Towards a Theory of Cell Assemblies

G. Palm

Max-Planck-Institut für biologische Kybernetik, Tübingen, FRG

Abstract. The term cell assembly, first introduced by D. O. Hebb, is defined in the framework of graph theory. This definition leads to some beautiful problems concerning the number and size of cell assemblies in large graphs. Some approaches to solve these problems are presented. In particular, the graphs $K_n \times K_m$ are constructed that have $n \cdot m$ points, $n + m - 2$ connections per point, and at least $2^n + 2^m - 4$ assemblies. Several new notions of connectivity in directed graphs are introduced and their relationships are investigated. The insight into these notions and their relationships will be helpful for further construction of graphs with many assemblies and/or high connectivity. The resulting graphs are not only important for the idea of cell assemblies in the context of neurodynamics, they may also find applications in the construction of communication networks and associative memories.

0. Introduction

The word "cell assembly" goes back to the psychologist Hebb (1949) and means a group of neurons in the brain that are strongly connected together and that represent a "concept" of our knowledge. The idea of a "cell assembly" has been used to answer several questions:

1. How are concepts and objects represented in our brain? *Answer*: Not in single neurons, but in cell assemblies.

2. How is information stored and recalled in our brain? *Answer*: It is stored in terms of cell assemblies and it is recalled by pattern completion when part of a cell assembly calls forth the rest of it.

3. How do we learn? *Answer*: By forming associations between concepts embodied in excitatory connections

between cell assemblies. In this way we may also form new cell assemblies.

4. How can we describe the electrical activity of all the neurons in the brain in a simplified way? *Answer*: As a succession of active cell assemblies governed by the rules of threshold control (cf. Braitenberg, 1978).

It seems that thinking in terms of cell assemblies may provide an intermediate description of the brain between the psychological and the electrophysiological level and with reasonably strong relations to both levels. These strong relations to both levels have lead to the question: Are they real?

From the anatomical point of view the idea of cell assemblies requires excitatory connections between all parts of the cortex (since all kinds of things can be associated with each other) and though the evidence for this is still incomplete there are indications that this is true (cf. Braitenberg, 1978).

From the physiological point of view the idea requires variable excitatory synapses that obey Hebb's rule (i.e. the connectivity is enhanced by coincident pre- and postsynaptic activity). This requirement is hardly accessible to direct experimental investigation, at least in man or higher vertebrates, and there is (to my knowledge) no evidence against it (compare also Cowan, 1976). Furthermore, it would be of interest to the physiologist how large cell assemblies should usually be, i.e. of how many cells they should be formed.

From the psychological point of view we need a very large number of cell assemblies, since we have a large number of concepts.

For example, cell assemblies can be regarded as the neuronal substrate for the "nodes" in a "semantic network" (like the one of Quilian, 1967, 1968). The flow of "activity" through such a network is somehow determined by the "links" in the network [the exact rules have not yet been worked out in the literature, as can be seen from the discussion in Collins and Loftus
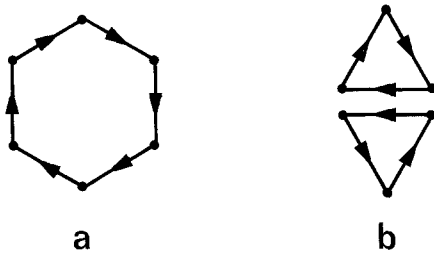
Fig. 1a and b. Both networks, a and b, consist of 6 elements and 6 connections. They both are homogeneous: Each element gives and receives one connection. Network b consists of two assemblies

(1975)]. This flow of activity corresponds to the succession of active cell assemblies in the cortex. Some first speculations on the mechanisms that control the succession of cell assemblies can be found in Braitenberg (1978). As for possible "links" between assemblies, one might consult Sect. 7.

But first of all we have to find out whether there is enough room in the brain for a sufficiently large number of cell assemblies. The problem concerning the number of cell assemblies is of course somehow connected to the question of their size.

This problem has already been tackled in some papers (e.g. Legendy, 1967, 1968). But I think it should be studied more systematically. In this article I want to suggest a mathematical formalism for the statement and investigation of this problem. In the first section I will try to present the problem more clearly; the following sections are devoted to an exact mathematical formulation.

1. Is the Cortical Network Sufficient to Contain all our Concepts?

Let me start with a rough picture of the cortical connectivity. The most striking feature of the cortical network is its homogeneity: in particular, every neuron receives and gives roughly the same number of connections. As has already been pointed out in Palm and Braitenberg (1979) it is important to distinguish the cortico-cortical connections in the "grey matter" from those through the "white matter". The first are local connections in one and the same area of the cortex and they are "metrical" in the sense that the chance of a connection between two neurons is dependent on their distance, being highest if the neurons are closest.

The second are global connections between different cortical areas and they are "ametrical" in the sense that the connection between two cells is not dependent on their distance in any simple way. It is now generally believed that inhibition is prominent in the local connections through inhibitory interneurons (although there is of course also local excitation

through axon collaterals of pyramidal cells), whereas the global connections (which are the axons of the pyramidal cells) are excitatory. The various "areas" in the brain can perhaps be viewed functionally as "regions of uniform context" (Braitenberg, 1974; Palm and Braitenberg, 1979), which can be interpreted as follows: Inside any one region (corresponding to one context) inhibitory local connections will help to differentiate between concepts (think of the literal meaning of "definition"), whereas the excitatory global connections serve to form the concepts in the first place (think of the literal meaning of "concept").

This interpretation of the cortical connectivity implies that cell assemblies are bound together mainly by the excitatory ametric long range connections and that they consist of cells distributed all over the cortex.

Therefore we can discard metrical considerations and inhibitory connections in the basic formulation of the problem (of the number of cell assemblies).

A cell assembly is a set of neurons that contribute more excitation to each other than they contribute to the average neuron.

Given the homogeneity of the cortical network, the first question is whether an assembly is possible in the cortex at all.

If we have a homogeneously and randomly connected network of N neurons, and each neuron has a probability p of firing, then the total postsynaptic activity a a fixed neuron A receives from the network, is a random variable. Let us now assume that A fires if the total postsynaptic activity a in its dendritic tree exceeds a threshold θ, then there is exactly one value θ_p for θ which yields again p as the probability of A to fire, i.e. there is exactly one number θ_p such that $pr[a > \theta_p] = p$. Thus to have a constant average activity of $p \cdot N$ neurons in the network, the average neuron has to have a threshold of $\theta = \theta_p$. If $\theta > \theta_p$ in the average neuron, the probability of firing will decrease which leads to a decrease in the postsynaptic activity and therefore to a further decrease in the probability of firing, and so on. Finally the activity will die out completely. If $\theta < \theta_p$, we get the opposite effect, leading finally to a complete activity of the whole network. In other words, the constant activity at level $N \cdot p$ is unstable and in particular very sensitive to changes of the threshold θ.

Computer simulations of randomly connected neuron networks as well as detailed statistical investigations on neurodynamics (Harth, 1970; Amari, 1974, 1977) have shown that it is easily possible to obtain a constant activity at some nontrivial level $p \cdot N$ $(0 < p < 1)$ in a randomly connected network and that this level does not change for small variations of θ. This means that the activity in these randomly connected networks is maintained in some subset of the set
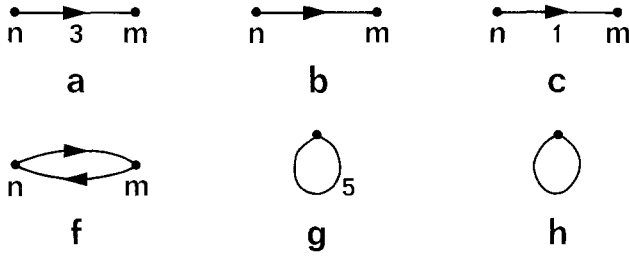
Fig. 2

Fig. 3   a   b

of all the N neurons. The neurons in this subset give more excitation to each other than to the rest (to sustain slight increase of θ and to avoid total excitation for slight decrease of θ).

Moreover, if we define a network as homogeneous, when every element receives and gives the same number of connections, then it is quite trivial to construct homogeneous networks containing such assemblies (Fig. 1).

In summary, it is possible that homogeneous networks contain assemblies, they even often occur in randomly connected networks.

Now only the one suspicion may be left that in a homogenous network the number of assemblies cannot be very large. To analyse this problem in detail we shall employ the mathematical language of graph theory (cf. Harari, 1969). A graph is just a set of points with some arrows or lines connecting them, like Fig. 1 above.

2. Weighted Graphs

To describe the dynamics of the cortical network, it is necessary to know the connectivity of the cortex. One could describe this connectivity by the so-called connectivity (or adjacency) matrix, i.e. by numbering the neurons and denoting by c_{ij} the connectivity from neuron i to neuron j.

The appearance of this matrix depends to a certain degree on the way the neurons are numbered. The connectivity is given in its purest way as a mapping $c: G \times G \to \mathbb{R}$, where G is the set of all neurons and $c(n, m)$ gives the strength of connectivity from neuron n to neuron m. As usual positive values of $c(n, m)$ mean an excitatory connection, negative values an inhibitory connection, and the value 0 means no connection at all.

A nice way to picture such a connectivity mapping c is by means of a graph: the neurons are denoted as points and the connections are indicated by arrows, e.g. $c(n, m) = 3$ is denoted as in Fig. 2a. Arrows with 0 connectivity are, of course, not drawn. For $c(n, m) = 1$ we might also write Fig. 2b instead of Fig. 2c. For $c(n, m) = c(m, n) = 1$ we may even write Fig. 2d or e instead of Fig. 2f. For $n = m$, $c(n, m) = 5$ is denoted as
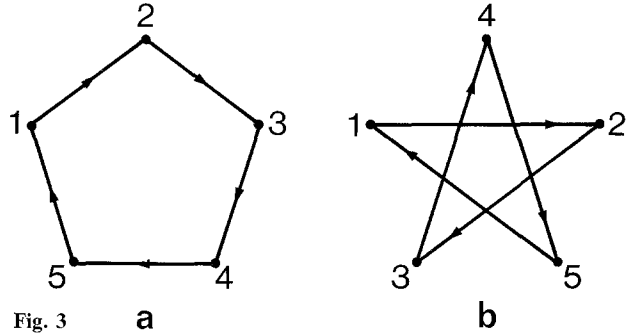
Fig. 2g, and $c(n, m) = 1$ simply as Fig. 2h. Such a connection is called a *self-connection* or *loop*.

For example the mapping

$$c: G \times G \to \{0, 1\}, \quad G = \{1, 2, 3, 4, 5\}$$

with

$$
\begin{aligned}
&c(1,1)=0 \quad c(2,1)=0 \quad c(3,1)=0 \quad c(4,1)=0 \quad c(5,1)=1 \\
&c(1,2)=1 \quad c(2,2)=0 \quad c(3,2)=0 \quad c(4,2)=0 \quad c(5,2)=0 \\
&c(1,3)=0 \quad c(2,3)=1 \quad c(3,3)=0 \quad c(4,3)=0 \quad c(5,3)=0 \\
&c(1,4)=0 \quad c(2,4)=0 \quad c(3,4)=1 \quad c(4,4)=0 \quad c(5,4)=0 \\
&c(1,5)=0 \quad c(2,5)=0 \quad c(3,5)=0 \quad c(4,5)=1 \quad c(5,5)=0
\end{aligned}
$$

can be described by the connectivity matrix

$$
C = \begin{pmatrix}
0 & 1 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 1 \\
1 & 0 & 0 & 0 & 0
\end{pmatrix}
$$

and can be pictured as in Fig. 3a or b.

Definition. A *weighted graph* is a pair $\langle G, c \rangle$, where G is a set and $c: G \times G \to \mathbb{R}$ a mapping. The elements of G are called *points*. For $x, y \in G$, $c(x, y)$ is called the *strength* or *weight* of the connectivity from x to y.

If $c: G \times G \to \{0, 1\}$ and $c(x, x) = 0$ for every $x \in G$, $\langle G, c \rangle$ is called a *directed graph*. If in addition $c(x, y) = c(y, x)$ for every x and y in G, $\langle G, c \rangle$ is called a *graph*.

Thus graphs, as well as directed graphs, do not contain loops.

I want to use such a graph as a model for the flow of activity in the brain. This can be done in the
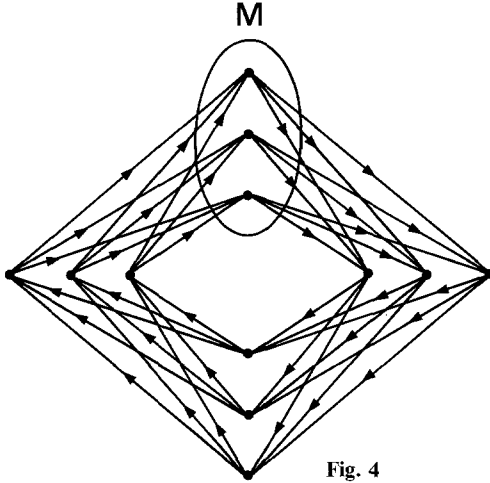
M

Fig. 4

M

Fig. 5

following way. The points are identified with the neurons and $c(x,y)$ gives the total strength of the synapses from neuron x to neuron y. Starting from a set M of "on"-neurons, we get the resulting flow of activity through the graph at threshold θ by iterating the mapping

$$f_\theta : \begin{cases} \mathscr{P}(G) \to \mathscr{P}(G) \\ M \mapsto \left\{ y \in G : \sum_{x \in M} c \in (x,y) \geqq \theta \right\}. \end{cases}$$

If the set M of neurons is active, this will in turn activate the set $f_\theta(M)$ at threshold θ, this in turn will activate $f_\theta^2(M)$, and so on.

3. Threshold Control

The basic idea of threshold control is that the basic neuronal activity evolves rather fast [it takes at most 5 ms from M to $f_\theta(M)$; this is a conservative estimate for the conduction time (axonal and synaptic) of a monosynaptic pathway from one cortical neuron to the next] and that it is controlled by comparatively slow variations of the parameter θ. In other words: in analysing the flow of activity we may keep θ fixed at first and let the activity evolve through M, $f_\theta(M)$, $f_\theta^2(M)$, ... to some final invariant state (or into some cycle). Then we change θ a bit and look for the new invariant state (that may occasionally be identical to the old one). We can use threshold control to detect cell assemblies: they occur if small variations in θ do not change the invariant state.

4. Cycles

Our graphic model for the dynamics of the brain is too exact in one respect: the activity proceeds from M to $f_\theta(M)$ and so on, in discrete time steps. In reality, the activity is "smeared out" in time at every synapse with
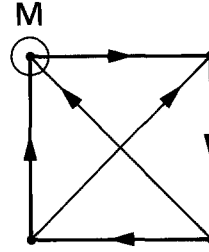
a time constant of a few milliseconds which is in the same range as the time needed by a monosynaptic pathway. Therefore in the long run cycles at fixed threshold θ are quite improbable in reality, although they will occur in the model.

For example, in the network of Fig. 4, starting with M, the activity will flow around in a cycle forever. In the corresponding real network, the flow of activity will show a cyclic structure at first, but due to the smearing out of activity, the whole net will finally be active.

Thus the real flow of activity in Fig. 4 will be similar to the sequence M, $f_\theta(M)$, $f_\theta^2(M)$, ... of Fig. 5.

For this reason we will not consider cycles as cell assemblies.

5. Inhibition

As I said in the first section we may disregard inhibition in the modeling of cell assemblies, since they are formed basically by the excitatory long range cortico-cortical connections.

Before doing so, it seems important to give a rough qualitative picture of the effects of inhibition that we have to keep at the back of our minds in the next section.

5.1. Specific Inhibition

This can occur between neighbouring cells in the same cortical area, and it implies that a certain part of one assembly selectively inhibits certain other neurons that are part of another assembly (or several other assemblies). Specific inhibition may for example correspond to the phenomenon that we cannot remember some name, because very often another name that is "too" similar in some respect comes to mind first and prevents the desired name from being remembered.

Specific inhibition may be helpful to define concepts from each other that are very similar in some respect. It may be learned through a synaptic mechanism analogous to Hebb's rule: some local inhibitory connections may be enhanced through common pre- and postsynaptic activity [for a theoretical analysis of this mechanism – although on a large global scale – see Kohonen (1977, Chap. 3.2)].
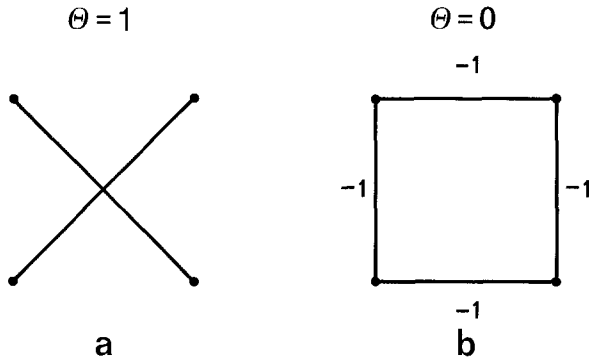
Fig. 6. b is obtained from **a** by subtracting 1 from the connectivities $c(m, n)$ for $m \neq n$

5.2. Diffuse Local Inhibition

At first glance one might believe that a certain level of diffuse inhibition is equivalent to general permanent increase of the threshold θ. This is not true as can be seen in the dynamics of Fig. 6.

Indeed, it turns out that homogeneous diffuse inhibition is equivalent to a "fast" threshold control whereby θ is increased proportionally to the number of active neurons (large numbers of active neurons distribute more inhibition than small numbers of active neurons).

This fast threshold control has two implications for the number of cell assemblies:

a) It tends to stabilize the number of active neurons, which is good for cell assemblies, since a constant activity (not zero and not total) implies the existence of a cell assembly.

b) It tends to decrease the number of cell assemblies, as can be seen in the network of Fig. 7.

Here we have three obvious assemblies, namely 1, 2, and 3. But also each combination of two of them, i.e. $(1, 2)$, $(1, 3)$, $(2, 3)$ could be regarded as an assembly since it is invariant and stable against small variations of θ.

However, a certain level of diffuse inhibition would forbid a combination – say $(1, 2)$ – of two "elementary" assemblies to stay active, simply because it is twice as large and causes twice as much diffuse inhibition. Therefore we would observe a "competition" between 1 and 2 and only one of them could stay active.

Thus, a certain level of diffuse inhibition will reduce the number of assemblies in the above network from 6 to 3.

A combination of two assemblies can only be an assembly again if there are some excitatory connections between the two (that help to overcome the increased amount of inhibition).

In the next chapter we shall ignore inhibition, but we incorporate this last requirement into the definition of a cell assembly.
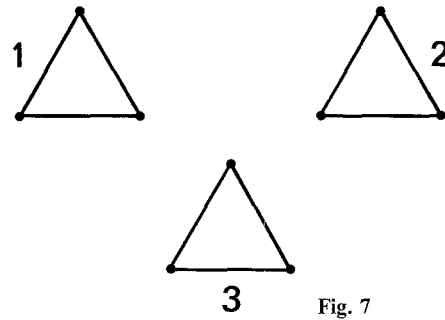

Let me finally discuss the possible psychological interpretation of the effects a) and b).

a) If M denotes a set of neurons (for example an assembly), $|M|$ denotes the number of neurons in the set M. The stabilization of $|M|$ may have the side effect that oscillations of $|M|$ around some mean value do occur. This would mean that some quite large part of an assembly is constantly active whereas other parts have just an oscillating activity. I think that these oscillations should not alter the concept represented by the assembly. Since we vary the threshold, we must have a large (for low threshold) and a small (for high threshold) set of neurons to represent the same concept, the small set being contained in the large set. Fluctuation in the size of the assembly may be regarded just as fluctuations in the "loudness" of the corresponding concept, as long as they stay within the boundaries of these two sets.

b) The competition between two concepts is a rather common phenomenon in psychology and psychophysics: think for example of ambiguous figures (Szenthagothai and Arbib, 1974, p. 412) and binocular rivalry (Breese, 1909).

6. Dynamics at Fixed Threshold

In this section the number θ is fixed, and we simply write f instead of f_θ. Moreover, we shall assume that $c(x, y) \in \mathbb{N}_0$ for every $x, y \in G$.

6.1. Definition. a) M *ignites* N (at θ), if there is a number $n \geq 1$, such that $N \subseteq f_\theta^n(M)$.

b) M *exhausts* N (at θ), if $N \subseteq M^* := \bigcup_{n=0}^{\infty} f_\theta^n(M)$, i.e. if for every element x of N there is a number $n \geq 0$, such that $f_\theta^n(M) \ni x$.

6.2. Definition. A subset M of G is called
invariant, if $f(M) = M$
persistent, if $f(M) \supseteq M$
weak, if there is an $n \in \mathbb{N} : f^n(M) = \emptyset$.

6.3. Definition. A sequence $(M_1, ..., M_l)$ is called a period of length l, if $f(M_i) = M_{i+1}$ for $i = 1, ..., l-1$ and $f(M_l) = M_1$.
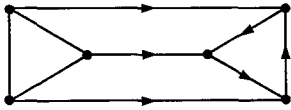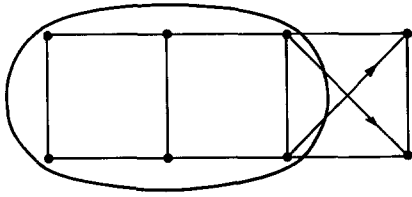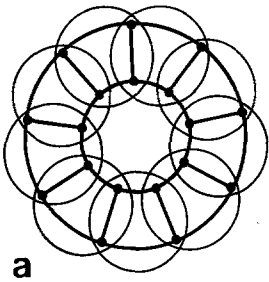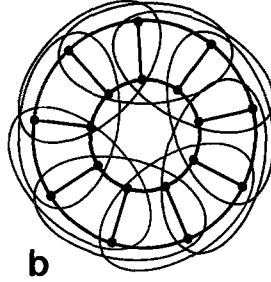
Fig. 8

Fig. 9

a   b

Fig. 10. a shows the 9 minimal persistent sets; b shows the 9 additional tight sets (which are assemblies)
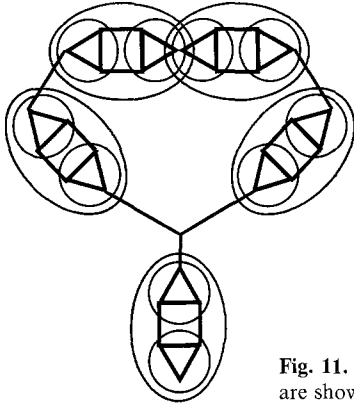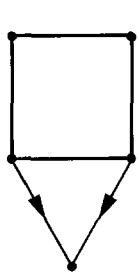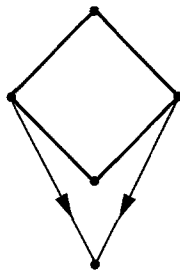

Fig. 11. All assemblies are shown

a   b   Fig. 12

6.4. Proposition. Let $M \subseteq G$. Exactly one of the following statements is true:

a) M is weak,
b) M ignites an invariant set,
c) M ignites a period.

Proof. This follows from the fact that $\mathscr{P}(G)$ is finite.

If M is persistent, we have $M \subseteq f(M) \subseteq f^2(M) \subseteq \dots$ and therefore we have case b). The invariant set generated by M is denoted by $\mathrm{cl}(M)$, the closure of M.

The next two propositions are obvious.

6.5. Proposition. a) $\mathrm{cl}(\mathrm{cl}(M)) = \mathrm{cl}(M)$ for M persistent,
b) $A \subseteq B$, A, B persistent, implies $\mathrm{cl}(A) \subseteq \mathrm{cl}(B)$.

6.6. Proposition. If A, B are persistent, then $A \cup B$ is persistent.

Next, we shall try to define an "assembly" (at θ) as a certain subset of G in terms of the dynamics in G at θ.

We shall use the following vague definition: "A cell assembly is a subset A of G such that every sufficiently large subset of A excites all of A." Here we have to specify the meaning of "sufficiently large" and "excites".

First of all, we shall require that a cell assembly has to be persistent. But this is not enough: For example, the graph of Fig. 7 is persistent at $\theta = 2$, but clearly we would not regard it as an assembly. Thus we could try the following definition of a cell assembly: "every persistent subset ignites the whole set". But this is perhaps a bit too strong. For example, Fig. 8 could well be regarded as an assembly, although the left triangle is persistent and does not ignite the rest. Figure 8 could be regarded as an assembly since the right triangle "needs" the left triangle in order to persist. Therefore we might use the following slightly weaker version: "every persistent subset whose complement is not weak, ignites the whole set". Also this definition is not yet perfect, since an assembly should be closed. This leads us to the final definition of an assembly.

6.7. Definition. a) A persistent set A is called *tight*, if every persistent subset of A whose complement in A is not weak, ignites the whole of A.

b) An assembly is the closure of a tight set. The example of Fig. 9 shows that the closure of a tight set does not need to be tight again:

6.8. Definition. A subset M of a graph G is called *minimal persistent*, if it is persistent and no proper subset of it is persistent.

6.9. Proposition. Every minimal persistent set is tight.

It is now possible to analyse the structure of weighted graphs (with positive weights) in terms of assemblies, tight sets, and minimal persistent sets. Let me give some examples (Figs. 10 and 11):

Further examples for assemblies are given in the next section.

7. Inner Structure of and Relations Between Assemblies

In this section I shall define some concepts to describe the inner structure of persistent sets, and especially assemblies. We still assume θ to be fixed and write f instead of f_θ. Let A be a persistent set.

We denote by $f_A : \mathscr{P}(A) \to \mathscr{P}(A)$ the mapping $M \mapsto f(M) \cap A$.

7.1. Definition. We say that a subset M of A *fills* A, if for every $x \in A$ there is an infinite sequence of numbers n_i such that $x \in f_A^{n_i}(M)$.

For example, in Fig. 12a at $\theta = 2$, only the square fills, whereas in Fig. 12b, two opposite points of the square fill as well.

7.2. Definition. a) A subset M of a persistent set A is called a *germ* of A, if it fills A and if no proper subset of M fills A.

b) The *kernel* $K(A)$ of a persistent set A is the union of all germs of A.

c) The *halo* $H(A)$ of a persistent set A is $\mathrm{cl}(A) - K(A)$.

7.3. *Examples* (Figs. 13–20)

7.4. Two assemblies may have an excitatory influence on each other in several different ways. In the following I will give examples for the most important cases I can think of.

  a) *Intersection.* Two assemblies A and B have some neurons in common.

In Fig. 21a and b the two assemblies form a superassembly.

  b) *Inclusion* (Fig. 22)

  c) *Projection* (Fig. 23)

  d) *Mutual projection* (Fig. 24)

In this case A and B together form a superassembly that holds at higher threshold.

8. Formulation of the Main Problem

Having defined the notion of an "assembly" we can now formulate precisely the main problem of the theory of cell assemblies: Given a weighted graph $\langle G, c \rangle$ with $c(x, y) \in \mathbb{N}_0$ for every x and y in G, we may ask for the number n_θ of assemblies at threshold θ and for the total number of assemblies.

This leads to some very specific graph-theoretical questions that I just want to pose in this section. I have not yet obtained an answer to any of them, but some preliminary results that are hopefully connected to these questions are given in Sect. 10.
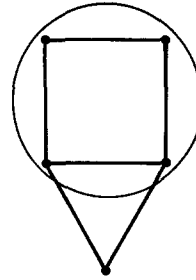

Fig. 13. This figure shows an invariant set; its kernel is circumscribed. The same conventions are used in Figs. 14–20
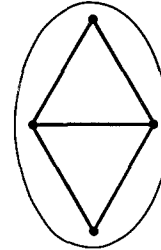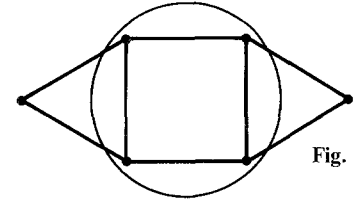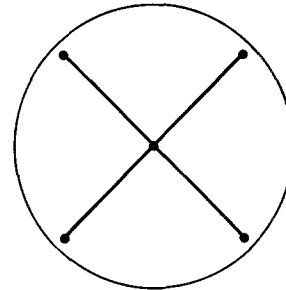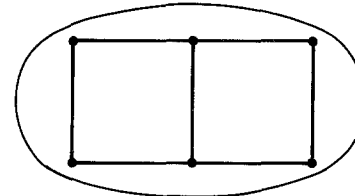
Fig. 14

Fig. 15

Fig. 16

Fig. 17

Fig. 18

Fig. 19

Fig. 20

a   b   c   Fig. 21
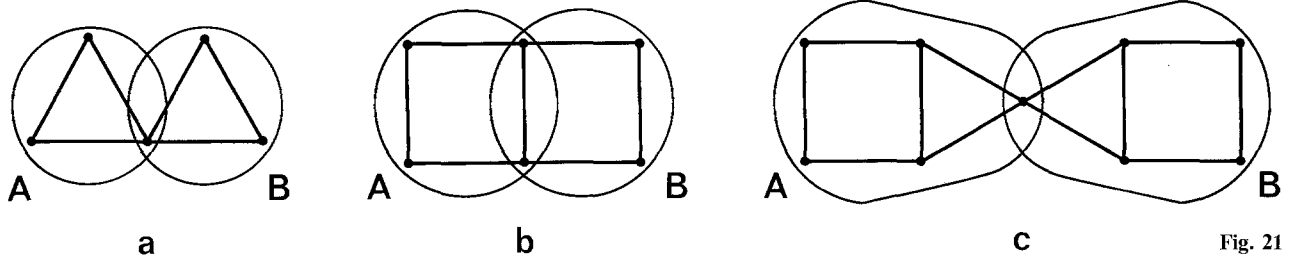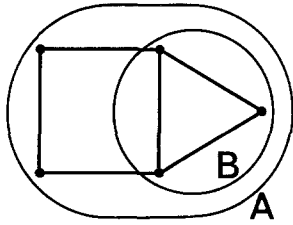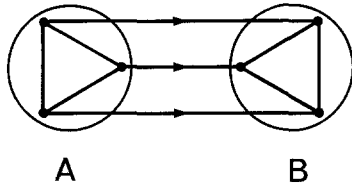

Fig. 22

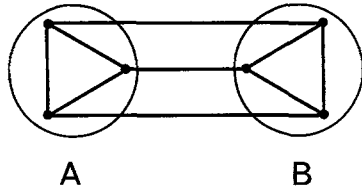A   B   Fig. 23
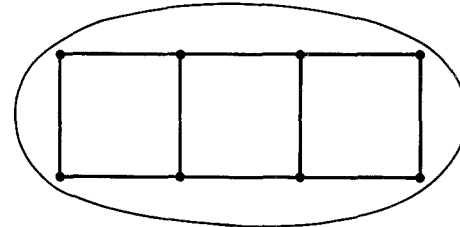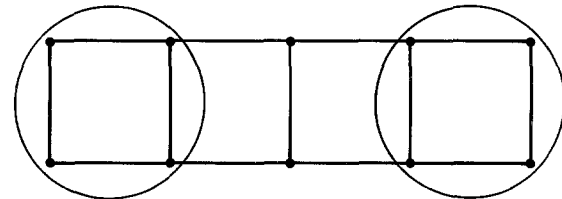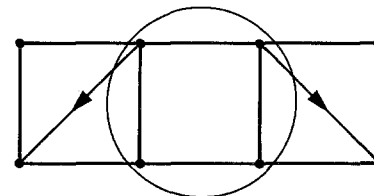
A   B   Fig. 24

In the next section I will introduce some further auxiliary concepts (especially notions of connectivity). To pose the questions we need one more definition:

8.1. Definition. A directed graph $\langle G, c \rangle$ is called *homogeneous*, if for any $x, x' \in G$ $\sum_y c(x,y) = \sum_y c(x', y)$ and

$$\sum_y c(y, x) = \sum_y (y, x').$$

Remark. This implies that for $e := \dfrac{1}{|G|} \sum_{x,y} c(x,y)$ and any $x \in G$ we have

$$\sum_y c(x,y) = e = \sum_y c(y,x).$$

Remember that $|G|$ denotes the number of elements (i.e. points) in G.

8.2. Question. Given two numbers k and a, determine a weighted graph $\langle G, c \rangle$ with $|G| = k$ and $e = a$ such that n is maximal.

8.3. Question. a) Is it possible to find a homogeneous weighted graph with this property?

b) Is it possible to find a strongly connected weighted graph with this property? (Notions of connectivity are defined in the next section.)

8.4. Question. How does the function $\theta \mapsto n_\theta$ look like, for such a graph?

8.5. Question. Given two numbers k and a, consider the set $\mathscr{G}$ of all (homogeneous) (connected) weighted graphs $\langle G, c \rangle$ with $|G| = k$ and $e = a$ and let $\theta > 0$. What is the average value for n_θ on the set $\mathscr{G}$? What is the average size of an assembly occuring at θ in a graph in the set $\mathscr{G}$?

The last question obviously contains several subquestions, which could even be answered in an asymptotic sense for $k, a \to \infty$. In this way one could sharpen the vague conjecture that large randomly connected networks contain many assemblies.

9. Some Characteristic Numbers and Properties of Weighted Graphs

In this section I shall define and discuss some characteristic numbers associated with weighted graphs, most of which are concerned with the "connectivity" of a graph.

9.1. Definition. $e := |G|^{-1} \sum_{x,y \in G} c(x,y)$ is called the average connectivity of G.

$\theta := \max\{t : G$ is persistent at $t\} = \min_{y \in G} \sum_{x \in G} c(x,y)$ is called the critical threshold of G.

$wc := \min_{A \subsetneq G} \sum_{x \in A} \sum_{y \in A^c} c(x,y)$ is called the weak connectivity of G.

$c := \max\{t : f_t(A) \cap A^c \neq \emptyset$ for every A with $|A| \geq s$ for some $s \leq t, s < |G|\}$ is called the connectivity of G.

Usually c coincides with c' which is given by the slightly more intuitive definition:
$c' := \max\{t : f_t(A) \cap A^c \neq \emptyset$ for every A with $|A| \geq t\}$.

Later I shall define some refinements of the definition of c. To this end a few somewhat different definitions will be helpful.

9.2. Definition. $i_\theta := \min\{n : |A| \geq n$ implies $A \longrightarrow G\}$ is called the ignition number of G.

$h_\theta := \min\{n : |A| \geq n$ implies A holds at $\theta\}$ is called the holding number of G.

$ic_\theta := \min\{n : |A| \geq n$ implies $f_\theta(A) \supsetneq A^c\}$ is called the immediate connection number of G.

$f_\theta := \min\{n : |A| \geq n$ implies A fills G at $\theta\}$ is called the filling number of G.

$s_\theta := \min\{n : |A| \geq n$ implies A is not weak$\}$ is called the survival number of G.

$d_\theta := \max\{n : |A| \leq n$ implies A is weak$\}$ is called the dying number of G.

$\mathrm{id}_\theta := \max\{n : |A| \geq n$ implies $f_\theta A = \emptyset\}$ is called the immediate dying number of G.

$n_\theta :=$ the number of assemblies at θ.

$n :=$ the total number of assemblies.

Usually I shall write i instead of i_θ, where θ is the critical threshold of G (Definition 9.1), and similarly for h, etc.

9.3. Proposition. a) $e \geq \theta$, b) $\theta \geq wc$ if $c(a,a) \geq 0$ for every $a \in G$.

Proof. a) $\sum_y \sum_x c(x,y) \geq |G| \min_y \sum_x c(x,y)$.

b) $A = G\backslash\{a\}$ implies

$$\sum_{x \in A} \sum_{y \in A^c} c(x,y) = \sum_{x \in A} c(x,a) \leq \sum_{x \in G} c(x,a).$$

Thus $\displaystyle \min_{|A| = G-1} \sum_{x \in A} \sum_{y \in A} c(x,y) \geq wc$.

9.4. Proposition. a) $h \leq ic + 1$, if $c(a,a) \geq 0$ for every $a \in G$.

b) $h \geq ic + 1$, if $c(a,a) \leq 0$ for every $a \in G$.

Proof. a) Let $|A| \geq ic + 1$ and $x \in A$. Then $f(A\backslash x) \ni x$, hence $f(A) \ni x$.

b) Let $|A| = h - 1$ and $x \notin A$. Then $f(A \cup \{x\}) \ni x$, hence $f(A) \ni x$.

9.5. Corollary. $i \leq ic + 1$, if $c(a,a) \geq 0$.

9.6. Proposition. $i \geq f \geq s > d \geq \mathrm{id}$.

Proof. Trivial.

9.7. Definition.

$c_3 := \max\{t : \mathrm{id}_t < |G|$ and $f_t(A) \cap A^c \neq \emptyset \, \forall A$ with $|G| > A > \mathrm{id}_t\}$.

$c_2 := \max\{t : \mathrm{id}_t < |G|$ and $A_t^* \supseteq A^c \quad \forall A$ with $|G| > A > \mathrm{id}_t\}$.

$c_1 := \max\{t : \mathrm{id}_t < |G|$ and A fills A^c at $t \, \forall A$ with $|G| < A < \mathrm{id}_t\}$.

$c_0 := \max\{t : \mathrm{id}_t < |G|$ and $f_t(A) \supseteq A^c \quad \forall A$ with $|G| > A > \mathrm{id}_t\}$.

9.8. Proposition. a) $c_3 \geq c_2 \geq c_1$

b) $\theta \geq c$, if $c(a,a) \geq 0$

Proof. a) Trivial.

b) We have to show that G is persistent at c: for $x \in G$, $f_c(G\backslash\{x\}) \ni x$.

9.9. Proposition. Let $\mathrm{id}_t < |G|$.

a) If $c(x,y) \in \mathbb{Z}$, then $\mathrm{id}_t \leq t - 1$.
b) If $c(x,y) \leq 1$, then $\mathrm{id}_t \geq t - 1$.

Proof. $\mathrm{id}_t < |G|$ means that there is an $x \in G$ and $M \subseteq G$ such that $\sum_{y \in M} c(y,x) \geq t$.

a) Let $A := \{y : c(y,x) > 0\}$ then $\sum_{y \in A} c(y,x) \geq t$. If $|A| \leq t$ we are done, if $|A| \geq t$ any subset B of A with $|B| = t$ will satisfy $\sum_{y \in B} c(y,x) \geq t$.

b) If $|M| \leq t - 1$ and $x \in G$ then $\sum_{y \in M} c(y,x) \leq t - 1$.

9.10. Corollary. a) If $c(x,y) \in \mathbb{Z}$ for every $x, y \in G$, then $c \geq c_3$.

b) If $c(x,y) \leq 1$ for every $x, y \in G$, then $c \leq c_3$.

Proof. Follows from 9.9.

9.11. Proposition. Let $c(x,y) \in \{0,1\}$ for every $x, y \in G$.

a) $c_3 = c \leq wc$.
b) Let $\vartheta \leq c$, then $|A| \geq \vartheta$ implies $f_\vartheta(A) \cap A^c \neq \emptyset$.

Proof. a) By 9.10, we have $c_3 = c$.

Let $A \subseteq G$, we have to show $\sum_{x \in A} \sum_{y \in A^c} c(x,y) \geq c$. If $|A| \geq c$, then $f_c(A) \cap A^c \neq \emptyset$, and therefore

$$\max_{y \in A^c} \sum_{x \in A} c(x,y) \geq c.$$

If $|A| =: m < c$, let $\sum_{x \in A} \sum_{y \in A^c} c(x,y) =: k$. Assume that $k < c$.

Take $B \supseteq A$ such that $|B| = c$ and B contains as many elements of $f_1(A)\backslash A$ as possible.

Take $x \in B^c$, then $\sum_{b \in B\backslash A} c(b,x) \leq |B\backslash A| = c - m$,

$$\sum_{b \in A} c(b,x) \leq \begin{cases} k - (c-m) & \text{if } |f_1(A)\backslash A| \geq c - m \\ 0 & \text{if } |f_1(A)\backslash A| \leq c - m, \end{cases}$$

and therefore $\sum_{b \in B} c(b,x) \leq \left\{ \begin{matrix} k \\ c - m \end{matrix} \right\} < c$.

This shows $f_c(B) \cap B^c = \emptyset$.

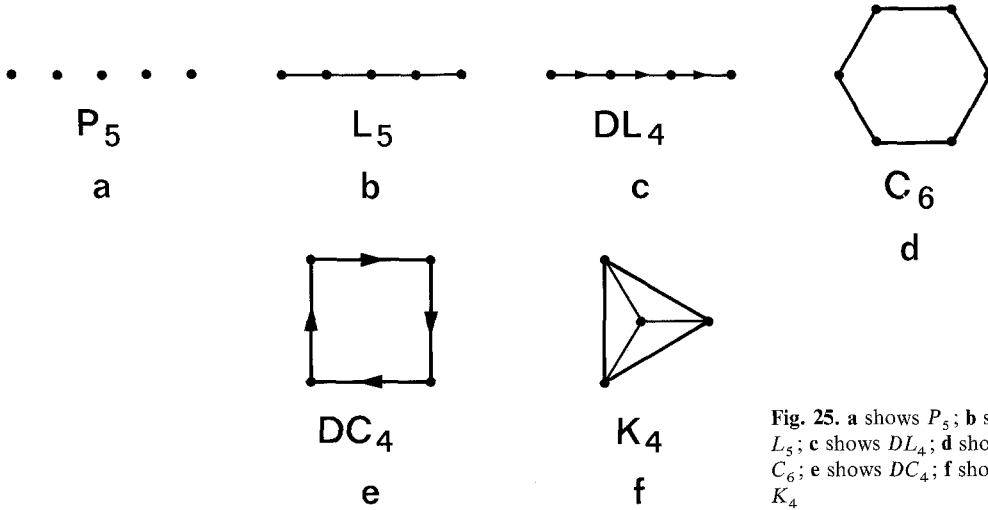b) Here the argument is similar to a), but simpler; it is left to the reader.

P$_5$

a

L$_5$

b

DL$_4$

c

C$_6$

d

DC$_4$

e

K$_4$

f

Fig. 25. a shows P_5; b shows L_5; c shows DL_4; d shows C_6; e shows DC_4; f shows K_4
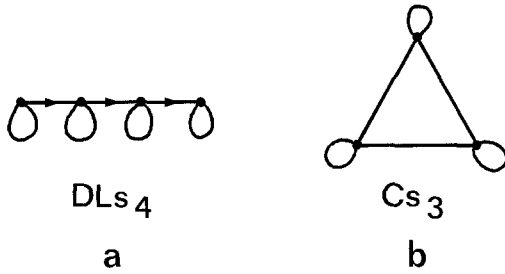
DLs$_4$

a

Cs$_3$

b

Fig. 26. a shows DLs_4; b shows Cs_3

9.12. Proposition. Let $c(x,y) \in \mathbb{Z}$ for every $x, y \in G$ and $wc \geqq 1$, then $c, c_3, c_2, c_1 \geqq 1$. (In this case the graph G is called *connected*.)

Proof. In view of 9.10 and 9.8, we have to show $c_1 \geqq 1$. It is sufficient to show that for $x, y \in G$ there is an $n \in \mathbb{N}$ such that $f_1^n(x) \ni y$. [Indeed, this implies $f_1^m(y) \ni x$ for some $m \in \mathbb{N}$ and therefore $f_1^{2n+m}(x) \supseteq f_1^{n+m}(y) \supseteq f_1^n(x) \ni y$, etc.]

Thus we have to show that $\{x\}_1^* = G$ for any $x \in G$. Assume $A := \{x\}_1^* \neq G$, then

$$f_1(A) \subseteq A \text{ implies } \sum_{x \in A} \sum_{y \in A^c} c(x,y) \leqq 0,$$

in contradiction to $wc \geqq 1$.

9.13. Proposition. Let $c(x,y) \in \mathbb{Z}$ for every $x, y \in G$.

If $c_0 \leqq \dfrac{|G|}{2}$, then $c_1 \geqq c_0$.

Proof. Let $|A| = \mathrm{id}_{c_0} + 1 \leqq c_0$

Then $|A^c| \geqq |G| - c_0 \geqq \dfrac{|G|}{2} \geqq c_0 \geqq \mathrm{id}_{c_0} + 1$

Therefore $f_{c_0}(A^c) \supseteq A$ and $f_{c_0}(A) \supseteq A^c$.
Thus A fills G at c_0.

This is a fortiori true for any B with $B \supseteq A$. This means that $|B| > \mathrm{id}_{c_0}$ implies that B fills G at c_0.

10. Construction of Graphs and Examples

Let me start this section by introducing some general graphs and some general ways of constructing new graphs from given ones.

10.1. Definition. 1) P_n denotes the graph G containing n separate points (Fig. 25a).

2) L_n denotes a single line containing n points (Fig. 25b).

2') DL_n denotes a directed line containing n points (Fig. 25c).

3) C_n denotes a circle with n points (Fig. 25d).

3') DC_n denotes a directed circle with n points (Fig. 25e).

4) K_n denotes the complete graph with n points (Fig. 25f).

10.2. Definition. The suffix s adds selfconnections to the graphs P_n, L_n, K_n, C_n, DL_n, and DC_n (compare Fig. 26).

10.3. Given any two directed graphs H and G we may construct the following graphs (compare Fig. 27):

1) $\tilde{G}$ has connections exactly where G has not, but $\tilde{G}$ does not have self connections.
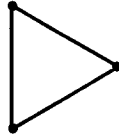
2) $G + H$ means that G and H are placed side by side without any connections.

3) $G +_c H$, called the connected sum (or join): G and H are placed side by side and every point of G is connected (both ways) with every point of H.

4) $G +_d H$, called the directed sum: G and H are placed side by side and there is a connection from every point of G to every point of H.
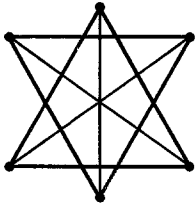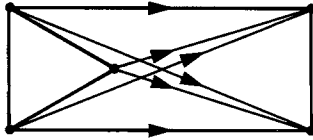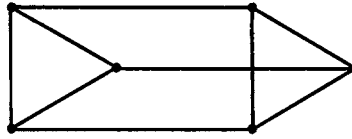
Fig. 27. a shows $\tilde{C}_6$; b shows $K_3 + K_2$; c shows $K_3 + _c K_2$; d shows $K_3 + _d K_2$; e shows $K_3 \times K_2$
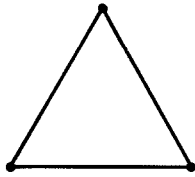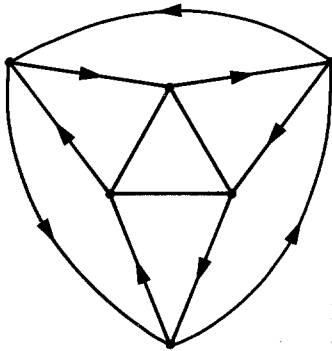

Fig. 28. $e = 2$, $\theta = 2$, $wc = 2$, $c = 1$

Fig. 29. $e = 2\frac{1}{2}$, $\theta = 2$, $wc = 2$, $c = 1$

5) $G \times H$: Every point of G is replaced by one version of H and every arrow of G is replaced by $|H|$ arrows connecting the corresponding points of the two versions of H that have replaced the two endpoints of the arrow.

10.4. Some exercises with these notions:

a) $K_2 = L_2$.
b) $K_3 = C_3$.
c) $\tilde{C}_4 = L_2 + L_2$.
d) $C_4 = K_2 \times K_2$.
e) $\tilde{C}_5 = C_5$.
f) $\tilde{C}_6 = K_3 \times K_2$.
g) $Ps_1 \times C_n = Cs_n$.
h) $Ps_2 \times C_n = Cs_n + Cs_n$.
i) $P_3 \times G = G + G + G$ for any graph G.
j) $P_i + P_j = P_{i+j}$.
k) $P_i \times P_j = P_{i \cdot j}$.
l) $K_i + _c K_j = K_{i+j}$.
m) $G \times H = H \times G$ for any two graphs G and H.

n) $G + _c H = H + _c G$ for any two graphs G and H.
o) $\overline{G + _d H} = \tilde{H} + _d \tilde{G}$ for any two graphs G and H.
p) $\overline{G + _c H} = \tilde{G} + \tilde{H}$ for any two graphs G and H.

10.5. Let me finally give the connectivities as defined in the last section for some specific graphs (Figs. 28–33).

$$L_n: e = 2\frac{n-1}{n} \qquad \theta = 1, wc = 1$$

$$DL_n: e = \frac{n-1}{n} \qquad \theta = 0, wc = 0$$

$$C_n: e = 2 \qquad \theta = 2, wc = 2, c = 1$$

$$DC_n: e = 1 \qquad \theta = 1, wc = 1$$

$$K_n: e = n-1 \qquad \theta = n-1, wc = n-1, c = c_3 = n-1,$$

$$c_2 = n-1, c_1 = \left\lceil \frac{n}{2} \right\rceil$$

$$\tilde{C}_n: e = n-3 \qquad \theta = n-3, wc = n-3, c = c_3 \approx \frac{n}{3},$$

$$c_2 = ?, \qquad c_1 = ?$$

$$C_n \times L_2: e = 3 \qquad \theta = 3, wc = 3, c = 1$$

$$L_n \times L_2: e = \frac{3n-2}{n}, \qquad \theta = 2, wc = 2, c = 1.$$

11. On the Construction of Graphs with Many Assemblies and/or High Connectivity

Let us take $|G| = 6$ and let us try to construct a graph with as many assemblies as possible. Of course, we hope that we should be able to get more than the 6 assemblies of the rather trivial construction Ps_6 (Fig. 34):

For example we could try Cs_6 (Fig. 35):

This graph is homogeneous and connected and it has 6 assemblies consisting of the 6 pairs of neighbouring points and 6 further assemblies consisting of the 6 triplets of neighbouring points. A set of 4 neighbouring points is no longer an assembly, since it is "combined of" two pairs of neighbouring points.
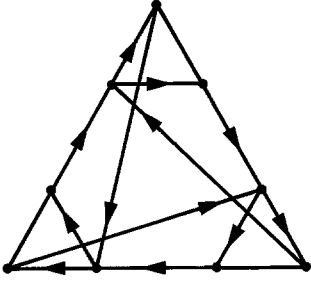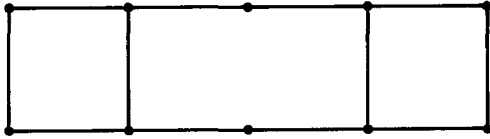
Fig. 30. $e=2$, $\theta=2$, $wc=2$, $c=1$

Fig. 31. $e=2.4$, $\theta=2$, $wc=2$, $c=1$
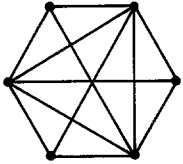

Fig. 32. $e=3$, $\theta=3$, $wc=2$, $c=1$

Fig. 33. $e=4$, $\theta=3$, $wc=3$, $c=c_3=3$, $c_2=2$, $c_1=2$
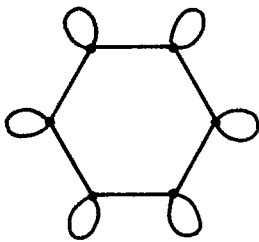

Fig. 34

Fig. 35

Fig. 36

Fig. 37

The following weighted graph contains both the assemblies of Ps_6 and those of Cs_6: see Fig. 36.

But using this strong self-excitation we can get a rather trivial solution to the problem, namely the graph G_1 obtained from K_6 by adding self excitation of the strength $c(i,i)=2$ ($i=1, ..., 6$): see Fig. 37.

In this graph every set of points forms an assembly, since any set of k points is minimal persistent and invariant at $\theta=k+1$. Thus, $n=2^6-1=63$.

In the following it will be more interesting to forbid selfconnections or to work only with directed graphs (i.e. to forbid numbers on the arrows). I will now
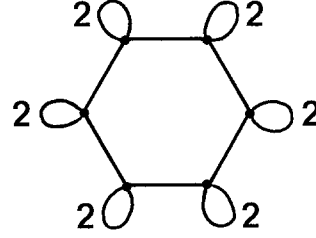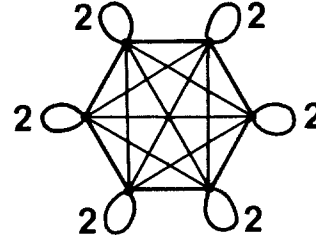
restrict myself to directed graphs without self-connections.

The following general strategy for constructing graphs with many assemblies may have emerged from the previous discussion: Use the above results with self-connectivity. Replace every point in a "good" graph G with self-connectivity of strength 1 (like Cs_6) by one exemplar of K_2, in other words: try $C_6 \times K_2$.

Replace every point in a "good" graph G with self-connectivity of strength 2 (like G_1 above) by one exemplar of K_3, in other words: try $K_6 \times K_3$.

For $|G|=6$, this strategy yields $P_3 \times K_2$ with $n=n_1=3$ and $K_2 \times K_3$ with $n=3$.

Furthermore I would like to mention the graph of Fig. 38 with $n=n_2=1$:

Up to now I could not find a graph with $|G|=6$ and $n>3$. At first sight this may look rather pessimistic but for larger $|G|$ the situation becomes much better:

Let me just show some graphs G with many assemblies for $|G|=36$. From the first strategy, we may try $K_{12} \times K_3$ with $n \geq 2^{12}$ or for example $G_2 \times K_2$ where G_2 is given in Fig. 39. Here we get $n \geq 2+8\cdot18=146$:

Let me give two more graphs: $L_6 \times L_6$ with $n=81$ (all at $\theta=2$) and $C_6 \times C_6$ with $n=99$ (where we get the 18 additional assemblies at $\theta=3$).

The champion among all these graphs is $K_{12} \times K_3$, a homogeneous graph with high connectivity ($wc=13$, $c=2$). This graph, however, needs quite a number of connections: the graph $K_n \times K_m$ has $e=n+m-2$.

Therefore, if we restrict the average number e of connections per point, graphs of the type $K_n \times K_m$ are certainly not the best ones: for example $K_6 \times K_6$ has $e=10$ and probably $n=125$ which is not as good as the example $G_2 \times K_2$ with $n \geq 146$ and $e=5$.

But still, the graphs $K_n \times K_m$ do illustrate that it is possible to contruct large graphs with a very large number of assemblies:

The graph $K_n \times K_m$ has $n \cdot m$ points, $(n \cdot m) \cdot (n+m-2)$ connections, i.e. $e = n+m-2$, and at least $2^n + 2^m - 4$ assemblies.

Let me close these considerations at this still very unsatisfactory state and let me add that I was quite surprised to get n as high as 2^{12} for $|G| = 36$ and that I am very curious to know the maximum value for n in this case.

12. Applications in other Areas

In this section I only want to hint at possible applications of well-constructed graphs with many assemblies in two other areas of research:

One is the problem of providing connectivity schemes for associative matrix memories.

The other is the problem of designing decentralized communication networks.

12.1. In Palm (1980) I have described associative matrix memories and especially the case of auto-association.

In the case of auto-association a 0, 1-sequence s of length n, $s = (s_1, ..., s_n)$ (called a "*pattern*") is "stored" in a 0, 1-matrix by forming $s \otimes s = (s_i \cdot s_j)_{i,j}$.

A set $\mathscr{S} = \{s^1, ..., s^z\}$ of such patterns is "stored" in the matrix

$$A = A_{\mathscr{S}} = \max_{k=1}^{z} s^k \otimes s^k .$$

If we interpret the matrix A as the connectivity matrix of a graph G_A with n points, we see that each pattern s^k is stored by connecting all the points of G_A that correspond to those places where the 0, 1-sequence $s^k = (s_1^k, ..., s_n^k)$ contains a "*1*", to a complete subgraph of G_A.

If these subgraphs do not overlap too much, they will form assemblies and therefore it will be possible to reconstruct the original patterns $s_1, ..., s_z$ from G_A by detecting assemblies in G_A.

The matrix A is called the *auto-association matrix* for the set $\mathscr{S}$ of patterns.

12.2. Now the problem is the following: Does this scheme still work if not every two points in G_A can be connected?

The answer to this question obviously depends on the restrictions that are given to the possibility of connections.

These restrictions are given in a *connectivity scheme* C. C is an $n \times n$ 0, 1-matrix, where $c_{ij} = 1$ means that i can be connected to j and $c_{ij} = 0$ means that it cannot.
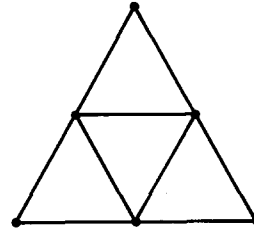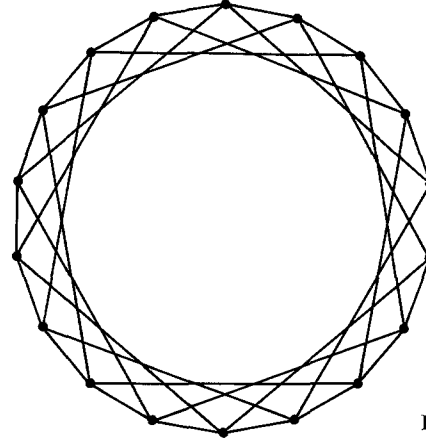

Fig. 38

Fig. 39

Of course the restriction can as well be described by the directed graph G_c corresponding to C. Given a set $\mathscr{S}$ of patterns, we now form the matrix $C_{\mathscr{S}} := A_{\mathscr{S}} \cdot C$, where $(X \cdot Y)_{ij} := x_{ij} \cdot y_{ij}$ and the corresponding subgraph G of G_c. Then we try to reconstruct the patterns in $\mathscr{S}$ by detecting the assemblies in G. Obviously, if G_c is the complete graph Ks_n, we have no restriction to the connectivity and we are in Sect. 12.1.

But can we design a connectivity scheme C with not too many connections such that the modified procedure still works?

12.3. To this end, we may assume that each pattern in $\mathscr{S}$ contains k ones. Then we should try to design a matrix C, or a graph G_c with small e and $h_t \leq k$ for a high value of t. This means that $ic_t \leq k-1$, since $h_t = ic_t + 1$ (Proposition 9.4). In fact, an optimal graph for this kind of problem can be found, but the solution turns out to require a discouragingly high number e of connections.

Let us try to construct a directed graph G with $|G| = n$ and $ic_t \leq k-1$. This means that for every subset S of G containing k points and every point $x \notin S$ there are at least t connections from S to x (this implies $k \geq t$).

Let us look at the complementary graph $\tilde{G}$: For every subset S of $\tilde{G}$ with k points and every point $x \notin S$ there are at most $k-1-t$ connections from S to x. This means exactly that every point $x \in \tilde{G}$ receives at most $k-1-t$ connections. Since we wanted to construct G with as few connections as possible, we have to construct $\tilde{G}$ with as many connections as possible. Thus in the optimal graph $\tilde{G}$, every $x \in \tilde{G}$ receives exactly $k-1-t$ connections. Therefore any homo-

geneous graph $\tilde{G}$ with $e=k-1-t$, and any homogeneous graph G with

$$e=(n-1)-(k-1-t)=n+t-k$$

is optimal.

12.4. The second problem that I announced for this section is the following:

Given n "participants" find a communication network for them with a minimal number of links which connects any two participants via not too many links.

12.5. Definition. For $M, N \subseteq G$ we define

$$t_\vartheta(M,N) := \min\{i : f_\vartheta^i(M) \cap N \neq \emptyset\}.$$

Then we define

$$t_\vartheta(k) := \max\{t_\vartheta(M,N) : |M|=k, |N|=1\}.$$

Then $l := t_1(1)$ denotes the number of links through which any two participants can be connected.

The problem can now be exactly formulated: Given two numbers n and k. Find a (homogeneous) graph G with $|G|=n$ and $l=k$, such that e is minimal. Moreover, find a graph G with the additional property that k does not increase (too much) if any point is removed from G.

The additional property (as well as the homogeneity requirement) is meant to represent the requirement that the network should be decentralized.

I believe that this problem is somehow related to the other problem of this section and also to the problem of cell assemblies, and the following theorem hints in this direction.

12.6. Theorem. Let G be a graph with $|G|=n$ and suppose that $t_\vartheta(k)=1$ (i.e. $ic_\vartheta \leq k$) for two numbers ϑ, $k \in \mathbb{N}$ with

$$\vartheta \leq k \leq \frac{n+\vartheta^2+1}{\vartheta+1}.$$

Then $t_\vartheta(\vartheta) \leq 2$.

12.7. Remark. This theorem can also be formulated as follows:

$$ic_\vartheta \leq \frac{|G|+\vartheta^2+1}{\vartheta+1} \quad \text{implies} \quad t_\vartheta(\vartheta) \leq 2.$$

And for $\vartheta=1 : ic_1 \leq \frac{|G|+2}{2}$ implies $l \leq 2$.

12.8. Remark. Figure 30 shows a graph with $l=3$ and a low number of connections ($e=2$). However, removing one point from this graph, may increase l to 5.

References

Amari, S.: A method of statistical Neurodynamics. Kybernetik **14**, 201–215 (1974)

Amari, S., Yoshida, K., Kanatani, K.: A mathematical foundation for statistical neurodynamics. SIAM J. Appl. Math. **33**, 95–126 (1977)

Braitenberg, V.: On the representation of objects and their relations in the brain. In: Physics and mathematics of the nervous system. Conrad, M., Güttinger, W., Dal Cin, M. (eds.) p. 290. Berlin, Heidelberg, New York: Springer 1974

Braitenberg, V.: Cortical architectonics: general and areal. In: Architectonics of the cerebral cortex. Brazier, M.A.B., Petsche, H. (eds.) p. 443. New York: Raven Press 1978

Braitenberg, V.: Cell assemblies in the cerebral cortex. In: Theoretical approaches to complex systems. Heim, R., Palm, G. (eds.), p. 171. Berlin, Heidelberg, New York: Springer 1978

Breese, B.B.: Binocular rivalry. Psychol. Rev. **16**, 410–415 (1909)

Collins, A.M., Loftus, E.F.: A spreading-activation theory of semantic processing. Psychol. Rev. **82**, 407–428 (1975)

Cowan, J.D.: Are there modifiable synapses in the visual cortex? In: Neural mechanisms of learning and memory. Rosenzweig, M.R., Bennett, E.L. (eds.), p. 133. Cambridge MA: MIT Press 1976

Harari, F.: Graph theory. Reading MA: Addison-Wesley 1969

Harth, E.M., Csermely, T.J., Beek, B., Lindsay, R.D.: Brain functions and neural dynamics. J. Theoret. Biol. **26**, 93–120 (1970)

Hebb, D.O.: The organization of behavior. New York: Wiley 1949

Hebb, D.O.: Textbook of psychology. Philadelphia, London, Toronto: Saunders 1958

Kohonen, T.: Associative memory. Berlin, Heidelberg, New York: Springer 1977

Legendy, C.R.: On the scheme by which the human brain stores information. Math. Biosci. **1**, 555–597 (1967)

Legendy, C.R.: How large are Hebb's cell assemblies? In: Cybernetic problems in bionics. Oestreicher, H.L., Moore, D.R. (eds.), p. 721. New York: Gordon and Breach 1968

Palm, G.: On associative memory. Biol. Cybern. **36**, 19–32 (1980)

Palm, G., Braitenberg, V.: Tentative contributions of neuroanatomy to nerve net theories. In: Progress in cybernetics and systems research. Trappl, R., Klir, G.J., Ricciardi, L. (eds.), Vol. 3, p. 369. London: Advance Publ. 1979

Quilian, M.R.: Word concepts: a theory and simulation of some basic semantic capabilities. Behav. Science **12**, 410–430 (1967)

Quilian, M.R.: Semantic memory. In: Semantic information processing. Minsky, M. (ed.). Cambridge MA: MIT Press 1968

Szenthagothai, J., Arbib, M.A.: Conceptual models of neural organization. NRP Bull. **12**, 3 (1974)

Dr. G. Palm
Max-Planck-Institut
für biologische Kybernetik
Spemannstrasse 38
D-7400 Tübingen
Federal Republic of Germany