

## **Dynamical Symmetries and Temporal Segmentation**

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**Summary.** Segmentation of a mixed input into recognizable patterns is a task that is common to many perceptual functions. It can be realized in neural models through temporal segmentation: formation of staggered oscillations such that within each period every nonlinear oscillator peaks once and is dominant for a short while. We investigate such behavior in a symmetric dynamical system. The fully segmented mode is one type of limit cycle that this system can exhibit. We discuss its symmetry classification and its dynamical characterization. We observe that it can be sustained for only a small number of segments and relate this fact to a limitation on the appearance of narrow subharmonic oscillations in our system.

**Key words:** segmentation, subharmonics, nonlinear oscillations, neural dynamics

### **1. Introduction**

Segmentation can be defined as the task of decomposing a pattern into subpatterns. In our paradigm the pattern is an input to a computational system whose elements (or particular combinations of them) are the subpatterns. This is the case for neural systems that perform cognitive computational tasks and use segmentation as a first processing step. Using the visual analysis of a scene as a convenient example, we note that a complicated picture is built out of elements that can be recognized separately. These elements are perceived simultaneously before the general meaning of the scene is grasped. Another example is auditory signal separation in the presence of several simultaneous inputs, known as the cocktail party effect (von der Malsburg and Schneider, 1986). We are able to listen to several conversations in parallel, at least to the extent of recognizing key words, by segmenting the information. A third example, taken from a third sensory function, is odor recognition and separation, which is being investigated in animals (Hopfield and Gelperin, 1989).

We will use a restricted definition of segmentation. It will mean the task of parallel retrieval of individual patterns that appear together in an input. To model

segmentation one may use a dynamical neural system that, in the presence of a given mixed input, can activate its various elements in such a fashion that they are all active within some common time window yet each one is dominant at different phases of this period. This implies the use of oscillatory phenomena, which are quite common in neural systems. For a general review of oscillations and their possible functions in neuronal systems, we refer to Gray (1994). Our definition of segmentation imposes restrictions on the possible waveforms that could model this task. Each oscillator should be dominant during a small fraction of the period and remain low for the rest of the period, while other oscillators take over sequentially. We should emphasize that phase-shifted identical waveforms will, in general, not fit our definition of segmentation.

The realization of temporal segmentation by oscillatory networks was demonstrated by Wang, Buhmann, and von der Malsburg (1990), by Horn and Usher (1991), and by von der Malsburg and Buhmann (1992). The way it works is that the activities of different memory patterns (clusters of oscillators) that are turned on by the input exhibit staggered oscillations, i.e., different memories have different phases. Moreover, due to the nonlinear character of the system, each memory is dominant for some very small time within the period that is relevant to information processing. This behavior satisfies a necessary condition for segmentation as defined above.

In Wang et al. (1990) the elements of the networks are oscillators by themselves, composed of excitatory-inhibitory pairs of neurons. Horn and Usher (1991) have worked with neurons that possess dynamic thresholds and exhibit adaptation: they vary as a function of the activity of the neurons to which they are attached. As such, they introduce time dependence that can turn a neural network from a dissipating system that converges onto fixed points into one that moves from one center of attraction to another (Horn and Usher, 1989, 1990).

Both models share a common problem: they have a limited segmentation power, i.e., for only a small number of common inputs they can lead to staggered oscillations. Assuming all inputs are constant and of similar magnitude, it has been shown (Wang et al., 1990; Horn and Usher, 1991) that for an input of more than approximately five memories the system will collapse. There is no general understanding why this happens, yet it is interesting to note that similar limits exist also in real neural systems. Miller (1956) has demonstrated in psychophysical experiments his  $7 \pm 2$  rule, which states that a limit of such small numbers exists for attention and short-term memory.

In this paper we study the phenomenon of segmentation in the context of a symmetric dynamical system. Rather than dealing with Hebbian cell assemblies of memories, we restrict ourselves to single oscillating neurons. Segmentation is obtained through phase separation of the different nonlinear neural oscillators, all of which are driven by the same constant input. Full segmentation is only one of the many possible limit cycles that our system possesses. We characterize its behavior by the symmetry group under which this solution is invariant. This characterization, as well as the computer search that is facilitated by the ensuing regular structures, is enabled through the choice of a permutation symmetric system. Another motivation for this choice is that all general types of waveforms are obtained as solutions.

Having a symmetric theoretical system allows us to investigate in a systematic manner some of the general questions we are interested in. These include the relative

importance of segmentation, its variation with the size of the probed system, and the dynamical reason for the limit on temporal segmentation. We believe that the lessons that one can learn from this theoretical model bear relevance to the phenomena observed in other models and systems, which may be more complicated and less symmetric than the model that we study.

Our model is explained in the next section. The following section describes the symmetry considerations and dwells on the  $n = 3$  case. Here we compare our results with recent literature on dynamics of coupled nonlinear oscillators. In the next section, dedicated to  $n \geq 4$ , we point out the interesting results that deviate from what is expected in weakly coupled systems (as in Ashwin and Swift, 1992). Finally we show that the limited  $n$  range for which full segmentation can be obtained may be understood in our model as a limited range for narrow subharmonic oscillations induced by the nonlinear equations that we employ.

## 2. Neural Networks as Dynamical Systems

Neural networks may be naturally expressed as systems of coupled first-order differential equations. Consider, for example, a system of  $n$  excitatory neurons  $i = 1, \dots, n$  interacting with one inhibitory neuron while receiving external inputs  $I_i$ :

$$du_i/dt = -u_i + m_i - am - br_i + I_i, \quad (2.1)$$

$$dr_i/dt = m_i - cr_i, \quad (2.2)$$

$$dv/dt = -gv - em + f \sum_i^n m_i \quad (2.3)$$

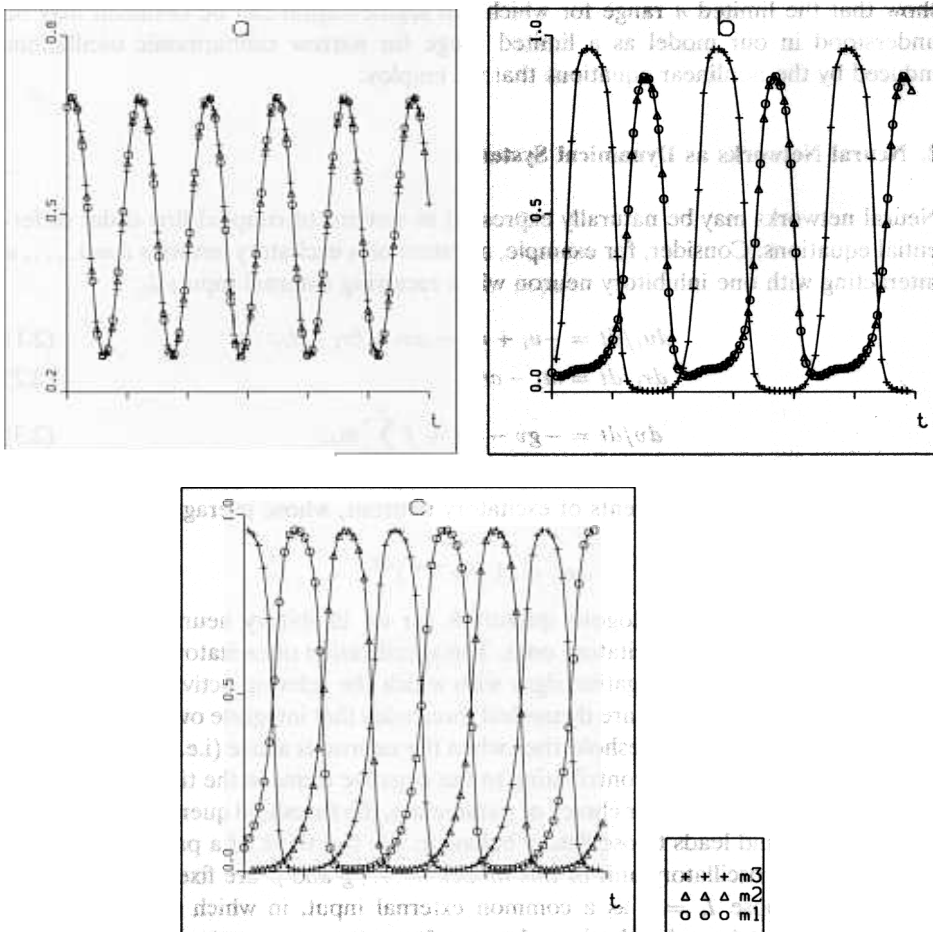
$u_i$  denote postsynaptic currents of excitatory neurons, whose average firing rates, or activities, are

$$m_i = (1 + e^{-\beta u_i})^{-1}, \quad (2.4)$$

whereas  $v$  and  $m$  are analogous quantities for an inhibitory neuron that induces competition between all excitatory ones. The specification of excitatory and inhibitory refers to the positive or negative signs with which the relevant activities couple into equations (2.1) and (2.3).  $r_i$  are dynamical thresholds that integrate over the activity of the neuron in time. The threshold rises when the neuron is active (i.e., its firing rate is high) for a long time, thus contributing to the negative terms in the time derivative of the current  $u_i$ . With a proper choice of parameters, the threshold quenches the activity of the neuron and leads to oscillatory behavior. We can think of a pair  $(u_i, r_i)$  as the basic nonlinear oscillatory unit of this model.  $a, \dots, g$  and  $\beta$  are fixed parameters.

Let us choose  $I_i = I$  as a common external input, in which case the system becomes symmetric under the interchange of any two neurons  $i \leftrightarrow j$ . This means that all oscillators are identical. As explained in the Introduction, this choice is motivated by theoretical considerations: obtaining general types of solution and being able to trace them systematically. In general, this dynamical system flows into a set of dynamic attractors. We will work in a regime where no fixed points exist. For three excitatory elements and constant input, we find then the following types of attractors: (a) common oscillatory mode; (b) two of the elements oscillate in phase and a third

out of phase (this solution has multiplicity 3 because we can choose two neurons out of three); (c) staggered oscillations of all elements (this solution has multiplicity 2 because there are two possible arrangements of the three neurons in a circle). The last type fits our understanding of temporal segmentation. Examples of all limit cycles are shown in Figure 1, which displays different solutions of  $m_i(t)$  obtained for some fixed values of parameters in the system of equations, but different initial conditions of the three excitatory neurons. All solutions shown in this work were obtained using



**Fig. 1.** Limit cycles of the  $n = 3$  system. Parameters were the following:  $a = 0.5$ ,  $b = 0.4$ ,  $c = 0.2$ ,  $g = 0.1$ ,  $e = 1.1$ ,  $f = 0.5$ , and  $\beta = 9$ . The different  $m_i$  are plotted versus time after transients have died away. The time scale is arbitrary but is chosen to be the same in all figures. Each  $m_i$  is represented by a different symbol. The limit cycles are (a) fully synchronous, a waveform which we denote by [123] and that has  $S_3$  symmetry (here  $I = 0.8$ ). (b) partial synchronous waveform [ $1_a 2_a 3_\beta$ ] forming the basis of an  $S_2$  symmetry ( $I = 0.4$ ); (c) full segmentation, [1,2,3] ( $I = 0.4$ ).

the fourth-order Runge–Kutta method for integrating a set of differential equations with time steps of  $dt = 0.005$ . Smaller time steps led to the same results.

We find it useful to introduce a notation for the repeated structure in the limit cycle. Let us start with case (b), where  $m_1 = m_2$  while  $m_3$  is different (and, incidentally peaks later in the cycle, a fact which will not be revealed by our notation). The notation we use is  $[1_\alpha 2_\alpha 3_\beta]$ , where  $\alpha$  and  $\beta$  refer to the two different waveforms of the same period. Case (c) will be denoted by  $[1_\alpha, 2_\alpha, 3_\alpha]$ , where the commas separate the overall period into substructures of equal temporal behavior. This can also be represented by  $[1, 2, 3]$  because all waveforms are of the same shape. Finally, case (a), which shows a limit cycle in which all  $m_i$  are equal, will be denoted by  $[123]$ , neglecting the common index  $\alpha$ , which becomes superfluous.

In order to estimate the basins of attraction of the various solutions, we have chosen random initial conditions over the seven dimensional space of initial conditions of the  $n = 3$  problem and have measured the probability of flow into the different limit cycles. Choosing the three  $u_i(0)$  uniformly in the domain  $[-1, 1]$ , the three  $r_i(0)$  in the domain  $[0, 1]$ , and  $v(0)$  in the domain  $[-1, 1]$ , for  $I = 0.4$ , we find  $P(a) = 0$ ,  $P(b) = 0.55$ , and  $P(c) = 0.45$ . This means that every one of the three attractors of type (b) and two attractors of type (c) have approximately the same size basin attraction.

It should be emphasized that the choice of parameters in the foregoing examples is quite arbitrary. The phenomena exist within a wide window of parameters. For example, dominance of modes (b) and (c) is obtained for  $0.3 < I < 0.65$  and  $0.5 < a < 0.7$ . We will continue and stick to the particular parameters specified in these examples while varying  $n$  in the study of our model.  $n$  was defined as the number of excitatory neurons in our model. If instead of choosing a common input  $I_i = I$  for all neurons, we present the input only to a subset, then all other excitatory neurons will remain inactive. Hence, for all practical purposes,  $n$  may be regarded as the number of excitatory neurons that are influenced by the common input.

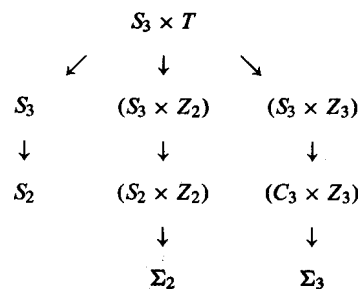
### 3. Symmetry Considerations

The attractors described in the previous section can be specified by regarding their invariance under symmetry operations. There are two types of symmetries that come into play: the permutation symmetry group  $S_n$  of the  $n$  nonlinear oscillators (excitatory neurons) and the finite translation operations  $Z_q$ , which map between  $q$  sections of the basic cycle, i.e., translate  $t \rightarrow t + \tau/q$ , where  $\tau$  is the period of the limit cycle. Although the system of differential equations is invariant under  $S_n$ , its solutions do not have to obey the full symmetry. They exhibit invariance under isotropy groups, which are subgroups of  $S_n \times T$ , where  $T$  is the group of continuous time translations. In the examples shown in Figure 1, only the  $[123]$  configuration of case (a) is invariant under the permutation group  $S_3$ . Case (b) is invariant under an  $S_2$  subgroup [generated by the permutation (12)]. Case (c) is invariant under a cyclic subgroup of the permutations and translations  $\Sigma_3 \subset C_3 \times Z_3$ , where  $C_3$  denotes a cyclic subgroup of  $S_3$  that is composed of the elements  $\{I, (123), (132)\}$ .  $\Sigma_3$  consists also of three elements; hence it is isomorphic to  $C_3$  and is generated by a permutation (123) multiplied by the translation of  $\tau/3$ .

This group-theoretic analysis follows the methodology of Golubitsky et al. (1988) and Ashwin and Swift (1992). An application to neuronal circuitry has been suggested recently by Collins and Stewart (1993), who have shown how the symmetries of a small neural network can be exploited to sort out biological operations (animal gaits in their paper). This is quite natural if we assume that the network controls these operations, with each network pattern corresponding to a particular behavioral pattern. Our interest lies in a different direction. We would like to understand the limitations on a particular mode—the segmentation mode—which, in the preceding example, obeys the symmetry  $\Sigma_3$ .

Before continuing to larger  $n$ , let us direct our attention to the symmetry reduction involved in the examples of  $n = 3$  (three nonlinear oscillators). The situation is summarized in Chart 1, where arrows represent reduction from a symmetry group to its subgroup.

All symmetry groups that we encounter are subgroups of  $S_3 \times T$ , where  $T$  is the continuous group of time translations. Clearly there is only one attractor (the common fixed point) that can be invariant under the whole group. All limit cycles are invariant, by definition, under translation by  $\tau$ . Some exhibit a substructure that allows for symmetry operations that combine permutations and finite time translation operations by  $\tau/q$ . The latter is realized by  $T_q = \exp(\frac{\tau}{q} \frac{d}{dt})$ , which generates the cyclic group  $Z_q$  when operating on a periodic waveform  $m(t)$ :  $T_q m(t) = m(t + \tau/q)$ . All direct products of permutation symmetries with  $Z_q$  are put in parentheses because they cannot be realized as isotropy groups. To see why this is so, consider the unit element of the group that is multiplied by  $Z_q$ . This would introduce group elements of shifts by  $\tau/q$ , which cannot be invariance operations if the smallest period is  $\tau$ . One possible isotropy group is not realized in our numerical studies. This is  $\Sigma_2$ , which would be a symmetry group of a structure like  $[1_\alpha 3_\beta, 2_\alpha 3_\beta]$ , which we have not obtained. That such an isotropy group is an allowed symmetry for a system of three coupled oscillators, was proved and demonstrated by Golubitsky and Stewart (1986), who considered systems with dihedral symmetry ( $D_n$ ), which for  $n = 3$  is isomorphic to  $S_n$ . In addition, we should also mention the completely asymmetric situation of  $[1_\alpha 2_\beta 3_\gamma]$ , which is also not obtained. The realized symmetries within the parameter space that we have studied are, as explained before,  $S_3$ ,  $S_2$ , and  $\Sigma_3$ , acting on the cases (a) (b) and (c) displayed in Figure 1.



**Chart 1.** Relation between symmetry groups for  $n = 3$ .

It is interesting to compare our analysis with that of Ashwin and Swift (1992). They prove that for  $n$  weakly coupled symmetric oscillators the different solutions correspond to all distinct ways of writing  $n = m(k_1 + k_2 + \dots + k_l)$ , where  $l, m$ , and  $k_j$  are integers with  $k_1 \geq k_2 \geq \dots \geq k_l \geq 1$ . The fully symmetric case (a) corresponds in their notation to  $m = 1, k = 3$ . Case (b) corresponds to  $m = 1, k_1 = 2, k_2 = 1$ , and case (c) corresponds to  $m = 3, k = 1$ . As can be seen,  $m$  corresponds to our number of temporal divisions (number of commas + 1), and the  $k_i$  denote the degeneracies of possible waveforms (our  $\alpha, \beta$ ). There is only one other case that fulfills their conditions, corresponding to the asymmetric state of  $m = 1, k_1 = k_2 = k_3 = 1$ . Their symmetries do not include the case of  $\Sigma_2$ , which could operate on a structure like  $[1_\alpha 3_\beta, 2_\alpha 3_\beta]$ . The reason is that they treat the weakly coupled case; hence they assume that all components display the same periodicity. A structure that is invariant under  $\Sigma_2$  involves different periodicities. This would not be the case for the example cited here. Admittedly we do not obtain such a solution in our analysis of  $n = 3$ ; however, different periodicities show up for higher  $n$  values, as will be demonstrated below in the subsequent text.

#### 4. Higher $n$ Values

Increasing the number of excitatory neurons from three to four more than doubles the number of possible symmetry groups of the limit cycles.  $S_4$ , the permutation symmetry of four objects, has 24 elements. Its reduction into subgroups that are relevant to our problem is described in Chart 2.

The subgroups of  $S_4$  include, in addition to lower permutation groups  $S_m$  and cyclic groups  $C_m$ , dihedral groups  $D_m$ . The ones appearing in Chart 2 are  $D_2 = S_2 \times S_2$ , an example of which is  $\{I, (12), (34), (12)(34)\}$ , and  $D_4$ , which can be composed of  $\{I, (12), (34), (12)(34), (14)(23), (13)(24), (1423), (1324)\}$ .  $D_2$  could be the symmetry of a structure of the type  $[1_\alpha 2_\alpha 3_\beta 4_\beta]$ , which, however, is not realized in our numerical evaluation.  $D_4$  leads to a possible symmetry group of our problem by outer multiplications with elements of  $Z_2$ . The result, which we call  $\Delta_4$ , is such that the

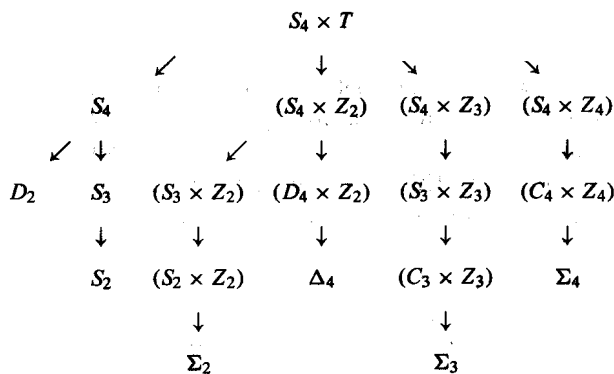
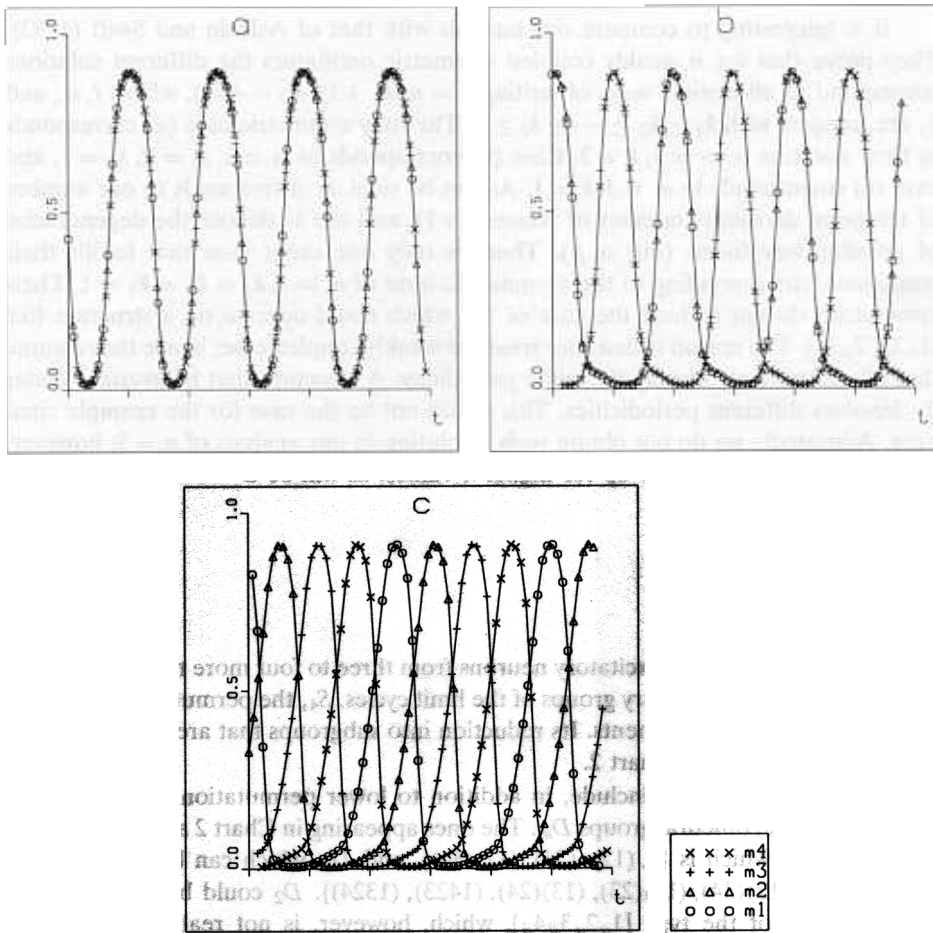


Chart 2. Relation between symmetry groups for  $n = 4$ .



**Fig. 2.** Three types of limit cycles of the  $n = 4$  problem: (a) Fully synchronous, [1234]; (b) partial segmentation, [12,34]; (c) full segmentation, [1,2,3,4]. Parameters are the same as in the  $n = 3$  problem shown in Figure 1 except for (a)  $I_i = 0.8$ ; (b)  $a = 0.55$ , and (c)  $a = 0.65$ ,  $I_i = 0.5$ .

four elements of  $D_4$  which do not belong to its  $D_2$  subgroup are multiplied by a shift of  $\tau/2$ . Clearly  $\Delta_4$  is isomorphic to  $D_4$ . An example of an oscillatory structure that is invariant under this group is  $[1_\alpha 2_\alpha, 3_\alpha 4_\alpha]$ , which we obtain as a possible limit cycle of this problem. This is shown in Figure 2 together with other possible solutions: The fully segmented structure [1, 2, 3, 4], which is invariant under  $\Sigma_4 = \{I, (1234) \times T_4, (13)(24) \times T_2, (1432) \times T_4^3\}$ , and the fully synchronous [1234].

Other solutions that we find, that are of the kind forbidden by Ashwin and Swift, are shown in Figure 3. These include waveforms of the type  $[1_\alpha 4_\beta, 2_\alpha 4_\beta, 3_\alpha 4_\beta]$ . This is quite evident in Figure 3a. It takes a second look to convince oneself that Figure 3b fits the same description. In the second example the basic waveform has two peaks of different heights for each component. The isotropy group of these structures is  $\Sigma_3$ ,



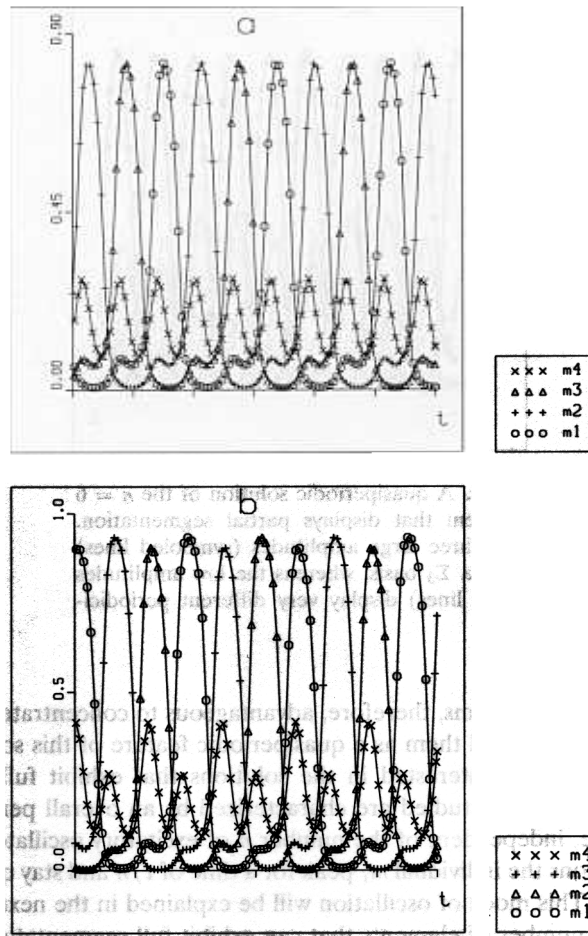
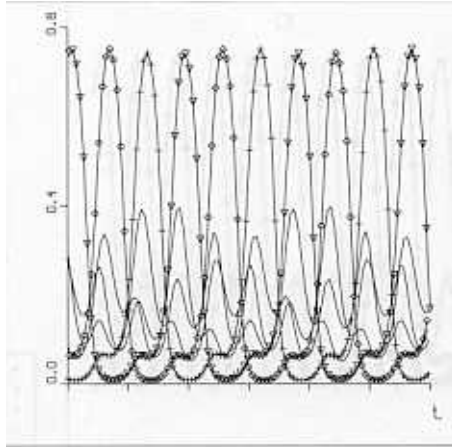


Fig. 3. Two solutions of the  $n = 4$  problem that can be obtained only for strong interactions ( $a > 0.54$ ). Both fit the description  $[1_\alpha 4_\beta, 2_\alpha 4_\beta, 3_\alpha 4_\beta]$ .

generated by the cyclic permutation (123) and a time shift of  $\tau/3$ . These examples differ from all previous ones by the different periods of their components and also by the different sizes of amplitudes. The latter is a natural consequence of the fact that no symmetry relation can exist between components that have different periodic structures. The phenomenon of multiple periods is a result of strong coupling in the system. In our case this comes about through the parameter  $a$  in equation (2.1). The solutions shown in Figure 3 were obtained for  $a = 0.65$ ; they disappear for  $a < 0.54$ .

Solutions of the type shown in Figure 3 become abundant for higher  $n$  values. An example is presented in Figure 4 which displays a result obtained in the case  $n = 6$ , which has three large waveforms and three small ones. Whereas the large amplitudes possess an effective  $\Sigma_3$  symmetry, the three small ones are not related by any obvious symmetry operation. In fact, their periods are much larger than those of



**Fig. 4.** A quasiperiodic solution of the  $n = 6$  problem that displays partial segmentation. The three large amplitudes (symboled lines) form a  $\Sigma_3$  basis, whereas the low amplitudes (solid lines) display very different periodicities.

the large waveforms. It seems, therefore, advantageous to concentrate on the leading waveforms only and regard them as a quasiperiodic feature of this solution.

We are particularly interested in the solutions that exhibit full segmentation. All the examples that we studied are characterized by an overall period  $\tau$ , which is roughly the same, independent of the number  $n$  of excitatory oscillators. In the fully segmented solutions the individual  $m_i$  peak for a time of  $\tau/n$  and stay quite low for the rest of the time. This mode of oscillation will be explained in the next section. There is a limit on the number of elements that can exhibit full segmentation. The highest  $n$  for which we find a fully segmented solution is  $n = 5$ . This is a numerical result obtained by a search in a wide parameter range. For higher  $n$  values we encounter only partial segmentation: either a quasiperiodic behavior in which some of the excitatory neurons participate, as in Figure 4, or segmentation of clusters of excitatory neurons, as in Figure 5, which corresponds to a waveform [12, 34, 56] for  $n = 6$ .

### 5. Segmentation as viewed by the Single Oscillator

In the system of equations that we study here, the interaction between all elements is provided by the inhibitory unit (2.3). The individual excitatory neuron  $i$ , described by (2.1) and (2.2), is influenced by all other units through the amplitude  $m$  of the inhibitory neuron in (2.1). The behavior of each  $m_i$  in any given solution can therefore also be viewed as the response of equations (2.1) and (2.2) to a driving term  $am(t)$ . All the waveforms that we encounter have an overall period that is roughly the same as that of the free oscillator ( $a = 0$ ). In a segmentation mode  $m(t)$  oscillates with a period of  $\tau/n$ . This can be seen in Figure 6, where we show  $m_1(t)$  and  $m(t)$  for the

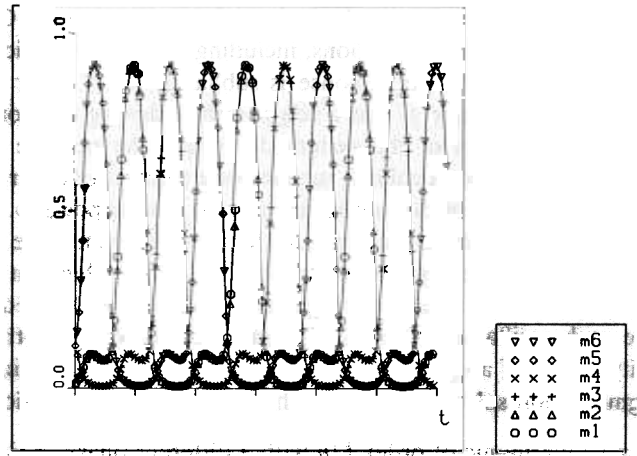


Fig. 5. Partial segmentation in the  $n = 6$  problem, through the formation of clusters of pairs of patterns that vary synchronously. This fits the description [12, 34, 56].

$n = 5$  segmentation.  $m_1$  has a waveform of period  $\tau$  whose local peaks have widths of  $\tau/n$ , as already emphasized in the previous section. If we think of  $m$  as the driving term, then the phenomenon observed here is that of subharmonic oscillation, which is known to exist in nonlinear oscillating systems (Mandelstam and Papalexi, 1932; Hayashi, 1964).

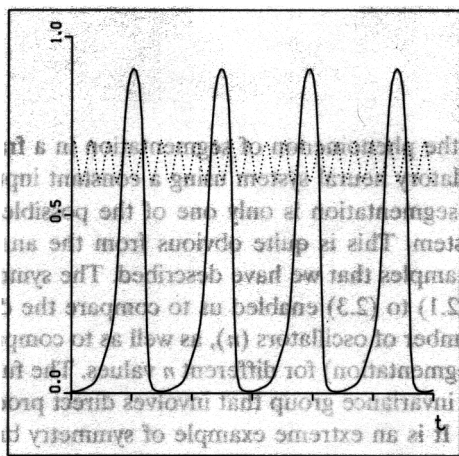


Fig. 6. The variation of  $m_1(t)$  (solid line) and  $m(t)$  (the inhibitory amplitude; dotted line) in the  $n = 5$  fully segmented limit cycle.  $m_1(t)$  oscillates with a frequency that is  $1/5$  of the frequency of the inhibitory neuron. This is evidently a subharmonic behavior.

A stable linear system follows the frequency of the driving term. Only nonlinear systems exhibit different periodic solutions, including the subharmonic ones that are of interest to us. We say that the response is subharmonic of order  $1/n$  when the system oscillates with frequency  $f/n$  as a response to a driving term of frequency  $f$ . The nonlinear characteristics of the system determine the possible orders of the subharmonic oscillations. In particular, a subharmonic solution of order  $1/v$  is likely to occur when one of the terms of the nonlinear function has the power  $v$ . Its realization depends, however, on stability conditions that have to be met. Note that any such solution has a  $v$ -fold degeneracy determined by the phase, which, in turn, strongly depends on the initial conditions. Full segmentation is a  $1/n$ -ordered subharmonic solution where each oscillator makes a different phase choice. Note that in our case the nonlinearity is that of a sigmoid function that, in principle, contains all powers.

A full segmentation solution of order  $n$  has to satisfy two conditions:

1. Each  $m_i$  is a subharmonic of order  $1/n$  with a different phase choice.
2. Each  $m_i$  is active during approximately  $\tau/n$  every cycle and stays quite low during the rest of the cycle.

In other words, full segmentation is a  $1/n$  subharmonic response of each nonlinear oscillator with a peak width of approximately  $\tau/n$ , which we call a narrow subharmonic. To test the subharmonic response of the system, we investigated the solutions of (2.1) and (2.2) when the driving term  $am(t)$  is replaced by a constant+sinusoidal amplitude with a tunable frequency. We were able to generate narrow subharmonic solutions of order  $1/2$  to  $1/5$ . From  $1/6$  onward the subharmonic solutions were no longer narrow, i.e., the peak width of  $m_i(t)$  was much larger than  $\tau/n$  (where  $1/n$  is the order of the subharmonic solution). This explains why a full segmentation solution is limited in our system to  $n \leq 5$ .

## 6. Summary

We have investigated the phenomenon of segmentation in a framework of a permutation symmetric oscillatory neural system using a constant input.

We saw that full segmentation is only one of the possible limit cycles that can be reached in this system. This is quite obvious from the analysis of  $n = 3$  and  $4$  and from the other examples that we have described. The symmetry imposed on the equations of motion (2.1) to (2.3) enabled us to compare the different modes of oscillation for a fixed number of oscillators ( $n$ ), as well as to compare the same mode of oscillation (e.g., full segmentation) for different  $n$  values. The full segmentation mode is characterized by an invariance group that involves direct products of permutations and time translations. It is an extreme example of symmetry breaking in our system because no degeneracy is left in the resulting solution.

We view segmentation as an important mode of oscillation because of the special role it may play in the analysis of mixed signals. Therefore, we look for an understanding of the limit on the number of segments. We find that it is related in our system to a limitation on the order of a narrow subharmonic solution. When the number of oscillators is larger than five, the mode of oscillation is, in general, partial

segmentation, i.e., there exist either clusters of oscillators or leading and nonleading waveforms. In either one of these cases the number of separate phases does not exceed five. The correspondence between full segmentation and subharmonics expresses another precondition for segmentation—nonlinearity. Both phenomena are indeed found only in nonlinear systems.

It is interesting to note that a similar limit on segmentation was reported by Hadley and Beasley (1987) in their study of arrays of Josephson junctions. They report that their system displays simple staggered oscillations only up to  $n = 3$ . For higher  $n$  values they obtain only more complicated phase distributions.

Although we believe that the general conclusions about the existence of a limit on staggered oscillations—the phenomenon we call segmentation—is valid, we should emphasize that our detailed results are specific to our model. The structure of the nonlinear oscillators is relevant to the specifics of the solutions, in general, and segmentation, in particular. Realistic neural systems are not expected to be permutation symmetric, and their inputs may well change with time. Nonetheless, the model shows us the general types of structures that can occur. The symmetry analysis can serve as a classification scheme. We have learned that some of the interesting structures come from the strong coupling domain and are therefore missed by mathematical analyses of weakly coupled oscillators. Segmentation is a very special case. In our system we were able to show its relation to subharmonic oscillations, thus explaining the intriguing limitation on the number of segmented sectors.

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