Neural Propagation of Beliefs

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Abstract

We continue to explore the hypothesis that neuronal populations represent and process analog variables in terms of probability density functions (PDFs). A neural assembly encoding the joint probability density over relevant analog variables can in principle answer any meaningful question about these variables by implementing the Bayesian rules of inference. Aided by an intermediate representation of the probability density based on orthogonal functions spanning an underlying low-dimensional function space, we show how neural circuits may be generated from Bayesian belief networks. The ideas and the formalism of this PDF approach are illustrated and tested with several elementary examples, and in particular through a problem in which model-driven top-down information flow influences the processing of bottom-up sensory input.

1 Introduction

1.1 Fundamental Hypothesis

This is the second of two papers elaborating upon the proposition (Anderson, 1994) that neural populations encode and process information about analog variables in the form of probability density functions (PDFs). As demonstrated in the first paper (Barber et al., 2001), explicit representation of probabilistic descriptors of the state of knowledge of physically relevant variables subserves a powerful strategy for modeling neural circuits. By exploiting mathematical tools developed

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within the theory of Bayesian inference, we can establish general procedures for building and understanding models of cortical circuits that carry out well-posed information-processing tasks.

Importantly, if neural populations encode the joint probability distribution over the variables of interest, then such neural networks are able to answer any probabilistic question about those variables. Motivated by this fact, we shall now extend the PDF hypothesis by devising methods for embedding joint probabilities into neural networks. This will enable us to construct neural circuit models that pool multiple sources of evidence, such as sensory inputs and any evolutionarily determined priors on the joint distribution. More specifically, we will focus on developing neural networks that use “bottom-up” sensory inputs to build an internal model of the data, which in turn uses “top-down” signals to impose global regularities on the sensory data. In the resulting neural networks, there will naturally arise distinct feedforward, feedback, and lateral connections, analogous to the neural pathways observed in the anatomy of the cerebral cortex (Van Essen et al., 1992).

Our treatment is based on Bayesian belief networks (Pearl, 1988; Smyth et al., 1997), graphical representations of probabilistic models that provide an efficient means for organizing the relations between the random variables of a given model. The resulting neural networks will have several properties of Bayesian belief networks, as well as more typical neural-network properties, so we will call them neural belief networks. Bayesian belief network have been previously utilized in the genesis of certain neural networks ((Neal, 1992; Zemel, 1999)), although with different methods for generating the neural network architecture and dynamics.

1.2 Three Levels of Representation

In the context of the PDF hypothesis (Anderson, 1996), we assert that a physical variable \( x \) is described by a neural population at time \( t \) in terms of a PDF \( \rho(x; t) \), rather than as a single-valued estimate \( x(t) \). In general, we consider a PDF described at time \( t \) in terms of a set of \( D \) parameters \( \{A_\mu\} \). Experimentally observed linear decoding rules (Georgopoulos et al., 1986; Schwartz, 1993) suggest that the PDFs may be represented as

\[
\rho(x; t) = \sum_{\mu=1}^{D} A_\mu(t) \Phi_\mu(x) \tag{1}
\]

The basis functions \( \Phi_\mu(x) \) are orthonormal functions which serve to define the PDFs that the neural circuit can represent, but the amplitudes \( A_\mu(t) \) cannot be interpreted as neuronal firing rates due to their
arbitrarily high precision and their ability to take on negative values. Therefore, we introduce an additional representation of the PDF in terms of firing rates $a_i(t)$ and decoding functions $\phi_i(x)$ assigned to $N$ neurons, so that

$$\rho(x; t) = \sum_{i=1}^{N} a_i(t)\phi_i(x)$$  \hspace{1cm} (2)

Unlike the basis functions $\Phi_\mu(x)$, the decoding functions $\phi_i(x)$ form a highly redundant, overcomplete representation ($N \gg D$) suitable for use with neuronal units having biologically realistic precision (some 2–3 bits; see Rieke et al., 1997).

The abstract representation defined by equation 1 will underlie the representation in the neuron space defined by equation 2. This allows us to deal with the issue of how PDFs can be precisely implemented in populations of neurons by focusing on the mapping between the minimal space and the space of neurons (Barber et al., 2001). Thus, neural belief networks can be developed in the theoretically convenient abstract representation, and then be implemented in more realistic networks of low-precision model neurons. Adopting the terminology of Zemel et al. (1998), we denote the set of physical variables as the implicit space and the measurable quantities as the explicit space. Extending their nomenclature, we denote the abstract space of equation 1 as the minimal space. The explicit space of neurons constitutes a biological implementation of the desired computations in the implicit space, while the minimal space, whose properties are more conducive to formal analysis, provides a valuable bridge between the two other spaces.

We have developed rules to transform between representations in the three spaces (Barber et al., 2001). Equations 1 and 2 respectively define how to transform representations in the minimal and explicit spaces into a representation (PDF) in the implicit space. With the remaining rules (summarized below), we can readily switch between the three representations and approach any task in the most appropriate space.

For the orthonormal basis $\{\Phi_\mu(x)\}$, the minimal space coefficients $A_\mu(t)$ are found using the encoding rule

$$A_\mu(t) = \int \Phi_\mu(x)\rho(x; t)\, dx$$  \hspace{1cm} (3)

The coefficients in the explicit space, i.e. the neural firing rates $a_i(t)$, cannot be found in this direct fashion. We utilize a set of encoding functions $\hat{\phi}_i(x)$ and an encoding rule of the form

$$a_i(t) = f\left(\int \hat{\phi}_i(x)\rho(x; t)\, dx\right)$$  \hspace{1cm} (4)
This explicit-space encoding rule is patterned after the neural responses associated with the population vector of Georgopoulos et al. (1986).

To relate the explicit and minimal spaces, we express the encoding and decoding functions in terms of the orthonormal basis, so that

$$\phi_i(x) = \sum_{\nu=1}^{D} \kappa_{i\nu} \Phi_\nu(x)$$ (5)

$$\hat{\phi}_i(x) = \sum_{\nu=1}^{D} \hat{\kappa}_{i\nu} \Phi_\nu(x)$$ (6)

The transformation coefficients $\kappa_{i\nu}$ and $\hat{\kappa}_{i\nu}$ also relate the $A_\mu(t)$ and $a_i(t)$, such that

$$A_\mu(t) = \sum_{i=1}^{N} \kappa_{i\mu} a_i(t)$$ (7)

$$a_i(t) = f \left( \sum_{\nu=1}^{D} \hat{\kappa}_{i\nu} A_\nu(t) \right)$$ (8)

Methods for determining the encoding functions $\hat{\phi}_i(x)$, decoding functions $\phi_i(x)$, and transformation coefficients $\kappa_{i\nu}$ and $\hat{\kappa}_{i\nu}$ have been addressed in detail in the earlier work (Barber et al., 2001).

2 Neural Belief Networks

2.1 Bayesian Belief Networks

In section 1.2, we have summarized methods for encoding and decoding probability density functions into and from the firing rates of populations of neurons. These methods are oriented towards encoding a single random variable (or vector), but we do not wish to restrict ourselves to only the simplest implicit spaces. In this work, we will explore ways in which we can apply the methods so far developed (Barber et al., 2001) to more complicated implicit spaces. In particular, we will use Bayesian belief networks to efficiently organize the implicit random variables, and then use these Bayesian belief networks to generate neural networks.

Bayesian belief networks are directed acyclic graphs that represent probabilistic models (Figure 1). Each node represents a random variable, and the arcs (or directed line segments) signify the presence of direct causal influences between the linked variables. The strengths of these influences are defined using conditional probabilities. The directionality of a specified link indicates the direction of causality (or, more simply, relevance); an arc points from direct cause to effect.
Bayesian belief networks have two properties that we will find very useful, both of which stem from the independencies shown by the graph structure. First, the value of a node $X$ is not dependent upon all of the other graph nodes. Rather, it depends only on a subset of the nodes, called a Markov blanket of $X$, that separates node $X$ from all the other nodes in the graph. The Markov blanket of interest to us can be readily determined from the graph structure. It is comprised of the union of the direct parents of $X$, the direct successors of $X$, and all direct parents of the direct successors of $X$. Second, the joint probability over the random variables is decomposable as

$$P(x_1, x_2, \ldots, x_n) = \prod_{i=1}^{n} P(x_i | \text{Pa}(x_i)) \quad (9)$$

where $\text{Pa}(x_i)$ refers to the (possibly empty) set of direct parent nodes of $X_i$. This decomposition comes about from repeated application of Bayes’ rule and from the structure of the graph.

### 2.2 Probabilistic Inference Performed by Neural Networks

Before exploring arbitrary Bayesian belief networks, it is enlightening to consider a BBN with a simple graph consisting of two connected nodes $X \rightarrow Y$. This graph represents any probabilistic model where a single random variable is inferred from one source of evidence. For convenience, we will work in the minimal space.

Our objective is to find the best marginal PDFs $\rho(y; t)$ and $\rho(x; t)$ to describe the system. We represent the PDFs using equation 1 and

$$\rho(y; t) = \sum_{\nu} B_{\nu}(t) \Psi_\nu(y) \quad (10)$$

In this network, we find values of the output firing rates $\{B_{\nu}(t)\}$ only,
with input firing rates \( \{A_\mu(t)\} \) assumed to be fully determined by an encoding process.

We define a cost function by

\[
E_y = \frac{1}{2} \int \left( \rho(y; t) - \int \rho(y | x) \rho(x; t) dx \right)^2 dy
\]

\[
= \frac{1}{2} \int \left( \sum_\nu B_\nu(t) \Psi_\nu(y) - \sum_\mu A_\mu(t) \int \rho(y | x) \Phi_\mu(x) dx \right)^2 dy
\]

(11)

The cost function has a minimum corresponding to taking a weighted average of the conditional probability \( \rho(y | x) \)

\[
\rho(y; t) = \int \rho(y | x) \rho(x; t) dx
\]

(12)

We assume in equation (12) that the relationship between \( x \) and \( y \) is independent of the values of the underlying parameters \( A_\mu(t) \) of the minimal space [Barber et al., 2001].

To minimize \( E_y \), we calculate the derivatives \( \partial E_y / \partial B_\nu \). Using gradient descent, we obtain the update rule

\[
\frac{dB_\nu(t)}{dt} = -\eta \frac{\partial E_y}{\partial B_\nu}
\]

\[
= -\eta \left( B_\nu(t) - \sum_\mu \Omega_{\nu\mu} A_\mu(t) \right)
\]

(13)

where \( \eta \) is a rate constant and we identify weights

\[
\Omega_{\nu\mu} = \iint \Psi_\nu(y) \rho(y | x) \Phi_\mu(x) dxdy
\]

(14)

Equations (13) and (14) define a network in the minimal space which can be converted to a neural network in the explicit space using equation (8).

Equation (13) has a fixed point at

\[
B_\nu(t) = \sum_\mu A_\mu(t) \iint \Psi_\nu(y) \rho(y | x) \Phi_\mu(x) dxdy
\]

(15)

This is identical to the result obtained by encoding the inference relation in equation (2) into the minimal space using equation (3).

### 2.3 Predictive and Retrospective Support

Neural belief networks can feature two distinct types of information propagation that provide support for the PDFs represented at each
graph node. Predictive support, also called causal support, is probabilistic information that propagates, along the directions of the graph links, from cause to effect (Pearl, 1988). The network considered in section 2.2 involves only predictive support.

The second type of support is retrospective, or diagnostic, support. In this case, information propagates against the directions of the graph links, from effect to cause, or, equivalently, from evidence to hypothesis (Pearl, 1988). By specifying $\rho(y;t)$ instead of $\rho(x;t)$, the $X \rightarrow Y$ inference network features only retrospective support.

Using the same minimal-space representation (equations 1 and 10) that we used for the predictive network, we determine the update rule for the retrospective network. We find

$$\frac{dA_{\mu}(t)}{dt} = \eta \left( \sum_{\beta} B_{\beta}(t) \Omega_{\beta\mu} - \sum_{\alpha} A_{\alpha}(t) \Upsilon_{\alpha\mu} \right) \tag{16}$$

with feedback weights

$$\Omega_{\beta\mu} = \iint \Psi_{\beta}(y) \rho(y|x) \Phi_{\mu}(x) dx dy \tag{17}$$

and lateral weights

$$\Upsilon_{\alpha\mu} = \int \left( \int \rho(y|x) \Phi_{\alpha}(x) dx \right) \left( \int \rho(y|x) \Phi_{\mu}(x) dx \right) dy \tag{18}$$

While the feedback weights $\Omega_{\beta\mu}$ of the retrospective network are identical to the feedforward weights of the predictive network (equation 13) in the minimal space, note that the resulting neural networks weights in the explicit space need not be identical. The lateral weights $\Upsilon_{\alpha\mu}$ provide a measure of the correlation between what the different basis functions in the parent node $X$ predict about the child node $Y$; these lateral connections act to ensure consistency between evidence and hypothesis.

Although the networks driven by retrospective support are closely related to the networks driven by predictive support, their function is quite different. For example, consider a network with $\rho(y \mid x) = \delta(y - |x|)$ as the underlying computation. In a predictive network, wherein we specify $\rho(x;t)$ and infer $\rho(y;t)$, the absolute-value relationship is approximated in a straightforward fashion (Figure 2a). Conversely, a retrospective network based upon the same conditional PDF is called upon to “invert” the absolute value, a non-invertible function. The inferred $\rho(x;t)$ decoded from the retrospective network (Figure 2b) captures both of the possible solutions—with positive and negative values—in response to a unimodal PDF $\rho(y;t)$. 

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Figure 2: Predictive and retrospective support of the absolute value function. The results shown here utilize spaces of dimension $D = 6$ to represent both $x$ and $y$ in the two networks. The structure of the spaces was determined from the singular value decomposition (Goldberg, 1991) of a discrete approximation of $\rho(y \mid x)$—the basis functions $\Phi_\mu(x)$ and $\Psi_\nu(y)$ are set to the singular vectors corresponding to the $D$ largest singular values. (a) The network with predictive support closely approximates the absolute value function. Specifying a PDF $\rho(x; t)$ centered about $x = -1/2$ yields an inferred PDF $\rho(y; t)$ of similar form centered about $x = +1/2$. (b) The network with retrospective support allows for both possible solutions. Specifying a unimodal PDF $\rho(y; t)$ centered about $x = +1/2$ yields an inferred bimodal PDF $\rho(x; t)$, with the modes centered about $x = -1/2$ and $x = +1/2$. 
2.4 Encoding Bayesian Belief Networks Into Neural Networks

Following a strategy similar to that presented in section 2.2, we can develop neural-network update rules from arbitrary Bayesian belief networks. We assume that the Bayesian belief network consists of \( R \) nodes, symbolizing random variables \( X_1, X_2, X_3, \ldots, X_R \). Introducing representations

\[
\rho(x_i; t) = \sum_\mu A^{(i)}_\mu(t) \Phi^{(i)}_\mu(x_i)
\]

for the marginal distributions in the minimal space, we define auxiliary cost functions, analogous to that in equation 11, with the forms

\[
E_i = \frac{1}{2} \int \left( \rho(x_i; t) - \int \rho(x_i | Pa(x_i)) \prod_j \rho(x_j; t) dx_j \right)^2 dx_i
\]

\[
= \frac{1}{2} \int \left( \sum_\mu A^{(i)}_\mu(t) \Phi^{(i)}_\mu(x_i) - \int \rho(x_i | Pa(x_i)) \prod_j \sum_{\nu_j} A^{(j)}_{\nu_j}(t) \Phi^{(j)}_{\nu_j}(x_j) dx_j \right)^2 dx_i
\]

(20)

where the index \( j \) for the product runs over the direct parents of \( X_i \).

We further define an aggregate cost function

\[
E = \sum_{i=1}^R K_i E_i
\]

(21)

The parameters \( K_i \) can be used to emphasize particular portions of the network; except where otherwise noted, we assume that \( K_i = 1 \) for all \( i \). Employing gradient descent to minimize \( E \), we find

\[
\frac{dA^{(k)}_\sigma}{dt} = -\eta \sum_{i=1}^R K_i \frac{\partial E_i}{\partial A^{(k)}_\sigma}
\]

(22)

Since \( A^{(k)}_\sigma \) does not appear in all of the cost functions, \( \partial E_i / \partial A^{(k)}_\sigma \) is nonzero only for \( i = k \) and when the graph node for \( X_i \) is one of the direct children of the graph node for \( X_k \). Thus,

\[
\frac{1}{\eta} \frac{dA^{(k)}_\sigma}{dt} = -K_k \frac{\partial E_k}{\partial A^{(k)}_\sigma} - \sum_{i \in \{i: X_i \in Ch(X_k)\}} K_i \frac{\partial E_i}{\partial A^{(k)}_\sigma}
\]

(23)

As was the case for the two-node inference network, the input PDF or PDFs will be specified by an encoding process rather than an update rule of this sort.
The derivatives in equation (23) are straightforward but lengthy to evaluate. We omit the details of the calculation and simply state the results

\[
\frac{1}{\eta} \frac{dA^{(k)}}{dt} = -K_k \left( A^{(k)}_\sigma - \prod_j A^{(j)}_{\nu_j} \Omega^{(k)}_{\sigma \nu_1 \nu_2 \cdots \nu_{j_{\text{max}}}} \right)
\]

\[
+ \sum_i K_i \sum_\mu \prod_{j \neq k} A^{(i)}_{\nu_j} \prod_j A^{(j)}_{\nu_j} \Omega^{(k)}_{\mu \nu_1 \nu_2 \cdots \nu_{j_{\text{max}}} \sigma}
\]

\[
- \sum_i K_i \prod_{j \neq k} \sum_\nu A^{(j)}_{\nu_j} \sum_\mu A^{(j')}_{\mu_j} \Omega^{(j'k)}_{\nu_1 \nu_2 \cdots \nu_{j_{\text{max}}} \mu_1 \mu_2 \cdots \mu_{j'_{\text{max}}} \sigma}
\]

(24)

where we have defined

\[
\Omega^{(k)}_{\sigma \nu_1 \nu_2 \cdots \nu_{j_{\text{max}}}} = \int \Phi^{(k)}_{\sigma} (x_k) \rho(x_k | \text{Pa}(x_k)) \prod_j \Phi^{(j)}_{\nu_j} (x_j) dx_j dx_k
\]

(25)

\[
\Omega^{(ik)}_{\mu \nu_1 \nu_2 \cdots \nu_{j_{\text{max}}} \sigma} = \int \Phi^{(i)}_{\mu} (x_i) \rho(x_i | \text{Pa}(x_i)) \Phi^{(k)}_{\sigma} (x_k) \prod_{j \neq k} \Phi^{(j)}_{\nu_j} (x_j) dx_j dx_i dx_k
\]

(26)

and

\[
\Upsilon^{(j'k)}_{\nu_1 \nu_2 \cdots \nu_{j_{\text{max}}} \mu_1 \mu_2 \cdots \mu_{j'_{\text{max}}} \sigma} = \int \left( \int \Phi^{(k)}_{\sigma} (x_k) \rho(x_k | \text{Pa}(x_k)) \prod_{j' \neq k} \Phi^{(j')}_{\mu_j} (x_{j'}) dx_{j'} dx_k \right)
\]

\[
\int \rho(x_i | \text{Pa}(x_i)) \prod_j \Phi^{(j)}_{\nu_j} (x_j) dx_j \right) dx_i
\]

(27)

The sums over the index \( i \) in equation (24) run over the children of \( X_k \). The products are over the parents of either node \( X_k \) (equation (24), first term in (24) or node \( X_i \) (equations (26) and (27), second and third term in (24)), possibly excluding node \( X_k \) itself. From these equations, it can be seen that the PDF represented at a node \( X_i \) is updated based only on its direct parents, its direct descendents, and the direct parents of its direct descendents, so that \( X_i \) is separated from all other nodes in the neural belief networks by an appropriate Markov blanket.

Equations (24) through (27) can be awkward to use directly. It can be more convenient to write out the cost functions for a specific prob-
abilitistic model using equation 20 and directly evaluate the necessary derivatives (specified by equation 23).

3 Applications of Neural Belief Networks

3.1 Bidirectional Propagation

So far, we have restricted our attention to developing neural networks that encode simple probabilistic models involving only a single source of evidence. Given suitable representations, we can design neural networks that capture a wide variety of probabilistic relations (Barber et al., 2001). Further, by regarding representations of probabilistic dependence models as Bayesian belief networks, we have seen that two types of information propagation come into play: predictive and retrospective.

In this section, we will examine several applications of neural belief networks. Unlike those considered before, the probabilistic models will now feature multiple sources of evidence, with bidirectional propagation of both predictive and retrospective support. The corresponding neural networks thus have neurons with both feedforward and feedback connections, as well as lateral connections.

3.2 Neural Propagation of Evidence in Trees

To facilitate investigation of information propagation in neural belief networks, we first focus on networks whose implicit spaces are specified by tree-structured Bayesian belief networks (Figure 3a). These implicit networks are general enough to illustrate the concepts, while yielding neural networks that are readily understood. We will examine binary trees, where each node has at most two children, but the results extend simply to more general tree structures.

We may assume that evidence is only available in the root node and the leaf nodes (although all such nodes need not provide evidence). The root node is the single node which has no father and is located at the top of the tree, while the leaf nodes are all the nodes which have no children. If another node $X$ were externally specified, the subtree rooted at $X$ could be broken off and treated separately. Conversely, the father node of $X$ is unaffected by the descendants of $X$, so they could be deleted from the original tree, leaving $X$ as a leaf node.

Clearly, an unspecified root node can only receive retrospective support, while an unspecified leaf node can only receive predictive support. All other unspecified nodes in the tree will receive both retrospective and predictive support. We will thus need to consider separately these three types of nodes when determining the update rules for the neural network.
Figure 3: Tree-structured Bayesian belief networks. (a) In this tree, node A is called the root, while nodes D, F, G, and H are called the leaves. For trees, the direct parent of a node is called its father, and its direct children are called its sons. Since each father has at most two sons, the tree shown here is a binary tree. (b) A small tree. Any of the nodes in this tree can be specified as evidence. The two leaf nodes could also provide evidence: both leaves can provide information to the root, but if the root and one of the leaves is specified, the other leaf will only be driven by the root (its Markov blanket). (c) A tree-like graph with the arrows reversed. Any two of the nodes can be specified and its information will propagate throughout the network. Unlike the case of the tree, the Markov blanket of any node is both of the other nodes. (d) Chains are special cases of trees. This three-node chain can feature both predictive and retrospective support.
An unspecified root node $X$ with children $Y$ and $Z$ receives feedback inputs (retrospective support) from both of them (Figure 3). We introduce the representations

\[ \rho(x; t) = \sum_{\alpha} A_{\alpha}(t) \Phi_{\alpha}(x) \]  

(28)

\[ \rho(y; t) = \sum_{\beta} B_{\beta}(t) \Psi_{\beta}(y) \]  

(29)

\[ \rho(z; t) = \sum_{\gamma} C_{\gamma}(t) \Theta_{\gamma}(z) \]  

(30)

Following the procedures described in section 2.4, the update rule for the root is

\[ \frac{1}{\eta} \frac{dA_{\mu}}{dt} = -K_y \frac{\partial E_y}{\partial A_{\mu}} - K_z \frac{\partial E_z}{\partial A_{\mu}} \]  

(31)

with

\[ \frac{\partial E_y}{\partial A_{\mu}} = \sum_{\alpha} A_{\alpha}(t) \int \left( \int \rho(y \mid x) \Phi_{\alpha}(x) dx \right) \left( \int \rho(y \mid x) \Phi_{\mu}(x) dx \right) dy \]

\[ - \sum_{\beta} B_{\beta}(t) \iint \Psi_{\beta}(y) \rho(y \mid x) \Phi_{\mu}(x) dx dy \]  

(32)

and

\[ \frac{\partial E_z}{\partial A_{\mu}} = \sum_{\alpha} A_{\alpha}(t) \int \left( \int \rho(z \mid x) \Phi_{\alpha}(x) dx \right) \left( \int \rho(z \mid x) \Phi_{\mu}(x) dx \right) dz \]

\[ - \sum_{\gamma} C_{\gamma}(t) \iint \Theta_{\gamma}(z) \rho(z \mid x) \Phi_{\mu}(x) dx dz \]  

(33)

Thus, the firing rates for the root node are driven by a sum of feedback inputs that individually are identical to the input produced by a single source of retrospective support (section 2.3). The parameters $K_y$ and $K_z$ need not be the same; different values may be used to give greater significance to one of the inputs.

The firing rates for an unspecified leaf node are also updated by a familiar rule. Consider a leaf node $X$ with father $U$. Using equation 28 and

\[ \rho(u; t) = \sum_{\delta} D_{\delta}(t) \Lambda_{\delta}(u) \]  

(34)

we obtain the update rule

\[ \frac{1}{\eta} \frac{dA_{\mu}}{dt} = -K_x \frac{\partial E_x}{\partial A_{\mu}} \]  

(35)
where
\[ \frac{\partial E_x}{\partial A_\mu} = A_\mu(t) - \sum_{\delta} D_\delta(t) \int \int A_\delta(u) \rho(x|u) \Phi_\mu(x) du dx \] (36)

This update rule is of course identical to the update rule for the \( X \rightarrow Y \) network with predictive support (section 2.2).

All nonroot, nonleaf nodes have similar update rules. For a node \( X \) with father \( U \) and sons \( Y \) and \( Z \), we impose the representations given above in equations 28 through 30 and equation 34. Applying the procedure of section 2.4 yields an update rule with form
\[ \frac{1}{\eta} \frac{dA_\mu}{dt} = -K_y \frac{\partial E_y}{\partial A_\mu} - K_z \frac{\partial E_z}{\partial A_\mu} - K_x \frac{\partial E_x}{\partial A_\mu} \] (37)

The partial derivatives of the cost functions are identical to those evaluated for the root and leaf nodes. The descendants and ancestors of \( X \) thus communicate, in the neural network, only through the intermediary of \( X \) itself. This is consistent with the tree structure of the underlying Bayesian belief network; given \( X \), the descendants of \( X \) are conditionally independent of the ancestors of \( X \) (Pearl, 1988).

With these update rules, evidence provided at the root node or at leaf nodes will propagate throughout the network. The manner in which evidence is specified will depend on how the probabilistic model is posed. Therefore, the same graph could have different nodes specified for different purposes. For instance, the small tree in Figure 3b could have any of its nodes represent sensory inputs.

If we specify the PDF for the root node, the leaf nodes \( Y \) and \( Z \) will receive predictive support from \( X \). By selecting appropriate representations for the PDFs and for the conditional probabilities associated with the links, the resulting neural network could subdivide a complex, highly general sensory input into simpler, more specialized components. For example, a visual input at a particular retinal location might be separated into contrast and color.

Conversely, if we specify PDFs for the leaf nodes, the root node \( X \) will receive retrospective support from \( Y \) and \( Z \). Amongst other possibilities, this provides a simple way to model redundant sensory inputs. If we take the conditional probabilities to be of narrow Gaussian form, \( \rho(y|x) = N(y;x, \sigma_y^2) \) and \( \rho(z|x) = N(z;x, \sigma_z^2) \), then the firing rates representing \( \rho(x;t) \) will be updated so as to pool the diagnostic information from both the sensory inputs, \( Y \) and \( Z \).

Similar arguments apply to larger trees. Additionally, larger trees may well have the root node and leaf nodes specified simultaneously (which is not of interest for the small tree discussed above). These nodes may correspond to sensory inputs, or can represent priors that are built into the neural network.

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It is important to recognize that the neural update rules developed above apply only to the binary trees. If the arrows in the binary tree graphs are reversed, rather different neural update rules are produced. For example, the directions of the small tree shown in Figure 3b can be reversed, as shown in Figure 3c. Specifying $Y$ and $Z$ yields the multiplicative update rule

$$\frac{1}{\eta K_x} \frac{dA_\alpha(t)}{dt} = -A_\alpha(t) + \sum_{\beta, \gamma} B_\beta(t)C_\gamma(t) \int \int \int \Phi_\alpha(x)\rho(x|y,z)\Psi_\beta(y)\Theta_\gamma(z)dxdydz$$

(38)

while specifying $X$ and $Z$ yields

$$\frac{1}{\eta K_x} \frac{dB_\nu(t)}{dt} = \sum_{\alpha, \gamma} A_\alpha(t)C_\gamma(t) \int \int \int \Phi_\alpha(x)\rho(x|y,z)\Psi_\nu(y)\Theta_\gamma(z)dxdydz - \sum_{\beta, \gamma_1, \gamma_2} B_\beta(t)C_{\gamma_1}(t)C_{\gamma_2}(t) \int \left\{ \left( \int \rho(x|y,z)\Psi_\beta(y)\Theta_{\gamma_1}(z)dydz \right) \left( \int \rho(x|y,z)\Psi_\nu(y)\Theta_{\gamma_2}(z)dydz \right) \right\} dx$$

(39)

This latter update rule features a feedforward term that is multilinear in the firing rates $\{A_\alpha(t)\}$ and $\{C_\gamma(t)\}$. It also features a nonlinear lateral combination of the firing rates $\{B_\beta(t)\}$ and $\{C_\gamma(t)\}$ which serves to ensure that the two parent nodes $Y$ and $Z$ are mutually consistent with the PDF of the child node $X$. If only $X$ is specified, there will be an additional update rule for the firing rates $\{C_\gamma(t)\}$ that is similar in form to equation 39.

Although the update rules are more complicated with the directions reversed in this manner, the probabilistic model may demand it. For instance, the Bayesian belief network in Figure 3c is appropriate for implementing the arithmetic operations (add, subtract, multiply, and divide).

An interesting application of these two types of neural belief networks (tree and reversed-tree) is the estimation of the velocity of a moving object. A small tree (Figure 3b) can generate two copies $Y$ and $Z$ of the input position $X$ by taking the conditional probabilities to be Dirac delta functions $\delta(y-x)$ and $\delta(z-x)$. We can set the
A neural belief network can estimate the velocity of a moving target. (a) The position of the target is copied into two different populations of neurons, with different time delays. (b) The time delay and the difference of the two copies of position are used to estimate the velocity. The results shown here were obtained with the PDFs for each of the random variables represented using minimal spaces spanned by two straight-line basis functions.

parameters $K_i$ so that the values of the copies will be held for different lengths of time. In particular, we can establish the relations

$$\rho(y,t) = \rho(x; t - \tau)$$  \hspace{1cm} (40)
$$\rho(z,t) = \rho(x; t - 2\tau)$$  \hspace{1cm} (41)

These copies of the position can then be used as the inputs to a Bayesian belief network of the type shown in Figure 3c. By setting $\rho(x | y, z) = \delta(x - (y - z)/\tau)$, the velocity (given here by $x$) at time $t - \tau$ can be estimated (Figure 4).

### 3.3 Top-Down Feedback From a High-Level Model

In section 3.2, we examined the neural update rules for Bayesian belief networks having binary-tree structure. By doing so, we examined the means by which information propagates throughout the network from one or more sources. In particular, we saw that conditional independence in the Bayesian belief network was preserved in the neural network connectivity.

We now turn from the general rules by which probabilistic information propagates in the neural network and investigate in more detail the effects that multiple sources of evidence have on the encoded PDFs. We consider PDFs encoded by chains of nodes with evidence provided...
at one or both ends. (Specifying the PDF for any other node breaks the chain into two chains that can be treated independently.) A chain is a special case of a tree, so the neural update rules can be obtained as in section 3.2.

For the chosen demonstration, we employ representations of higher dimensionality than those generally used in the preceding developments. For each graph node, the interval $[-1, 1]$ is covered with ten Gaussians (Figure 5a), from which an orthonormal basis is generated. This makes it possible to represent a variety of PDFs, including multimodal distributions.

The neural firing rate patterns in the explicit space are also assumed to be of Gaussian form. To eliminate any possibility of negative firing rates, the nonlinear activation function is taken to be rectification.

We have already studied at some depth the behavior of chains consisting of two nodes (sections 2.2 and 2.3). These chains are able to transmit probabilistic information from one node of the graph to another, with the accuracy limited by the representations adopted. For the predictive network, a feedforward input $X$ drives the output $Y$.

To keep the focus on the interaction of multiple sources of evidence, we take the conditional probability to be a Dirac delta function, $\rho(y|x) = \delta(y - x)$. Of course, this defines a version of the communication channel that we have extensively considered, but the goal is now to duplicate the PDF rather than a particular numerical value. As seen in Figure 5b, the input PDF $\rho(x;t)$ is copied with great fidelity by the output PDF $\rho(y;t)$.

Every chain with three or more nodes will admit both predictive and retrospective support. The behavior of all such chains is well characterized by a chain with three nodes: the update rule for any node depends only on the neighboring nodes, so a chain with three nodes covers all possibilities (only predictive support, only retrospective support, and both predictive and retrospective support). Therefore, we consider the effect of adding a third node to the chain (Figure 3d). We set $\rho(z|y) = \delta(z - y)$ along with $\rho(y|x) = \delta(y - x)$ and use identical parameters $K_y$ and $K_z$.

The first possibility is just to add the third node without adding any additional evidence to the network. We decode $\rho(y;t)$ and $\rho(z;t)$ from neural firing rates determined using update rules derived previously for more general trees. For the same input PDF as above, $\rho(y;t)$ is unchanged by the addition of the retrospective support from the third node, and the structure of $\rho(z;t)$ is identical to that of $\rho(y;t)$.

Since the same evidence was presented to the network, the introduction of a third node did not change the behavior of the original nodes. This is entirely appropriate, given the probabilistic foundations of the neural belief networks. However, it is feasible that, by adjusting the $K_i$ parameters or the PDFs representable by the minimal spaces, there
Figure 5: Propagation of evidence in chain-structured neural belief networks. (a) Gaussian functions spanning the minimal spaces for the chain-structured neural belief networks under consideration. Orthonormal bases for the minimal spaces are formed from these functions. (b) A neural belief network accurately transmits PDFs in a chain of two nodes. The decoded output PDF $\rho(y;t)$ is very similar to the encoded input PDF $\rho(x;t)$. (c) Multiple sources of evidence can help to resolve ambiguous information. Here, the inferior mode of a bimodal, bottom-up input $\rho(x;t)$ is damped by a more specific top-down signal $\rho(z;t)$. (d) A high-level model can be dynamically generated in a neural belief network with a population $Z$ of winner-take-all neurons. An ambiguous input signal at $X$ is propagated to the winner-take-all neurons through $Y$. The winner-take-all neurons only respond to the stronger mode of the bimodal input, which damps the inferior mode in $\rho(y;t)$. The functions $\rho(y;t)$ and $\rho(z;t)$ are only approximations to PDFs, since they can take on negative values.
can be a change in the dynamics of neural networks extended in this fashion. For example, appropriate parameter choice could produce a slowly varying PDF in $Z$ that is relatively stable against noise, thus stabilizing a more rapidly varying PDF in $Y$.

A more proactive role that the third node $Z$ can play is as an additional source of evidence. We directly specify $\rho(z;t)$ and encode it into the neural network. The neural firing rates for $Y$ are driven by predictive support from $X$ and retrospective support from $Z$, and then decoded to find $\rho(y;t)$. One possible use of this second source of evidence is to resolve an ambiguous input; the inferior mode of a bimodal predictive input can be de-emphasized using more specific retrospective evidence (Figure 5c).

Although this use of the retrospective evidence resolves the ambiguous predictive input, it does not explain how the retrospective evidence comes about. Ideally, we would like to build up a high-level model of the predictive input, and use this model to generate a top-down signal that imposes global regularity on the bottom-up predictive input. The uniform priors that we have assumed throughout this work are somewhat of a hindrance for this purpose. With these priors, probabilities account well for multiple possibilities, but here we want to choose only one of those possibilities.

In principle, we could restrict the allowed PDFs for $\rho(z;t)$ by imposing a prior on the PDFs and rederiving our neural update rules. However, we will adopt a more direct approach that illustrates the first steps towards implementing decision theory (Raiffa, 1968) in neural networks and take the neurons representing $\rho(z;t)$ to be winner-take-all units. Only one of these neurons will be active at a time, based on a simple utility function: the neurons compete to be active, and the single neuron that is most strongly driven will be the one that is activated. The manner of implementation of the winner-take-all units is immaterial, so we directly choose the most strongly driven neuron in the computer simulations. (It is possible to implement a set of winner-take-all units in a real network through a suitable choice of nonlinear activation function and lateral weights. One may let each neuron inhibit the others and have a self-excitatory connection. See Hertz et al., 1991.)

Since only the most strongly driven winner-take-all neuron is activated, this strategy provides us with a way to generate a high-level model that selects the dominant mode of a multimodal input distribution. We allow $Z$ to be driven by the predictive support from $Y$, and the winner-take-all nature of the $Z$ neurons permits only narrow Gaussian PDFs to be represented. Thus, $\rho(z;t)$ serves as our high-level model, and can resolve ambiguous inputs, as demonstrated in Figure 3d. This type of neural network could be used as the starting point for coherent theoretical accounts of attentive effects in the
primate visual system, of the electrosensory system of weakly electric fish, and of other neural systems where an internal model is built up to impose global constraints on neural representations of information.

4 Conclusions

We have extended the hypothesis that neural networks represent information as probability density functions. These PDFs are assumed to be obtainable by a linear combination of some implicit decoding functions, with the decoder for each neuron being weighted by its firing rate. The firing rates in turn are obtainable from the PDF using a complementary set of encoding functions.

Success in representing an individual PDF with a population of neurons ([Barber et al., 2001]) has led us to inquire whether more complex probabilistic models can be represented and implemented in neural terms. To this end, we have adopted graphical representations of probabilistic dependence models, in the form of Pearl's Bayesian belief networks, to organize and simplify the relations between the random variables in such a model.

In summary, we have introduced, analyzed, and applied three ways to represent probabilistic information. These are the implicit model, depicted as a Bayesian belief network; the representation of the probabilistic model in the minimal space; and the representation of the probabilistic model as a neural network in the explicit space. Further, we have devised rules that permit us to convert one type of representation into another type. This formalization of the representation and processing of information in neurobiological computation therefore suggests a general protocol by which probabilistic models can be embedded in neural networks. First, we specify the probabilistic model, using a Bayesian belief network to organize the random variables. We then consider what sorts of functions are exemplars of the PDFs describing the random variables and use these exemplars to define the minimal space. Finally, we utilize the relations between the minimal space and the explicit space to generate the neural network itself.

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References

Anderson, C. (1994). Basic elements of biological computational systems. *International Journal of Modern Physics C*, 5(2):135–7.

Anderson, C. (1996). Unifying perspectives in neuronal codes and processing. In Ludeña, E., Vashishta, P., and Bishop, R., editors, *Condensed Matter Theories*, volume 11, pages 365–374, Commack, NY. Nova Science Publishers.

Barber, M., Clark, J., and Anderson, C. (2001). Neural representation of probabilistic information. Submitted to Neural Comput.

Georgopoulos, A., Schwartz, A., and Kettner, R. (1986). Neuronal population coding of movement direction. *Science*, 233(4771):1416–19.

Goldberg, J. (1991). *Matrix Theory With Applications*. McGraw-Hill, Inc., New York, NY.

Hertz, J., Krogh, A., and Palmer, R. (1991). *Introduction to the Theory of Neural Computation*. Addison-Wesley Publishing Company, Reading, MA.

Neal, R. (1992). Connectionist learning of belief networks. *Artificial Intelligence*, 56:71–113.

Pearl, J. (1988). *Probabilistic Reasoning in Intelligent Systems: Networks of Plausible Inference*. Morgan Kaufmann Publishers, Inc., San Mateo, CA.

Raiffa, H. (1968). *Decision Analysis: Introductory Lectures on Choices Under Uncertainty*. Addison-Wesley.

Rieke, F., Warland, D., de Ruyter van Steveninck, R., and Bialek, W. (1997). *Spikes: Exploring the Neural Code*. MIT Press, Cambridge, MA.

Schwartz, A. (1993). Motor cortical activity during drawing movements: Population representation during sinusoid tracing. *J. Neurophysiol.*, 70(1):28–36.

Smyth, P., Heckerman, D., and Jordan, M. (1997). Probabilistic independence networks for hidden Markov probability models. *Neural Comput.*, 9:227–69.

Van Essen, D., Anderson, C., and Felleman, D. (1992). Information processing in the primate visual system: an integrated systems perspective. *Science*, 255(5043):419–23.
Zemel, R. (1999). Cortical belief networks. In Hecht-Neilsen, R., editor, *Theories of Cortical Processing*. Springer-Verlag, Berlin.

Zemel, R., Dayan, P., and Pouget, A. (1998). Probabilistic interpretation of population codes. *Neural Comput.*, 10(2):403–30.