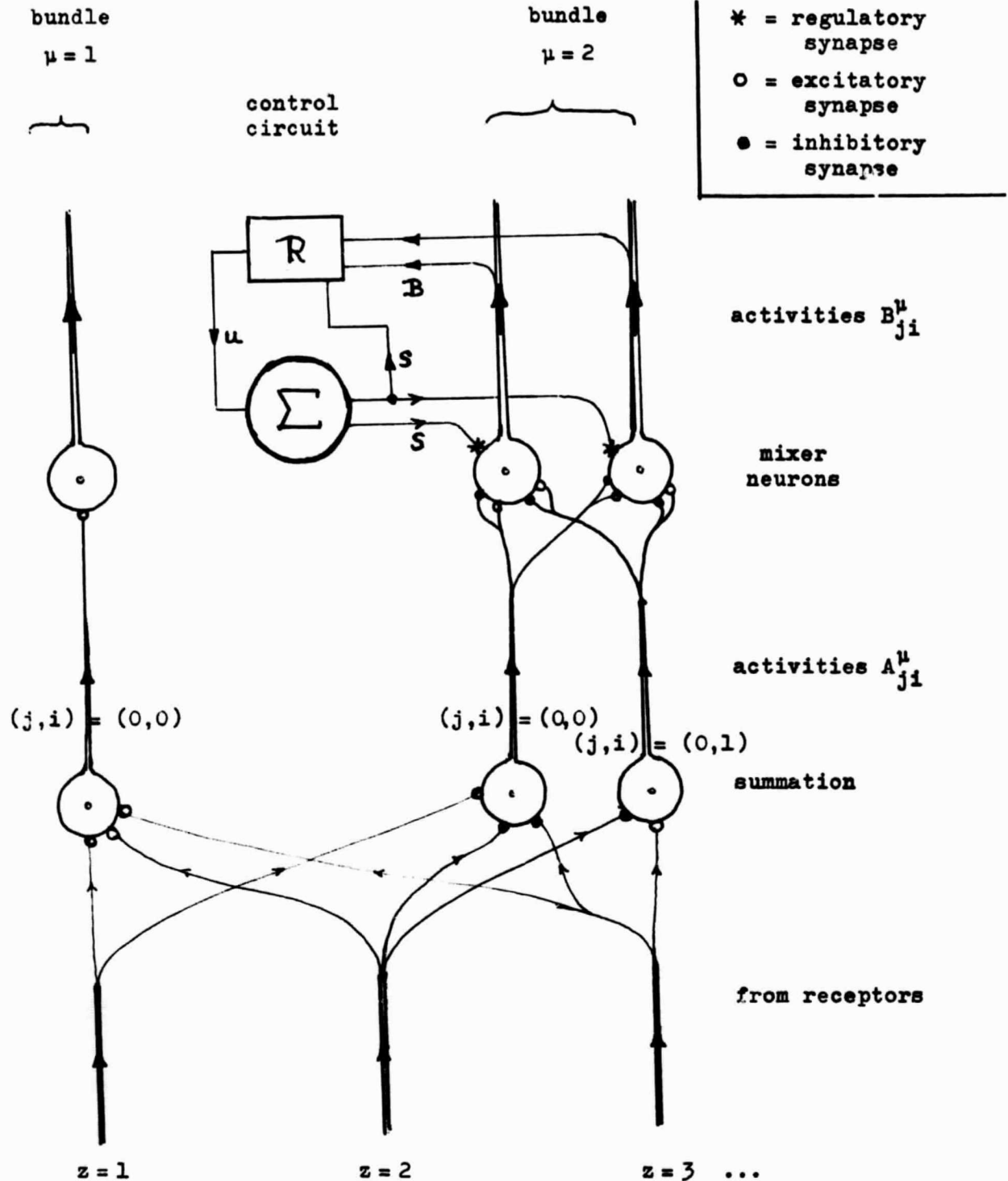


Fig.3 Neuronal implementation.

For explanation see text, Secs.5 and 6. The regulator "R" is described by Eqs(R) and (6.18), and the system "Σ" by Eqs. (Σ1) and (Σ2) of Sec.6. The activities A_{ji}^μ are computed according to Eq.(4.13), and the activities B_{ji}^μ according to Eqs.(M1) and (M3) of Sec.6.