

# TOWARDS THE SYNTHESIS OF NEURAL AND EVOLUTIONARY LEARNING

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## Abstract

This chapter focusses on the intersection of neural and evolutionary learning and shows basic aspects of and current approaches to the combination of these two learning paradigms. Advantages and difficulties of such a combination are described. Approaches from both the field of artificial intelligence and the neurosciences are surveyed. A number of related works as well as extensive references to further literature are presented.

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# 1. INTRODUCTION

Learning, defined as any change in the knowledge base of a system that enables the system to improve its performance in the future, is a many-faceted phenomenon. One can distinguish several paradigms for learning, two of which are the neural and the evolutionary paradigm: according to the former, learning consists of modifying the connection weights of a neural or neural-type network of simple computational elements; according to the latter, learning consists of applying the evolutionary operators mutation, recombination and selection to individuals that represent specific points in a search space. This chapter focusses, from the viewpoints of artificial intelligence and the neurosciences, on the intersection of neural and evolutionary learning.

In the field of artificial intelligence neural and evolutionary learning have been investigated separately from and independently of each other until very recently. Neural learning is one of the central areas of research on artificial neural networks; the major goal is the development of learning procedures that work efficiently even for complex real-world tasks, and much progress has been made in achieving this goal in the last decade. Table 1 provides an overview of basic neural learning approaches; for details see (Hinton, 1989; Weiss, 1990).

Against that, evolutionary learning is typically considered in the context of research on evolutionary search. The most common formal techniques of evolutionary search are Rechenberg's evolution strategy (Rechenberg, 1973; Schwefel, 1977) and, most intensively studied, Holland's

NEURAL LEARNING		
SUPERVISED LEARNING	REINFORCEMENT LEARNING	UNSUPERVISED LEARNING
i. e. learning with full training feedback specifying the desired actions	i. e. learning with partial training feedback specifying only the quality of the performed actions	i. e. learning without any training feedback
e. g. backpropagation (Rumelhart et. al, 1986), Boltzmann learning (Hinton & Sejnowski, 1986)	e. g. associative reward-penalty learning (Barto & Anandan, 1985), the reinforcement-comparison algorithms (Sutton, 1984, 1985), the REINFORCE algorithms (Williams, 1987)	e. g. feature maps (Kohonen, 1988), adaptive resonance theory (Grossberg, 1988), Linsker-type learning (Linsker, 1988)

**TABLE 1:** *An overview of basic neural learning approaches in artificial intelligence.*

1. Initialize a population of structures  $P$
2. Evaluate the structures in  $P$
3. while the desired structure is not contained in  $P$  do
  - 3.1. create a new population  $Q$  by applying the evolutionary operators to the structures in  $P$
  - 3.2.  $P \leftarrow Q$
  - 3.3. Evaluate the structures in  $P$

**TABLE 2:** *The evolutionary search cycle. Evolutionary search works with populations of structures, where each structure (genotype) codes for a specific solution (phenotype) in the search space. A structure is evaluated by assigning a measure (fitness value) to the solution it codes for. The initialization is usually done at random. Evolution proceeds by selecting structures according to their fitness values and by randomly changing (mutating) and recombining (crossing) the structures with some (low) specified probability. The search stops when a structure is found that codes for a solution whose fitness value exceeds some predefined threshold.*

genetic algorithm (Dorigo, 1990; Goldberg, 1989; Holland, 1975). Although these techniques differ with respect to several implementational details, conceptually they are nearly identical (Hoffmeister & Bäck, 1990). Table 2 shows how evolutionary search realized by them works in principle. Up to now two types of evolutionary machine learning systems have been proposed: Holland’s classifier systems (Booker, Goldberg & Holland, 1989; Holland, 1986; Holland & Reitman, 1978; Wilson & Goldberg, 1989) and Smith’ LS systems (Smith, 1980, 1983; Schaffer, 1984, 1985); a learning system that combines features of classifier systems and LS systems was presented by Grefenstette (1988a). Roughly, these are parallel, message-passing, rule-based systems that use the genetic algorithm for discovering new rules. The primary difference between the classifier systems and the LS systems is that the former apply the evolutionary operators to individual rules whereas the latter apply them to entire rule sets (see (de Jong, 1988; Grefenstette, 1988b) for a more detailed comparison).

The idea of combining neural and evolutionary learning has received much attention in the last few years and now there are a number of approaches to such a combination. These approaches as well as related works from artificial intelligence and other fields are surveyed in section 2.

In the neurosciences learning is investigated at different levels of brain organization, including the molecular level, the level of individual synapses and neurons, and the level of whole groups of neurons (e.g., Changeux & Konoshi, 1986; Neuroscience Research, 1986; Trends in

Neurosciences, 1988). Several neuroscientific theories have been proposed that combine aspects of neural and evolutionary learning and, in particular, postulate that selective processes operating at these brain levels in somatic time (i.e. during the life time of an individual) are fundamental to neural learning. These theories — the evolutionary selection circuits model, the theories of selective stabilization of synapses and pre-representations, and the theory of neuronal group selection (neural Darwinism) — are described in section 3.

## **2. HYBRID APPROACHES IN ARTIFICIAL INTELLIGENCE**

### **2.1. Evolutionary Design of Artificial Neural Networks**

Experimental data reported in the literature show that there is a strong connection between the structure (size and connectivity) and the function of an artificial neural network (ANN). This connection concerns aspects of both learning and representation. In particular, the structure greatly affects the performance in learning the desired function, that means, the speed and accuracy (including criteria like noise resistance and generalization ability) with which this function is learned, as well as the comprehensibility of the representation of the learned function, that means, the transparency or opaqueness of this function's representation. However, apart from some vague statements, nothing is known about the principles and laws underlying this structure–function connection.<sup>1</sup> There is no method for a priori specifying an appropriate network structure, neither in view of the learning performance nor in view of the representational comprehensibility, and this causes the network design to be the weak point of the process of developing an ANN. (“Network design remains something like a black art”, as was radically formulated in (Miller, Todd & Hedge, 1989).) Therefore it is not surprising that there is a rapidly growing interest in the automated design of network structure (e.g. see (Barna, 1990)).

#### **2.1.1. Improving Learning Performance and Representational Comprehensibility**

There are several approaches to the automated design of ANNs which employ the technique of evolutionary search, typically in the form of Holland's genetic algorithm, in order to find an appropriate network structure. Following the above considerations, these approaches can be classified as follows.

Approaches to the automated network design which deal with the aspect of learning performance were described in (Hancock, 1990; Harp, Samad & Guha, 1989a, 1989b; Lehar & Weaver, 1987; Merrill & Port, 1988b; Miller, Todd & Hedge 89; Nolfi, Elman & Parisi, 1990; Schiffmann, 1989; Schiffmann & Mecklenburg, 1990; Schiffmann, Joost & Werner, 1990;

Wilson, 1990). The intention underlying these approaches was to improve the speed and accuracy achieved by conventional learning procedures for ANNs. Examples of the application tasks used by these approaches are the XOR problem (Harp, Samad & Guha, 1989a, 1989b; Miller, Todd & Hedge, 1989), T–C discrimination (Merrill & Port, 1988b), Boolean multiplexer (Wilson, 1990), digit/face recognition (Harp, Samad & Guha, 1989a, 1989b; Hancock, 1990), and food searching in a simple environment (Nolfi, Elman & Parisi, 1990). The experimental results were very encouraging; in particular, the evolved networks showed an improved learning behavior in comparison with the initial ones (esp. see the approaches of Harp et. al. and Miller et. al.). It is interesting that evolutionary search often produced appropriate structures which are quite different from those (e.g. layered feedforward or simple recurrent structures) typically used in the ANN field.

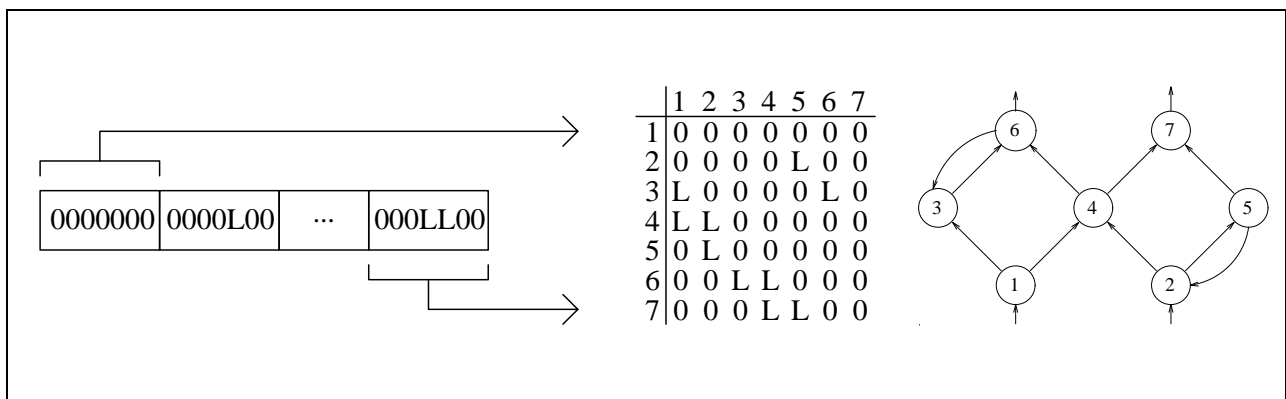
An approach to automated network design which deals with the aspect of representational comprehensibility was depicted in (Dolan & Dyer, 1987a, 1987b). This work focusses on the question of how symbolic schemata might be implemented at the subsymbolic, neural-like (connectionist) level. Thereby Dolan and Dyer took the view that networks learning by constructing opaque representations “may yield little to our understanding of human cognitive information processing” (1987b, p. 123) and that “in order to learn large symbolic structures of the type that people use, specific architectures will be required” (1987a, p. 8). (A similar argumentation is contained in (Feldman, 1988).) The primary intention for applying the evolutionary search technique was to demonstrate that there is a plausible evolutionary path along which network structures suitable for symbol processing can evolve. The experiments performed by Dolan and Dyer indicated that the low-structured networks were less robust (hence more flexible) as regards mutational changes than the high-structured ones (also see (Gierer, 1989)); particularly, these experiments showed an evolutionary tendency towards complex, hierarchically organized structures. (Another hybrid approach which may be viewed under the aspect of representational comprehensibility was presented in (de Garis, 1990a); see section 2.2. Another work carried out at the symbolic–subsymbolic intersection was described in (Mühlenbein & Kindermann, 1989).)

### 2.1.2. Genotypic Representation of Neural Networks

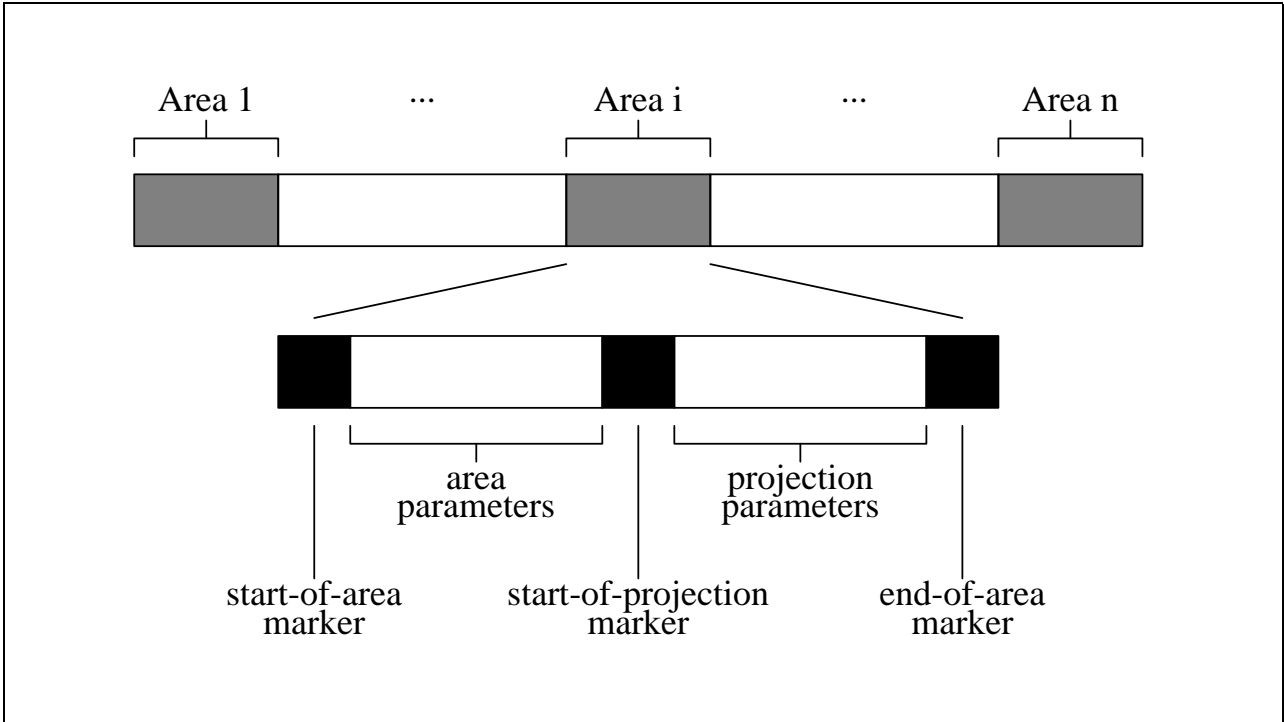
Employing the evolutionary search technique requires that the network structures be encoded in specific representations or “genotypes” upon which the evolutionary operators mutation and recombination (crossing over) can act. One can distinguish between two types of representational schemes used in the approaches mentioned above. First, the low-level scheme according to which the structure is specified more or less directly by the *network connectivity* (e. g., Miller, Todd & Hedge, 1989; Schiffmann & Mecklenburg, 1990). Second, the high-level scheme according to which the structure is specified in a relatively abstract way by *network parameters* like the number of layers or units (total or within a layer), the degree and

the types of connectivity between and within the layers, the size of the units' receptive fields, and so forth (e. g., Dolan & Dyer, 1987a, 1987b; Harp, Samad & Guha, 1989a, 1989b; Lehar & Weaver, 1987; Merrill & Port, 1988b).<sup>2</sup> The figures 2 and 3 give an example of these representational schemes. (Other genotypes that have been used code for “non-structural network properties” like the magnitude of the units' thresholds or the magnitude and decay rate of the connection- or layer-specific learning coefficient.) As it was pointed out by Harp, Samad and Guha (1989a, 1989b), the major characteristics of these representational schemes is that the low-level one is suited for the precise and deterministic handling of the connectivity patterns of small networks, whereas the high-level one is suited for the handling of the structural regularities of large networks. However, up to now there are no performance studies comparing the low- and high-level schemes. It has to be noted that these two types of schemes establish representational extremes between which many “mixed” genotypic representations are possible.

An alternative (high-level) representation scheme according to which the structure of an ANN is specified by simple *growth rules* was proposed in (Mjolsness & Sharp, 1986; Mjolsness, Sharp & Alpert, 1987, 1988; Mjolsness, Sharp & Reintz, 1990).<sup>3</sup> This scheme is biologically more plausible than the others, particularly, it enables a more realistic transition from the genotypes to the phenotypes (i.e. the networks themselves). (Wilson (1987, 1989) considered growth rules from a more general point of view.)



**FIGURE 1:** Example of a low-level network representation according to (Miller, Todd & Hedge, 1989). The figure shows the genotypic representation (left) of the connectivity constraint matrix (middle) of a simple neural net (right). The matrix entry  $(i,j)$  specifies the type of constraint on the connection from unit  $j$  to unit  $i$ ; thus, row  $i$  of the matrix represents the constraints on the connections to unit  $i$ , and column  $j$  represents the constraints on the connections from unit  $j$ . Entry “0” means “weight fixed at zero”, and entry “L” means “learnable”; other constraint types mentioned by Miller et. al. are “weight fixed at some constant value” and “weight restricted to positive (negative) values”. (The mutation operator randomly chooses new connection constraints, and the crossover operator randomly chooses a row number and exchanges that row between two “parents”.)



**FIGURE 2:** Example of a high-level network representation according to (Harp, Samad & Guha, 1989a, 1989b) (details omitted). A network “blueprint” is genotypically represented by a bit string that consists of several segments. Each segment specifies (i) the structure (e. g. the number of units and their spatial arrangement) of some area of the network by means of area parameters and (ii) the connections (e.g. their density and projection field) from this area to other areas by means of projection parameters. This kind of blueprint representation allows a compact specification even of very complex networks. (The mutation operator randomly changes entries of the bit string, the crossover operator swaps corresponding segments between two strings.)

The choice of the genotypic representation and the evolutionary operators is decisive to the efficiency of the evolutionary search technique. Particularly, this choice affects important aspects like

- *structural completeness* (“Which structures of which size and connectivity are available?”),
- *structural correctness* (“Do all mutated and recombined genotypes specify correct (meaningful) structures?”),
- *structural level of operator application* (“At which network level — individual connections, whole sub-networks — do mutation and recombination operate?”), and
- *structural sensibility to operator application* (“To what degree do mutation and recombination change the structures?”).

(Note that mutation and recombination are syntactic operators that are applied to the genotypes without regard to the semantics (function) of the respective phenotypes.) The last two aspects give rise to some controversy over the applicability of the recombination operator. On the one side, assuming that small structural changes are more likely to lead to acceptable functional changes than large ones, its applicability appears to be questionable (cf. (Bergman & Kerszberg, 1987) and the considerations of structure–function gradualism in (Lehar & Weaver, 1987; Conrad, 1988)). On the other side, assuming that sub–networks are functional units, its applicability, at least at this level, appears to be useful (cf. the concepts of local networks (3.2), cell assemblies (3.3) and neuronal groups (3.4)).

### 2.1.3. Hybrid Learning

Generally, all the approaches mentioned above (no matter which type of representational scheme they are using) realize a crossing of neural and evolutionary learning according to the hybrid learning cycle shown in table 3. (In this cycle the genotypes and the phenotypes are not explicitly distinguished; remember that the mutation and crossing–over operators act on the genotypes whereas the selection operator acts on the phenotypes.) Of course, the individual approaches differ greatly in detail; this concerns, in particular, the population size (ranging from one upwards), the parent–offspring replacement strategy (e. g. with/without substitution), the evolutionary operators (e. g. sometimes the recombination operator was not used for reasons discussed above), the learning procedures (typically back–propagation or Hebb–type learning), the performance criteria (which can be distinguished into learning criteria — speed and accuracy — and cost criteria — number of units and/or connections), and the desired results with regard to these criteria (e. g. “maximal speed in a minimal network”)

As it was pointed out in (Miller, Todd & Hedge, 1989), there are several reasons for using evolutionary search/genetic algorithms in designing networks. In particular, both enumera-

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|--|
| <ol style="list-style-type: none"> <li>1. Creation of the next population of ANNs by means of fitness–oriented reproduction. This includes both selection, mutation and recombination. (The initial population is created at random.)</li> <li>2. Training of the ANNs by conventional neural learning procedures.</li> <li>3. Evaluation of the ANNs’ fitness values according to some given performance criteria.</li> <li>4. If the desired result is obtained then stop, otherwise goto step 1.</li> </ol> |
|--|

**TABLE 3:** *The hybrid learning cycle.*



tive, random, gradient-descent and heuristic-knowledge-guided search methods are unsuited because the search space (defined by the fitness values above the space of all possible network structures) is infinitely large (since there are infinitely many different structures), undifferentiable (since changes in the structure are discrete but can have discontinuous effects on the network performance), deceptive (since structurally similar networks can have different fitness values) and multimodal (since structurally different networks can have similar fitness values).

The price that has to be paid for using the technique of evolutionary search for automated network design is that of high computational costs. These costs can be reduced by employing the “natural parallelism” being inherent in this technique (cf. the various approaches to parallel versions of Holland’s genetic algorithm contained in the proceedings of the second and third international conference on genetic algorithms).

A term sometimes used within the frame of these approaches is that of a genetic neural network. Following the expositions in (Bergman, 1988; Mühlenbein & Kindermann, 1989), such a network is defined by four components: a language whose sentences represent the genotypes of networks; a procedure realizing the genotype-phenotype transition; a procedure mutating the genotypes; and a procedure (fitness function) measuring the phenotypes’ performance values. (This definition is general enough to be also applicable to the hybrid approaches described in the next section.)

## **2.2. Evolutionary Training of Artificial Neural Networks**

One of the recent developments in the field of artificial neural learning is that of using the technique of evolutionary search instead of conventional learning procedures for training artificial neural nets (ANNs); see (Caudell & Dolan, 1989; de Garis, 1990a; Dodd, 1990; Heistermann, 1990; Höffgen & Siemon, 1990; Merrill & Port, 1988a; Montana & Davis, 1989; Nolfi, Elman & Parisi, 1990; Scholz, 1990; Whitley, 1988; Whitley & Hanson, 1989; Whitley, Starkweather & Bogart, 1989; Wieland, 1990).

The major idea underlying these approaches is to interpret the weight matrices (or vectors) of the ANNs as genotypes and to change the connection weights by means of specific evolutionary operations. Typically Holland’s genetic algorithm or variants of it have been used.

Perhaps the most striking argument for evolutionary network training is that this technique, in contrast to the conventional gradient descent learning procedures, inherently tends to avoid getting stuck in local minima of the error surface over the weight space (where the error is defined as the difference between the actual and the desired network outputs). Evolutionary training was successfully applied to tasks like the XOR/424-encoder/adder problem (Whitley & Hanson, 1989), the construction of networks that approximate functions (Höffgen & Siemon,

1. Training of the ANNs. This includes
  - 1.1. fitness-oriented selection and
  - 1.2. weight modification by means of recombination and/or mutation
 and results in a new population of ANNs.
2. Evaluation of the ANNs' fitness values, where the error produced by an ANN serves as the performance measure.
3. If the desired result is obtained then stop, otherwise goto step 1.

**TABLE 4:** *The evolutionary-training cycle.*

1990), categorization (Montana & Davis, 1989), robot-arm positioning (deGaris, 1990a), and the standard pole balancing problem and variations of it (Wieland, 1990).

Generally, the learning cycle performed by the evolutionary-training approaches is as shown in table 4. (As it is the case with the hybrid learning approaches (2.1.2), the evolutionary-training approaches show great differences in detail, too. Again this concerns, in particular, the population size, the replacement strategy, and the performance criteria used by them.)

Finally, a brief outline of some individualities of the evolutionary-training approaches mentioned above.

Caudell and Dolan (1989) a network model that combines optical and electronic components was introduced. The weighting of the electro-optical networks is constrained by *parametric connectivity*, that means, it is controlled by specific parameters in such a way that the number of these parameters is generally smaller than the number of the connection weights. This discrepancy leads to intricate dependencies between the weights and, with that, to a highly complex error surface over the parameter space.

In (Montana & Davis, 1989) various specific mutation and crossover operators were defined and tested; thereby the *real-valued* weights themselves (and not a — binary — encoding of them as would be typical for genetic algorithms) constituted the genotypes.

In (de Garis, 1990a) the concept of *genetic programming* was introduced (see also (Conrad, 1988b) and (Koza, 1990) for different uses of this term). According to this concept, both network modules and their control circuits were trained by the genetic algorithm. Further aspects of this kind of automated evolutionary network design were described in (de Garis, 1990b).

In (Whitley, 1989; Whitley & Kauth, 1988) a specific genetic algorithm called GENITOR was used. It differs in two important aspects from the standard genetic algorithm. Firstly,

a technique called *ranking* (Baker, 1985) was employed in order to avoid selective–pressure problems and, hence, the necessity of scaling (cf. (Goldberg, 1989) for details); according to this technique, the number of offsprings of an ANN is a function of its rank in the performance–sorted population. Secondly, it does not work on the conventional generational reproduction mechanism but employs a *one-at-a-time reproduction*, that means, one new genotype at a time replaces the lowest ranking genotype. A distributed version of GENITOR called GENITOR II was described in (Whitley & Starkweather, 1990).

## 2.3. Further Hybrid Approaches and Related Works

This section provides a loose overview of further hybrid approaches and of various works (both from artificial intelligence and other fields) which do not explicitly aim at the combination of neural and evolutionary learning but are related to this subject.

**2.3.1.** Whitley and Bogart (1990) employed the technique of evolutionary search (in form of a rank–based genetic algorithm, cf. 2.2) for pruning unnecessary connections of already backpropagation–trained, fully connected artificial neural networks (ANNs). The underlying idea was to develop nets that are smaller and therefore faster than the initial ones but still able to solve the desired tasks. The weights of the starting nets were used to initialize the pruned nets which, in turn, were re–trained with an increased number of backpropagation cycles.

Another relevant work combining neural and evolutionary learning was presented by Belew, McInerney and Schraudolph (1990). Here two different approaches were investigated. First, the GA was successfully used for tuning parameters (learning rate and momentum) of the standard backpropagation algorithm; this approach may be viewed as a typical application of the GA. Second, and very interesting, the GA was used for searching the space of initial weights of the networks’ connections, from which conventional learning methods (conjugate gradient and backpropagation) proceed. The idea underlying the latter approach is to effectively combine the global sampling performed by the GA with the local search performed by the conventional methods. The encoding of the real–valued network weights into the binary genotypes is done according to a mechanism called dynamic parameter encoding (Schraudolph & Belew, 1990) which allows an adaptive refinement of the mapping from the binary genotypes to real numbers.

Mühlenbein and Kindermann (1989) provided a survey of formal models describing the dynamics of genotype–phenotype evolution (including the models of Mendelian and ecological genetics) and of evolutionary algorithms based on these models (including the algorithms of Rechenberg and Holland). Additionally, genotype and phenotype learning were compared with the help of the Iterated Prisoner’s Dilemma, and an artificial system called Pandemonium II that combines these two types of learning was outlined.

A work done at the intersection of computer science, artificial intelligence, and Darwinian evolution was presented in (Dress, 1987, 1988, 1989; Dress & Knisley, 1987). Based on some

general, theoretical considerations on the simulation of complex systems, Dress and his colleagues focussed on the evolution of synthetic intelligent systems. (The word “synthetic” is used in a twofold meaning: as a synonym for “assembled from interacting functional modules”, and as a generic term for “real” and “simulated”.) Simulation experiments were done with a synthetic organism (presented as an insect) composed of an adaptive, frequency-coded neural network and sensors and effectors for the environmental interaction; thereby evolutionary search was used for optimizing the feature-detection capabilities of the organism’s non-adaptive retina. The population size was restricted to one, and no recombination operator was applied. The experiments run with two types of selection: positive selection, i.e. selection for higher fitness, and negative selection, i.e. selection against lower fitness. (The optimization of the feature-detection capabilities of an artificial retina by means of evolution strategy was also treated by Lohmann (1990).)

Koza (1990) described how LISP-represented artificial neural networks can evolve by applying the genetic operators to the LISP-expressions encoding the nets.

Another work that was inspired, in a broad sense, by the concept of evolution was presented in (Hagiwara & Nakagawa, 1989). Here the intention was to use selection (of the unit which produces the maximum error value) and mutation (of this unit’s weights) in order to escape from local error minima in backpropagation-trained ANNs.

Lee and Peterson (1989) used the principles of mutation and selection to enable unsupervised learning networks (more exactly, generalized versions of Kohonen’s self-organizing feature maps) to change their structure adaptively.

Some of the evolutionary-design and evolutionary-training approaches treated in the preceding sections are capable of modifying the number of units of the networks at each successive generation; especially see (Harp, Samad & Guha, 1989a, 1989b) and also (Mjolsness & Sharp, 1986; Mjolsness, Sharp & Alpert, 1987, 1988). This capability brings them in close contact to various other, “non-evolutionary” approaches to networks of variable size; e. g. (Ash, 1989; Fahlman & Lebiere, 1990; Honavar & Uhr, 1988; Mezard & Nadal, 1989; Mozer & Smolensky, 1989; Sietsma & Dow, 1988) and (Baum 89). Common to these evolutionary and non-evolutionary approaches is that they enable learning by modifying both the connection weights and the number of units/connections.

Works done at the intersection of classifier systems (cf. chapter 1) and ANNs were described in e. g. (Belew & Gherrity, 1989; Compiani, Montanari, Serra & Valastro, 1989; Davis, 1988, 1989; Schmidhuber, 1989). Some analogies between classifier systems and ANNs were shown in (Belew & Forrest, 1988). A general comparison between genetic and connectionist models was drawn by Laussermair (1988).

A bibliography of works relating ANNs and evolutionary search was provided in (Rudnick, 1990).

The first steps towards the use of the evolutionary principles of mutation and selection in

the field of ANNs were described in (Selfridge, 1958; Klopff & Gose, 1969).

**2.3.2.** In (Bergman & Kerszberg, 1987; Kerszberg & Bergman, 1988) the evolution of computational abilities in competing automata was studied. The automata consisted of threshold-like units that interact via unmodifiable (positive or negative) connections; the evolutionary process proceeds by mutation and selection only, recombination was not used (for the reason mentioned in section 2.1). In accounting for the nature-versus-nurture problem — “at what extend is the brain/behavior genetically determined?” —, automata having differently constrained connectivity patterns were considered. The application task was to recognize similarities in successively presented input patterns. Simulation experiments showed that in the course of evolutionary learning specific connectivity patterns develop, where the automata having neither a too weakly nor a too strongly constrained connectivity pattern learned best. This observation seems to be consistent with work done in in the field of neurobiology (see 2.3.3).

Another interesting aspect, the evolution of the learning capability itself, was explored by Chalmers (1990). Here the underlying idea was to encode the dynamic weight-space properties of a network into a genotype and then see whether any interesting learning mechanisms evolve. Chalmers focussed on supervised learning of (linearly separable) mappings in single-layer feed-forward networks having a fixed structure; the weight-space dynamics of the networks is described by a parametrized weight-update function. Chalmers concluded that “the methods of genetic search and connectionism can be combined to provide a demonstration that the capacity for learning (adaptation within the lifetime of an individual) may evolve in a natural fashion under the pressures of evolution (adaptation over the history of a population)” and that “this double adaptive loop seems to be a powerful mechanism for coping with a diverse environment”.

The question under which conditions and how quickly learning could evolve was investigated within the frame of the work described in (Miller & Todd, 1990; Todd & Miller, 1990, 1991). Miller and Todd performed experiments with artificial creatures that have a simple brain and live in a hypothetical environment consisting of food and poison. Food and poison each have specific colors and smells within one creature’s life (e.g. food–green–sweet and poison–red–sour), where the smell accuracy depends on the actual environmental conditions; furthermore, the smell–object relations are fixed, but the color–object relations vary between creatures (e.g. poison may be red for one creature but green for another). Consequently the learning task was to build up associations between color and object. The experiments indicated an interesting relationship between the smell accuracy and the time taken to evolve color learning: the time was shortest for accuracies around 75 percent and increased for accuracies diverging from that middle range. In their interpretation of this relationship Miller and Todd argued that the U–shape emerges indirectly “from a trade–off between the phylogenetic adaptive pressure to evolve learning (during species–wide evolution), and the ontogenetic ease of learning (during each individual creature lifetime)”. (See also 2.3.4.)

The evolution by mutation and selection of Boolean automata was investigated in (Kauffman, 1969, 1984, 1986; Kauffman & Smith, 1986; Kauffman & Levin, 1987). This work was greatly motivated by the various open questions concerning the stability of ontogenetic development, particularly its genetic regulation and its capability to evolve. The Boolean automata consisted of interconnected binary components, each realizing one of the possible Boolean functions, and they were classed by the (uniform) number of input connections per component. The theoretical and experimental studies concentrated on the dynamic behavior of the automata (in terms of state cycles and their basins of attraction, where at each time the state of an automata is determined by the states of its components) and its evolution given a specific fitness landscape.

**2.3.3.** An interesting question related to the approaches treated in sections 2.1 and 2.2 is how and to what extent real brains are genetically determined. Although there is little known about the details underlying this brain–genetics connection, in biology the following general statements are commonly accepted (esp. cf. Changeux, 1983a, 1985; Changeux, Heidmann & Patte, 1984; Gierer, 1988).

The degree of genetic brain determinism decreases from evolutionary lower to higher animals. This determinism is almost absolute in invertebrates and implies an a priori specified, more or less precise point–to–point wiring; against that, it is less strict in vertebrates and allows variability in the brain connectivity (even between genetically identical individuals). Particularly in vertebrates and especially in mammals, the brain development depends on both genetic and epigenetic factors and requires the organism’s interaction with its environment.

In view of the nature–versus–nurture problem it can be said that the initial brain state of a vertebrate is neither “tabula rasa” nor “completely pre–programmed”; instead, the genes code for some (species–specific) brain invariants and for general rules for brain development. As it was pointed out by Gierer (1988, p. 19), “genetically specified initial conditions of the neural network taking into account of features which vary rarely or not at all in different situations would provide the organism with a clear head start as compared with a ‘tabula rasa’ state even if the latter allows, in principle, to deal with any conceivable kind of information processing input ... given enough time”.

AI works that take these nature–versus nurture aspects in one or another way into account were described in (Bergman & Kerszberg, 1987; Kerszberg & Bergman, 1988) and (Mjolsness, Sharp & Alpert, 1988). A work that focusses on the construction of a genetic–like code for ANNs was presented by Boseniuk (1990); the intention was to use this code, which controls interactions between simulated processes like cell growth or cell division, as an object of evolutionary optimization. Stork, Walker, Burns and Jackson (1990) used the GA for experimentally illustrating how genetically specified preadaptations may lead to anomalous neural connections.

Gierer (1988) focussed on question of how much genetic information controls the brain development. In short, Gierer arrived at the following two interesting suggestions: on the one

hand, only a small number of genes may be required for generating a highly structured brain; on the other hand, a large number of genes may be involved in the specification of the connection strengths. The total number of genes contributing to brain development “is presumably determined by a balance between evolutionary pressures in favour of fine tuning facilitating performance under common conditions, and those in favour of maintaining versatility and responsiveness for coping with uncommon situations” (p.19).

**2.3.4.** The Weismann doctrine states that there is no — Lamarckian — retranslation from the phenotype to the genotype, that means, phenotypic modifications acquired by learning or environmental factors cannot be translated into the genotype (and, hence, are not inheritable). However, according to a hypothesis sometimes called the Baldwin effect (Baldwin, 1896; Morgan, 1896) it is nevertheless possible that learning guides evolution without violating the Weismann doctrine. The idea underlying this hypothesis may be sketched as follows: the ability to learn influences the degree of adaptability and, by this way, the number of descendants; this, in turn, leads to a modified evolutionary search space. In (Belew, 1989; Hinton & Nowlan, 1987; Maynard Smith, 1987; Nolfi, Elman & Parisi 1990; Plotkin 1988) this hypothesis was recently reconsidered. Hinton and Nowlan performed experiments demonstrating that learning can speed up evolution given a fixed environment. Belew mathematically analyzed the Hinton–Nowlan model and extended it by incorporating culture (reduced to a real number) as an additional factor influencing an individual’s fitness value. A strong interaction between learning and evolution is also indicated by the experiments reported by Nolfi et. al.

The question how evolution and cognition are related to each other is the subject of evolutionary epistemology (Lorenz, 1973; Vollmer, 1975). According to the main thesis of this discipline, which may be viewed as the “biological and philosophical basis” particularly of the evolutionary–design approaches treated in section 2.1, the subjective cognitive structures are adapted to the structures in the real world since they are a result of the biological evolution, and they coincide (at least partially) with the real structures since only such a coincidence enables survival (Vollmer, 1975, p. 102). Further considerations on the evolutionary epistemology are contained in e. g. (Lorenz & Wuketits, 1983; Riedl, 1982; Riedl & Wuketits, 1987, Vollmer, 1988). Other publications focussing on the evolution–cognition relation are e. g. (Lewontin, 1990; Piatelli–Palmarini, 1989; Seitelberger, 1989).

Further literature: (Hastings & Waner, 1985, 1986; Hastings, Waner & Wu, 1989; Waner & Wu, 1987a, 1987b) and (Ackley, 1985, 1987; Bateson, 1984; Dewdney, 1985; Fedanzo, 1986; Oosthuizen, 1989; Stolorz & Hoffmann, 1988).

### 3. SELECTIVE THEORIES IN THE NEUROSCIENCES

#### 3.1. General Aspects

In the neurosciences several theories have been proposed that combine aspects of neural and evolutionary learning; these are the evolutionary selection circuits model, the theories of selective stabilization of synapses and pre-representations, and the theory of neuronal group selection.

Essential to these theories is the assumption that the brain, or the nervous system in general, works on the principle of selection; in other words, selection is assumed to play the same role in the brain in somatic time as it does in biological evolution in phylogenetic time. This view of the brain as a selective system, or as a “Darwin machine” as Calvin (1987) said, has some important implications; in particular, it requires that there is a great variety in the neural tissue which is prior to any environmental interaction and upon which selection can act in a fitness-oriented, eliminative manner. (Of course, this requirement for variety has to be met by all selective systems.)

The selective theories are radically opposed to the instructive theories which assume that the development of the brain is directed epigenetically during the organism’s interaction with the environment by rules for the precise brain wiring. The two basic arguments underlying the controversy between the supporters of the selective and the instructive theories are the following: from the “selective view” the instructive theories have to be rejected since they imply a pre-existing order in the world which is transferred into the brain; against that, from the “instructive view” it is argued that the selective theories go wrong since they imply a pre-existing wiring of all the potentially learnable things. Currently it is not definitely known whether the instructive or the selective theories are the correct ones; however, there are several neurobiological facts (e. g., Edelman, 1987, pp. 37–42) which indicate that, in one or another way, selective mechanisms may be fundamental to the brain development. (Selective-instructive disputes have some tradition in biology: remember the controversial theories of antibody production or of biological evolution.)

The following sections give an overview of the four selective theories mentioned above. The main emphasis is on the basic claims made by them; additionally, each section contains a brief guide to additional literature. Further selectionist views of the brain proposed in the field of the neurosciences that are not considered in this chapter were described in (Jerne, 1967; Young, 1973, 1975).

#### 3.2. The Evolutionary Selection Circuits Model

The evolutionary selection circuits model (Conrad, 1974, 1976), ESCM for short, con-



ceptually describes neural learning as the gradual modification of the information–processing capabilities of enzymatic neurons through a process of variation and selection in somatic time. In order to put this more precisely, first a closer look is taken at enzymatic neurons, and then the fundamental claims of the ESCM are described.

The ESCM starts from the view that the brain is organized into various types of local networks which contain enzymatic neurons, that is, neurons whose firing behavior is controlled by enzymes called excitases. (For details of this control and its underlying biochemical processes see (e. g., Conrad, 1984, 1985).) These neurons incorporate the *principle of double dynamics* (Conrad, 1985) by operating at two levels of dynamics: at the level of readin or tactilization dynamics, the neural input patterns are transduced into chemical–concentration patterns inside the neuron; and at the level of readout dynamics, these chemical patterns are recognized by the excitases. Consequently, the enzymatic neurons themselves are endowed with powerful pattern–recognition capabilities where the excitases are the recognition primitives. Both levels of dynamics are gradually deformable as a consequence of the *structure–function gradualism* — “slight changes in the structure cause slight changes in the function” — in the excitases.<sup>4</sup>

There are three fundamental claims made by the ESCM: redundancy of brain tissue, specificity of neurons, and existence of brain–internal selection circuits. According to the claim for redundancy, there are many replicas of each type of local network; that means, the brain consists of local networks which are interchangeable in the sense that they are highly similar or even identical with regard to the connectivity (including the synaptic strengths) and the properties of their neurons. The claim for specificity says that the excitases are capable of recognizing specific chemical patterns and, with that, cause the enzymatic neurons to fire in response to specific input patterns. According to the third claim, the brain contains selection circuits which direct the fitness–oriented, gradual modification of the local network’s excitase configurations. These selection circuits include three systems: a *testing system* which allows to check the consequences (e.g., pleasure or pain) of the outputs of one or several local networks for the organism; an *evaluation system* which assigns fitness values to the local networks on the basis of these consequences; and a *growth–control system* which regulates (stimulates or inhibits) the production of the nucleic acids which code for the local networks’ excitases on the basis of these fitness values. The nucleic acids, whose variability is ensured by random somatic recombination and mutation processes, diffuse to neighbouring networks of the same type (where they perform the same function because of the interchangeability property mentioned above).

These claims imply that neural learning proceeds by means of the gradual modification of the excitase configurations in the brain’s local networks through the repeated execution of the following evolutionary learning cycle:

1. Test and evaluation of the enzymatic neuron–based local networks. As a result, a fitness value is assigned to each network.

2. Selection of the local networks. This involves the fitness-oriented regulation of the production of the excitase-coding nucleic acids, as well as their spreading to adjacent interchangeable networks.
3. Application of somatic recombination and selection to these nucleic acids. This maintains the range of the excitase configurations.

The execution stops when a local network having a sufficiently high fitness is found. Conrad emphasized that this evolutionary learning cycle is much more efficient than natural evolution because the selection circuits enable an intensive selection even if there is hardly a difference between the fitness values of the interchangeable networks.

Finally, further works of reference. The ESCM is part of extensive work focussing on the differences between the information processing capabilities of biological (molecular) systems and conventional computers; the interested reader is referred to (Conrad, 1985, 1988a, 1989) and the references therein.

A computational specification of the ESCM which concentrates on the pattern-processing capabilities of the enzymatic neurons, together with its successful application to a robot-control task, was presented by Kampfner and Conrad (1983a). Investigations of this computational variant were described in (Kampfner & Conrad, 1983b; Kampfner, 1988). Another computational specification which concentrates on the intraneuronal dynamics of enzymatic neurons is described by Kirby and Conrad (1984). Kirby and Conrad (1986) described a combination of these two specifications. Furthermore, see (Akingbehin & Conrad, 1989; Conrad et. al., 1989).

### **3.3. The Theories of Selective Stabilization of Synapses and Pre-Representations**

The **theory of selective stabilization of synapses** or briefly TSSS was proposed by Changeux and his co-workers (Changeux, Courrege & Danchin, 1973; Changeux & Danchin, 1976). It accounts for neural learning *during development* by postulating that a somatic selection mechanism acts at the level of synapses and contributes to the wiring pattern in the adult brain. Subsequently the neurobiological basis and the major claims of the TSSS are depicted.

The neurobiological basis of the TSSS comprises aspects of both neurogenesis and neurogenetics.

In vertebrates one can distinguish several processes of brain development. These are the cellular processes of cell division, movement, adhesion, differentiation, and death, and the synaptic processes of connection formation and elimination. (For details see (Cowan, 1978; Cowan et. al., 1984; Purves & Lichtman, 1985).) The TSSS focusses on the “synaptic aspect” of neurogenesis; it deals with the *outgrowth and stabilization of the synapses*, and it takes the developmental stage where *maximal synaptic wiring* exists as its initial state.

The neurogenetic attitude of the TSSS constitutes a compromise between the preformist (“specified-by-genes”) and the empirist (“specified-by-activity”) view of brain development. It is assumed that the genes involved in brain development, the “genetic envelope”, only specify the *invariant characters* of the brain; this includes, in particular, the connections between the main categories of neurons (i. e. between groups of neurons which are of the same morphological and biochemical type) and the rules of synaptic growth and stabilization. These rules allow for an activity-dependent, *epigenetic synapse formation* within the neuronal categories. (As Changeux (1980, p. 193) formulated: “The genetic envelope offers a hazily outlined network, the activity defines its angles.”)

The TSSS makes three major claims. First, at the critical stage of maximal connectivity there is a significant but limited redundancy within the neuronal categories as regards the specificity of the synapses. Second, at this time of so-called “structural redundancy” any synapse may exist under (at least) three states of plasticity: labile, stable, and degenerate. Only the labile and stable synapses transmit nerve impulses, and the acceptable state transitions are those from labile to either stable or degenerate and from stable to labile. Especially, the state transition of a synapse is epigenetically regulated by all signals received by the postsynaptic soma during a given time interval. (The maximal synaptic connectivity, the mechanisms of its development, and the regulative and integrative properties of the soma are determinate expressions of the genetic envelope.) Third, the total activity of the developing network leads to the selective stabilization of some synapses, and to the regression of their functional equivalents. As a consequence, structural redundancy decreases and neuronal singularity (i. e., individual connectivity) increases. This provides a plausible explanation of the connection elimination naturally occurring during neural development.

For further readings in the TSSS see (Changeux, 1983a, 1983b, 1985; Changeux, Heidmann & Patte, 1984).

The **theory of selective stabilization of pre-representations** (TSSP), which may be viewed as an extension of the TSSS, provides a selectionist view of neural learning in the adult brain (Changeux, 1983b; Changeux, Heidmann & Patte, 1984; Heidmann, Heidmann & Changeux, 1984). The theory postulates that somatic selection takes place at the level of neuronal networks. Similar to Edelman’s theory of neuronal group selection (see 3.4), the TSSP may be viewed as an attempt to show how neurobiology and psychology are related to each other. (There are several parallels between the works of Changeux and Edelman; however, an investigation of these parallels is beyond the scope of this chapter.) In what follows, the two major claims of this theory are outlined.

The first claim is that there exist mental objects or “neural representations” in the brain. A mental object is defined, in a general manner, as the physical state achieved by the correlated and transitory (both electrical and chemical) activity of a cell assembly consisting of a large number of neurons having different singularities.<sup>5</sup> According to the TSSP, three classes of

mental objects are distinguished. First, *primary percepts*; these are labile mental objects whose activation depends on the direct interaction with the outside world and is caused by sensory stimulations. (Primary percepts may exist before birth and are located at the primary and secondary areas of the cerebral cortex.) Second, *stored representations*; these are memory objects whose evocation does not demand environmental interaction and whose all-or-none character of activity results from a stable, cooperative coupling between the neurons. Third, *pre-representations*; these are mental objects which are generated before and concomitant with any environmental interaction. Pre-representations are labile and of great variety and variability; they result from the spontaneous but correlated firing of neurons or groups of neurons.

The second claim made by the TSSP is that learning in the adult brain corresponds to the selective stabilization of pre-representations, that means, the transition from selected pre-representations to stored representations. As stated by Changeux, this requires, in the simplest case, the interaction with the environment; in this case the criterion of selection is the resonance (spatial overlapping or firing in phase) between a primary percept and a pre-representation.

Further literature on the TSSP: (Changeux & Dehaene, 1989) (here the two theories, TSSS and TSSP, were embedded in more general considerations on the neural basis of cognition) and (Dehaene, Changeux & Nadal, 1987; Toulouse, Dehaene & Changeux, 1986) (here a formal model of neural learning on the basis of the TSSP was described).

### 3.4. The Theory of Neuronal Group Selection

Among the selective theories the theory of neuronal group selection (abbreviated to TNGS) or “neural Darwinism” (Edelman, 1978, 1987) is both the most rigorous and elaborate one. This theory, which has attracted much attention especially in the last few years, bridges the gap between biology and psychology by postulating that somatic selection is the key mechanism which establishes the connection between the structure and the function of the brain. As done in the preceding sections, below the major ideas of the TNGS are described.

There are three basic claims. First, during (prenatal and early postnatal) development, *primary repertoires* of degenerate neuronal groups were formed epigenetically by selection. Thereby a neuronal group is considered as a local anatomical entity which consists of hundreds to thousands of strongly connected neurons, and degenerate neuronal groups are groups that have different structures but carry out the same function more or less well (they are nonisomorphic but isofunctional). This concept of *degeneracy* is fundamental to the TNGS; it implies both structural diversity and functional redundancy and, hence, ensures both a wide range of recognition and the reliability against the loss of neural tissue. Degeneracy naturally originates from the processes of brain development (cf. section 3.3) which are assumed to occur in an epigenetic manner and to elaborate several selective events at the cellular level.<sup>6</sup> According

to the *regulator hypothesis*, these complex developmental processes, as well as the selective events accompanying these processes, are guided by a relatively small number of cell adhesion molecules.

Second, in the (postnatal) phase of behavioral experience, a *secondary repertoire* of functioning neuronal groups is formed by selection among the preexisting groups of each primary repertoire. This group selection is accomplished by epigenetic modifications of the synaptic strengths without change of the connectivity pattern. According to the *dual rules model*, these modifications are realized by two synaptic rules that operate upon populations of synapses in a parallel and independent fashion: a presynaptic rule which applies to long-term changes in the whole target neuron and which affects a large number of synapses; and a postsynaptic rule which applies to short-term changes at individual synapses.<sup>7</sup> The functioning groups are more likely to respond to identical or similar stimuli than the non-selected groups and, hence, contribute to the future behavior of the organism. A fundamental operation of the functional groups is to compete for neurons that belong to other groups; this competition affects the groups' functional properties and is assumed to play a central role in the formation and organization of cerebral cortical maps. (All these hypotheses have been integrated in a model, sometimes called the confinement-competition-selection model, which accounts for the development of topographic maps in the adult brain.)

Third, reentry — phasic signaling over re-entrant (reciprocal and cyclic) connections between different repertoires, in particular between topographic maps — allows for the *spatiotemporal correlation* of the responses of the repertoires at all levels in the brain. Reentry is viewed as an important mechanism supporting group selection and as being essential both to categorization and the development of consciousness. Two fundamental structures based on reentry are that of a *classification couple* — re-entrant repertoires that can perform classifications more complex than a single involved repertoire could do — and that of a *global mapping* — roughly, re-entrant repertoires that correlate sensory input and motor activity.

Some brief notes on how the TNGS accounts for psychological functions. Following Edelman's argumentation, categories do not exist apriori in the world (the world is “unlabeled”) and categorization is the fundamental problem facing the nervous system. This problem is solved by means of group selection and reentry. Consequently, categorization largely depends on the organism's interaction with its environment and turns out to be the central neural operation required for all other operations. Based on this view of categorization, Edelman suggests that memory is “the enhanced ability to categorize or generalize associatively, not the storage of features or attributes of objects as a list” (Edelman, 1987, p. 241) and that learning, in the minimal case, is the “categorization of complexes of adaptive value under conditions of expectancy” (Edelman, 1987, p. 293).

There is a large body of literature on the TNGS. The most detailed depiction of the theory was provided in Edelman's book (Edelman, 1987). In order to test the TNGS, a series of

computer models which embody the theory's major ideas have been constructed. These are the Darwin I model (Edelman, 1981), the Darwin II model (Edelman & Reeke, 1982; Reeke & Edelman, 1984; Edelman, 1987), and the Darwin III model (Reeke & Edelman, 1988; Reeke, Sporns & Edelman, 1988).

Edelman sharply criticizes both the symbolic and the subsymbolic (connectionist) artificial intelligence approach. The main arguments underlying his criticism are that here it is assumed that the world is pre-labeled and that the brain acts in an instructionist mode like a computer (Edelman, 1987; Reeke & Edelman, 1988; Reeke, Sporns & Edelman, 1988).

Recently appeared reviews of the TNGS: (Crick, 1989; Michod, 1989; Nelson, 1989; Smoliar, 1989; Patton & Parisi, 1989).

#### 4. CONCLUDING REMARKS

In this chapter a broad overview has been provided of works carried out at the intersection of the neural and the evolutionary learning paradigm. This overview has shown that the combination of these two learning paradigms is of great interest for several reasons: generally, it may prove useful in explaining the structure–function connection of neural or neural–type networks; in particular, from the perspective of artificial intelligence it offers new possibilities in improving both the learning performance and the representational transparency of artificial neural nets, from the perspective of the neurosciences it has a major impact on our understanding of the neural–level processes that underly the higher cognitive abilities, and from the perspective of evolutionary theory and psychology it sheds new light on the relationship between evolution and learning.

The combination of neural and evolutionary learning establishes a very young research area in artificial intelligence that has a strongly interdisciplinary character (affecting aspects and problems that have been traditionally treated within the frame of either the neurosciences, or genetics, or evolution theory or computer science). For answering the questions existing and arising in this area a lot of experimental and theoretical work has to be done in a close interdisciplinary cooperation; however, this work is worth doing since there is the justified hope that it will lead to results that are useful and profitable for all the involved disciplines.

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## NOTES

- 1 Examples of such vague statements about the structure–function connection are: “the more complex the problem the more hidden units have to be used”; “networks being too large may lose their generalization ability”, see e. g. (Huyser & Horowitz, 1988); “learning a function requires a larger network than implementing it”, see e.g. (Mozer & Smolensky, 1989; Sietsma & Dow, 1989; Whitley & Bogart, 1990); “unstructured networks produce incomprehensible representations”, see e.g. (Dolan & Dyer, 1987a; Feldman, 1988).
- 2 Merrill and Port (1988) introduced the term “fractally configured neural networks”. This term indicates that the space of all possible network structures was partitioned into regions of connectivity and non–connectivity in a way similar to the fractal partitioning of the complex plane into regions of attraction and infinite growth. (The evolved structures themselves were not fractal.)
- 3 One of the major assumptions underlying this work of Mjolsness and his co–workers is that structured networks, unlike unstructured ones, offer the possibility of automated functional scaling–up, that means, of automatically generating nets that solve bigger problems from nets that solve small ones.
- 4 As Conrad (1988a) pointed out, this structure–function gradualism is the key to natural evolution/evolutionary learning in general and it is a condition for the evolutionary adaptability of biological systems in particular; thereby evolutionary adaptability is the extent to which mechanisms of variation and selection can be utilized in order to survive in uncertain and unknown environments.
- 5 The concept of a cell assembly was introduced by Donald Hebb (1949). Roughly, in the original formulation, a cell assembly is viewed as a set of strongly interconnected neurons which is used as an elementary unit in higher cognitive processes. Thereby the connections alter during experience according to a particular rule, nowadays known as the Hebb rule, suggesting that the synaptic strength between any two neurons increases whenever they are simultaneously active.
- 6 Such selective events are strongly indicated by the developmental processes of cell death and connection elimination. A mechanism which may account for these regressive processes is the competition for quantitatively limited trophic factors; see (Purves & Lichtman, 1985).
- 7 An important property of this dual rules model, as stressed by Edelman and his co–workers, is that the pre– and postsynaptic modifications are functionally indistinguishable at the level of the individual synapse. It is interesting to note that the postsynaptic rule may be viewed as a general case of the Hebb rule (see note 5); however, because the former depends on global population effects whereas the latter only depends on local firing behavior, these two rules differ largely in their actions.