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**Running head:** Neural networks and synaptic efficacy
Abstract

Markram and Tsodyks, by showing that the elevated synaptic efficacy observed with single-pulse LTP measurements disappears with higher-frequency test pulses, have critically challenged the conventional assumption that LTP reflects a general gain increase. Redistribution of synaptic efficacy (RSE) is here seen as the local realization of a global design principle in a neural network for pattern coding. As is typical of many coding systems, the network learns by dynamically balancing a pattern-independent increase in strength against a pattern-specific increase in selectivity. This computation is implemented by a monotonic long-term memory process which has a bidirectional effect on the postsynaptic potential via functionally complementary signal components. These frequency-dependent and frequency-independent components realize the balance between specific and nonspecific functions at each synapse. This synaptic balance suggests a functional purpose for RSE which, by dynamically bounding total memory change, implements a distributed coding scheme which is stable with fast as well as slow learning. Although RSE would seem to make it impossible to code high-frequency input features, a network preprocessing step called complement coding symmetrizes the input representation, which allows the system to encode high-frequency as well as low-frequency features in an input pattern. A possible physical model interprets the two synaptic signal components in terms of ligand-gated and voltage-gated receptors, where learning converts channels from one type to another.

1 Introduction

The traditional experimental interpretation of long-term potentiation (LTP) as a model of synaptic plasticity is based upon a fundamental hypothesis: “Changes in the amplitude of synaptic responses evoked by single-shock extracellular electrical stimulation of presynaptic fibres are usually considered to reflect a change in the gain of synaptic signals, and are the most frequently used measure for evaluating synaptic plasticity.” (Markram & Tsodyks, 1996, p. 807) Paired action-potential experiments by Markram and Tsodyks (1996) call into question the LTP gain-change hypothesis by demonstrating a dramatic dependence of synaptic efficacy upon test-pulse frequency. In that preparation, following an interval of pre- and postsynaptic pairing, neocortical pyramidal neurons are seen to exhibit LTP, with the amplitude of the post-pairing response to a single test pulse elevated to 166% of the pre-pairing response. If LTP were a manifestation of a synaptic gain increase, the response to higher frequency test pulses would also be 166% of the pre-pairing response. Although the Markram–Tsodyks data do show an amplified response to the initial spike in a test train ($EPSP_{init}$), the degree of enhancement of the stationary response ($EPSP_{stat}$) declines steeply as test pulse frequency increases (Figure 1). In fact, post-pairing amplification of $EPSP_{stat}$ disappears altogether for 23 Hz test trains; and then, remarkably, reverses sign, with test trains of 30-40 Hz producing post-pairing stationary response amplitudes which are less than 90% the size of pre-pairing amplitudes. Pairing is thus shown to induce a redistribution, rather than a uniform enhancement, of synaptic efficacy.

Figure 1: Markram & Tsodyks (1996) $EPSP_{stat}$ data
As Markram, Pikus, Gupta, & Tsodyks (1998) point out, redistribution of synaptic efficacy has profound implications for modeling as well as experimentation: "Incorporating frequency-dependent synaptic transmission into artificial neural networks reveals that the function of synapses within neural networks is exceedingly more complex than previously imagined." (p. 497) Neural modelers have long been aware that synaptic transmission may exhibit frequency dependence (Abbott, Varela, Sen, & Nelson, 1997; Grossberg, 1968), but most network models have not so far needed this feature to achieve their functional goals. Rather, the assumption that synaptic gains, or multiplicative weights, are fixed on the time scale of synaptic transmission has served as a useful cornerstone for models of adaptive neural processes and related artificial neural network systems. A "bottom-up" modeling approach might now graft a new process, such as redistribution of synaptic efficacy, onto an existing system. While such a step would add complexity to the model’s dynamic repertoire, it may be difficult to use this approach to gain insight into the functional advantages of the added element. Indeed, adding the Markram–Tsodyks effect to an existing network model of pattern learning would be expected to alter drastically the dynamics of input coding — but what could be the benefit of such an addition? *A priori*, such a modification even appears to be counterproductive, since learning in the new system would seem to reduce pattern discrimination, by compressing input differences and favoring only low-frequency inputs.

A neural network model called distributed ART (dART) (Carpenter, 1996, 1997; Carpenter, Milenova, & Noeske, 1998) features redistribution of synaptic efficacy (RSE) at the local synaptic level as a consequence of the implementation of system design goals at the global pattern processing level. This "top-down" approach to understanding the Markram–Tsodyks data suggests, by example, how the apparently paradoxical phenomenon of RSE may actually be precisely the element needed to solve a critical pattern coding problem at a higher processing level. In a dART network, RSE serves the functional purpose of dynamically limiting memory changes, thereby to make stable/fast learning possible. Other competitive learning systems do not achieve this same result.

The original goal in designing the dART network was to combine the computational advantages of multilayer perceptrons, including noise tolerance and code compression, with the complementary advantages of adaptive resonance theory (ART) networks (Carpenter & Grossberg, 1987, 1993; Carpenter, Grossberg, & Reynolds, 1991; Carpenter, Grossberg, Markuzon, Reynolds, & Rosen, 1992), including code stability. In particular, dART represents a real-time model of pattern learning which permits fast as well as slow adaptation, without catastrophic forgetting. Both ART and dART models employ competitive learning schemes for code selection, and both are designed to stabilize learning. However, because ART networks use a classical steepest-descent paradigm called instar learning (Grossberg, 1972), these systems require winner-take-all coding to maintain stability with fast learning. A new learning law called the distributed instar (dlInstar) (section 2.1) allows dART code representations to be distributed across any number of network nodes. Both ART and dART also employ a preprocessing step called complement coding (Carpenter, Grossberg, & Rosen, 1991), which presents to the learning system both the original input vector and its complement. This device is analogous to on-cell/off-cell coding found in the early visual system. Complement coding solves a category proliferation problem pointed out by Moore (1989). It also suggests a computational solution to the tendency of Markram-Tsodyks RSE to enhance only low-frequency inputs: if an input component is
consistently large with respect to a given code, then the network can embody this fact in the complementary component, which can be enhanced since it will be consistently small.

The dynamic behavior of an individual dART synapse is seen in the context of its role in stabilizing distributed pattern learning, rather than as a primary hypothesis. RSE here reflects a tradeoff between frequency-dependent and frequency-independent synaptic signal components which support a tradeoff between pattern selectivity and a nonspecific path strengthening at the network level (Figure 2). Models that implement distributed coding via gain adaptation alone tend to suffer catastrophic forgetting and require slow or limited learning. In dART, each increase in frequency-independent synaptic efficacy is balanced by a corresponding decrease in frequency-dependent efficacy. With each frequency-dependent element assumed to be stronger than each frequency-independent element, the net result of learning is redistribution, rather than nonspecific enhancement, of synaptic efficacy. The system uses this mechanism to achieve the goal of a typical competitive learning scheme, enhancing network response to a given pattern while suppressing the response to mismatched patterns. At the same time, the dART network learning law protects prior codes against catastrophic forgetting. It does so by formally replacing the traditional multiplicative weight with a dynamic weight (Carpenter, 1994), equal to the rectified difference between target node activation and an adaptive threshold, which embodies the long-term memory of the system. The dynamic weight permits adaptation only at the most active coding nodes, which are limited in number due to competition at the target field. In addition, thresholds, which are initially zero, become increasingly resistant to change as they become larger.

Note that, although thresholds following a minimal dinstar learning law can only increase, complement coding allocates two thresholds for each component of the original input. Although an individual neuron can learn to enhance only low-frequency signals in the complement coded pattern, high-frequency and low-frequency component of the original input pattern are treated symmetrically. The network is thus able to encode a full range of input features. Elements of the dART network which are directly relevant to the discussion of Markram-Tsodyks RSE are defined quantitatively in the following sections.

**Figure 2**: Dynamic balance of signal components for pattern coding

## 2 Results

### 2.1 The Distributed ART Model Equations.** The net excitatory signal $T$ in a dART synapse is a function of two components with dual computational properties: a frequency-dependent component $S$, which depends on the current presynaptic input $I$, and a frequency-independent component $\Theta$, which is independent of $I$. Both components depend on the postsynaptic voltage $y$ and on the adaptive threshold $\tau$:

\[
\begin{align*}
\text{Frequency-dependent:} & \quad S = I \wedge [y - \tau]^+ \\
\text{Frequency-independent:} & \quad \Theta = y \wedge \tau \\
\text{Total signal:} & \quad T = S + (1 - \alpha)\Theta
\end{align*}
\]
In (2.1), \( a \land b \equiv \min\{a, b\} \) and \( [a]^+ = \max\{a, 0\} \). Parameter \( \alpha \) is assumed to be between 0 and 1, corresponding to the network hypothesis that a pattern-specific signal contributes more to postsynaptic activation than a nonspecific signal, all other things being equal. The dynamic weight, defined formally as \([y - \tau]^+\), specifies an upper bound on the size of \( S \); for smaller \( I \), the frequency-dependent signal is directly proportional to \( I \). Note that \([y - \tau]^+ = y - y \land \tau = y - \Theta\).

The adaptive threshold \( \tau \), initially 0, increases monotonically during learning, according to the \( \text{dInstar} \) learning law:

\[
\frac{d}{dt} \tau = [(y - \tau)^+ - I]^+
\]

The distributed instar represents a principle of atrophy due to disuse, whereby a dynamic weight that exceeds the current input “shrinks to fit” that input (Figure 2). When the coding node is embedded in a competitive network, the bound on total network activation across the target field causes dynamic weights to impose an inherited bound on the total learned change any given input can induce, with fast as well as slow learning. Note that \( \tau \) remains constant if \( y \) is small or if \( \tau \) is large, and that:

\[
\frac{d}{dt} \tau = (y - \tau)^+ - (y - \tau)^+ \land I
\]

\[
= y - y \land \tau - (y - \tau)^+ \land I
\]

\[
= y - \Theta - S
\]

When a threshold increases, the independent, or nonspecific, component \( \Theta \) (equation 2.1) becomes larger for all subsequent inputs, but the input-specific component \( S \) becomes more selective. For a high-frequency input, a nonspecifically increased component is neutralized by a decreased frequency-dependent component. The net computational effect of a threshold increase (e.g., due to pairing) is an enhancement of the total signal \( T \) subsequently produced by small presynaptic inputs, but a smaller enhancement, or even a reduction, of the total signal produced by large inputs.

**Figure 3:** dART model of the Markram-Tsodyks \( EPSP_{stat} \) data

**2.2 The Distributed ART Model Predicts Redistribution of Synaptic Efficacy.** Figure 3 illustrates the frequency-dependent and frequency-independent components of the signal \( T \), and shows how these two competing elements combine to produce RSE. In this example, model elements, defined by equation (2.1), are taken to be piecewise linear, although this choice is not unique. In fact, the general dART model allows a broad range of form factors that satisfy qualitative hypotheses. The model presented here has been chosen for minimality, including only those components needed to produce computational capabilities, and for simplicity of functional form. Throughout, the superscript \( b(\text{before}) \) denotes values measured before the pairing experiment; and the superscript \( a(\text{after}) \) denotes values measured after the pairing experiment. The graphs show each system variable as a function of the presynaptic test frequency \( (I) \). Variable \( I \) is scaled by a factor \((I \text{ Hz})\) which converts the dimensionless input
(equation 2.1) to frequency in the experimental range. The dimensionless model input equals the experimental test frequency divided by \( T \).

In the dART network, postsynaptic nodes are embedded in a field where strong competition typically holds a pattern of activation as a working memory code which is largely insensitive to input fluctuations of the external inputs. When a new input arrives, an external reset signal briefly overrides internal competitive interactions, which allows the new pattern to determine its own unbiased code. This reset process is modeled by momentarily setting all postsynaptic activations \( y = 1 \). The resulting initial signals \( T \) then lock in the subsequent activation pattern, as a function of the internal dynamics of the competitive field. Thereafter, signal components \( S \) and \( \Theta \) depend on \( y \), which is small at most nodes due to normalization of total activation across the field. The Markram-Tsodyks experiments use isolated cells, so network properties are not tested, and Figures 3 and 4 plot dART model equations (2.1) with \( y = 1 \).

Figure 3a shows the frequency-dependent component of the dART signal before pairing \( (S^b) \) and after pairing \( (S^a) \). The frequency-dependent component is directly proportional to \( I \), up to a saturation point, which is proportional to \( (1 - \tau) \). Tsodyks and Markram (1997) have observed this phenomenon: "The limiting frequencies were between 10 and 25 Hz ... above the limiting frequency the average postsynaptic depolarization from resting membrane potential saturates as presynaptic firing rates increase." (p. 720) The existence of such a limiting frequency confirms a prediction of the phenomenological model of synaptic transmission proposed by Tsodyks and Markram (1997), as well as the prediction of distributed ART (Carpenter, 1996, 1997). The dART model also predicts that pairing lowers the saturation point, as the frequency-dependent component becomes more selective.

Figure 3b illustrates that the frequency-independent component in the dART model is independent of \( I \) and that it increases during training. Moreover, the increase in this component \( \Delta = \Theta^a - \Theta^b = \tau^a - \tau^b \) balances the decrease in the frequency-dependent component at large \( I \), where \( S^b - S^a = \Delta \).

Figure 3c shows how the frequency-dependent and frequency-independent components combine in the dART model to form the net signal \( T \). Using the simplest form factor, the model synaptic signal is taken to be a linear combination of the two components: \( T = S + (1 - \alpha)\Theta \) (equation 2.1). For small \( I \) (below the post-pairing saturation point of \( S^a \)) pairing causes \( T \) to increase, since \( S \) remains constant and \( \Theta \) increases. For large \( I \) (above the pre-pairing saturation point of \( S^b \)) pairing causes \( T \) to decrease: because \((1 - \alpha) < 1\), the frequency-independent increase is more than offset by the frequency-dependent decrease. The neutral frequency, at which the test pulse \( I \) produces the same synaptic signal before and after pairing, lies between these two intervals.

Figure 3d combines the graphs in Figure 3c to replicate the data of Markram and Tsodyks, which are redrawn on this plot. The graph of \( T^a / T^b \) is divided into three intervals,
determined by the saturation points of $S$ before pairing $\left( I = I(1 - \tau^b) = 25.8 \text{Hz} \right)$ and after pairing $\left( I = I(1 - \tau^a) = 20.3 \text{Hz} \right)$ (Figure 3a). The neutral frequency, at which the test pulse produces the same signal after pairing as before pairing, lies between these two values.

System parameters of the dART model were chosen, in Figure 3, to obtain a quantitative fit to the Markram-Tsodyks (1996) experimental results. In that preparation, the data exhibit the reversal phenomenon where, for high-frequency test pulses, post-pairing synaptic efficacy falls below its pre-pairing value. Note that dART system parameters could also be chosen to fit data that might show a reduction, but not a reversal, of synaptic efficacy. This might occur, for example, if the test pulse frequency of the theoretical reversal point were beyond the physiological range. Across a wide parameter range, the qualitative properties illustrated here are robust and intrinsic to the internal mechanisms of the dART model.

**Figure 4:** dART prediction of learning transients

Analysis of the function $T = S + (1 - \alpha)\Theta$ suggests how this synaptic signal would vary with presynaptic spike frequency if responses to test pulses were measured at transitional points in the adaptation process, after fewer than the 30 pairing intervals used to produce the original data (Figure 4). In particular, the saturation point where the curve modeling $T^a/T^b$ flattens out at high presynaptic spike frequency depends only on the state of the system before pairing, so this location remains constant as adaptation proceeds. On the other hand, as the number of pairing intervals increases, the dART model predicts that the neutral point, where the curve crosses the 100% line and $T^a = T^b$, moves progressively to the left. That is, as the degree of LTP amplification of low-frequency inputs grows, the set of presynaptic frequencies that produce any increased synaptic efficacy shrinks.

3 Discussion

3.1 Redistribution of Synaptic Efficacy Supports Stable Pattern Learning. Markram and Tsodyks (1996) report measurements of the initial, transient, and stationary components of the excitatory postsynaptic potential in neocortical pyramidal neurons, bringing to a traditional LTP pairing paradigm a set of non-traditional test stimuli that measure postsynaptic response at various test pulse frequencies. The dART model analysis of these experiments focuses on how the stationary component of the postsynaptic response is modified by learning. This analysis places single-cell observations in the context of a large-scale neural network for stable pattern learning, thus providing a functional explanation for decreased responses to high-frequency test pulses.

In the dART model, the synaptic location of a frequency-independent bias term, realized as an adaptive threshold, leads to dual postsynaptic computations that imply the Markram–Tsodyks RSE. However, producing this effect was not a primary design goal — in fact, model specification preceded the data report. Rather, replication of the experimental findings was a secondary result of seeking to design a distributed neural network that does not
suffer catastrophic forgetting. The dInstar learning law (2.2) allows thresholds to change only at highly active coding nodes. This rule stabilizes memory because total activation across the target field is assumed to be bounded, so most of the system's memory traces remain constant in response to a typical input pattern. Defining long-term change in terms of dynamic weights thus allows significant new information to be encoded quickly at any future time, but also protects the network's previous memories at any given time. In contrast, most neural networks with distributed codes suffer unselective forgetting unless they operate with restrictions such as slow learning.

The first goal of the dART network is the coding process itself. In particular, as in a typical coding system, two functionally distinct input patterns need to be able to activate distinct activation patterns at the coding field. The network accomplishes this by shrinking large dynamic weights just enough to fit the current pattern (Figure 2). Increased thresholds enhance the net excitatory signal transmitted by this input pattern to currently active coding nodes because learning leaves all frequency-dependent signal components unchanged while causing frequency-independent signal components to increase wherever thresholds increase. On the other hand, these changes can depress the signal transmitted by a different input pattern to these nodes, since a higher threshold in a high-frequency path would now cause the frequency-dependent component to be depressed relative to its previous size. If this depression is great enough, it can outweigh the nonspecific enhancement of the frequency-independent component. Local RSE, as illustrated in Figure 3, is an epiphenomenon of this global pattern learning dynamic.

A learning process represented as a simple gain increase would only enhance network responses. Recognizing the need for balance, models dating back at least to the McCulloch-Pitts neuron (McCulloch & Pitts, 1943) have included a nodal bias term. In multilayer perceptrons such as back propagation (Rosenblatt, 1958, 1962; Werbos, 1974; Rumelhart, Hinton, & Williams, 1986), a single bias weight is trained along with all the pattern-specific weights converging on a network node. The dART model differs from these systems in that each synapse includes both frequency-dependent (pattern-specific) and frequency-independent (nonspecific bias) processes. All synapses then contribute to a net nodal bias. The total increased frequency-independent bias is locally tied to increased pattern selectivity. Although the adaptation process is unidirectional, complement coding, by representing both the original input vector and its complement, provides a full dynamic range of coding computations.

3.2 A Physical Realization of dInstar Learning. During dInstar learning, the fact that the decrease in the frequency-dependent signal component $S$ balances the increase in the frequency-independent component $\Theta$ suggests a possible physical model. The model realizes learning as the conversion of synaptic elements (e.g., receptor channels) from a state where activation depends upon the presynaptic frequency to a state where activation is independent of the presynaptic frequency. In this physical realization, channels responsible for the component $S$ are interpreted as jointly ligand- and voltage-gated, since $S$ depends on both $I$ and $\gamma$; while channels responsible for the component $\Theta$ are interpreted as voltage-gated. The gated receptor interpretation specifies one possible mechanism for the synaptic signal function $T$, since both types of channels are know to exist (e.g., Nicholls, 1994, Chapter 4). However, the computational hypotheses needed for pattern learning by the global dART model are not so
narrow as to constrain a unique physical prediction. The idea that learning converts ligand- and voltage-gated channels to (weaker) voltage-gated channels, through atrophy due to disuse, serves as one realization of the minimal, piecewise-linear model described in equations (2.1) and (2.2). Models that focus more on the Markram-Tsodyks paradigm with respect to the detailed biophysics of the local synapse, including transient dynamics, are now reviewed.

3.3 Local Models of the Markram-Tsodyks Data. In the Tsodyks-Markram (1997) model, the limiting frequency, beyond which $EPSP_{stat}$ saturates, decreases as a depletion rate parameter $U_{SE}$ (utilization of synaptic efficacy) increases. In this model, as in dART, pairing lowers the saturation point (Figure 3c). Tsodyks and Markram discuss changes in presynaptic release probabilities as one possible interpretation of system parameters such as $U_{SE}$. The formal dART model could be interpreted in terms of either presynaptic or postsynaptic mechanisms. The ART 3 model (Carpenter & Grossberg, 1990), for example, includes a frequency-dependent partition of synaptic resources which admits a natural presynaptic interpretation which is somewhat analogous to the Tsodyks-Markram system. In a postsynaptic interpretation of the Markram-Tsodyks preparation, where long-term memory is thought of as a transformation of certain ligand-gated channels into voltage-gated channels, depending on pre- and postsynaptic activation levels during pairing, the limiting frequency would correspond to the point where all ligand-gated channels are saturated. The postsynaptic channel interpretation provides one concrete example of how a simple learning law could simultaneously cause a synapse to become both nonspecifically strengthened (Figure 3b) and more selective (Figure 3a). However, the dART model does not uniquely imply a pre- or a postsynaptic mechanism.

Abbott, Varela, Sen, and Nelson (1997) also model some of the same experimental phenomena discussed by Tsodyks and Markram, focusing on short-term synaptic depression. In other model analyses of synaptic efficacy, Markram, Tsodyks, et al. (Markram, Pikus, Gupta, & Tsodyks, 1998; Markram, Wang, & Tsodyks, 1998) add a facilitating term to their 1997 model in order to investigate differential signaling arising from a single axonal source. Tsodyks, Pawelzik, and Markram (1998) investigate the implications of these synaptic model variations for a large-scale neural network. Using a mean field approximation, they "show that the dynamics of synaptic transmission results in complex sets of regular and irregular regimes of network activity." (p. 821) However, their network is not constructed to carry out any specified function, neither is it adaptive. Tsodyks, Pawelzik, and Markram conclude with the statement: "An important challenge for the proposed formulation remains in analyzing the influence of the synaptic dynamics on the performance of other, computationally more instructive neural network models. Work in this direction is in progress." (pp. 831-832) Because the Markram-Tsodyks data follow from the intrinsic functional design goals of a complete system, dART is, to date, unique among neural network models in meeting this challenge.

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Figure 1: Relative amplitude of the stationary postsynaptic potential $EPSP_{stat}$ as a function of presynaptic spike frequency ($I$): adapted from Markram & Tsodyks, 1996, Figure 3c, p. 809. In the Markram–Tsodyks pairing paradigm, sufficient current to evoke 4-8 spikes was injected, pre and post, for 20 msec; and this procedure was repeated every 20 sec for 10 min. Data points show the $EPSP_{stat}$ after pairing as a percent of the control $EPSP_{stat}$ before pairing, for $I = 2, 5, 10, 23, 30, 40$ Hz; plus the low-frequency “single-spike” point, shown as a weighted average of the measured data: $2 \times 0.25$ and $17 \times 0.067$ Hz. If pairing had produced no adaptation, $EPSP_{stat}$ would be a function of $I$ that was unaffected by pairing, as represented by the lower dashed line (100% of control). If pairing had caused an increase in a gain, or multiplicative weight, then $EPSP_{stat}$ would equal the gain times a function of $I$, as represented by the upper dashed line (166% of control). Markram and Tsodyks fit their data with an exponential curve, approximately $1 + 0.104 \left[ e^{-\frac{(I-14.5)}{7.23}} - 1 \right] \cdot 100\%$, which crosses the neutral point at $I=14.5$ Hz.
Figure 2: During dART learning, active coding nodes tend simultaneously to become more selective with respect to a specific pattern and to become more excitable with respect to all patterns. This network-level tradeoff is realized by a synaptic-level dynamic balance between frequency-dependent and frequency-independent signal components. During learning, “disused” frequency-dependent elements, at synapses where the dynamic weight exceeds the input, are converted to frequency-independent elements. This conversion will strengthen the signal transmitted by the same path input (or by a smaller input), which will subsequently have the same frequency-dependent component but a larger frequency-independent component. Network dynamics also require that an active frequency-dependent (pattern-specific) channel contribute more than the equivalent frequency-independent (nonspecific) channel, which is realized as the hypothesis that parameter $\alpha$ is less than 1 in equation (2.1). This hypothesis ensures that, among those coding nodes that would produce no new learning for a given input pattern, nodes with learned patterns that most closely match the input are most strongly activated.
Figure 3: dART model and Markram–Tsodyks data. (a) The dART frequency-dependent signal component $S$ increases linearly with the presynaptic test spike frequency $I$, up to a saturation point. During pairing, the model adaptive threshold $\tau$ increases, and the saturation point of the graph of $S$ is proportional to $(1 - \tau)$. The saturation point therefore declines as the coding node becomes more selective. Pairing does not alter the frequency-dependent response to low-frequency inputs: $S^d = S^b$ for small $I$. For high-frequency inputs, $S^d$ is smaller than $S^b$ by a quantity $\Delta$, which is proportional to the amount by which $\tau$ has
Figure 3 (cont.)

increased during pairing. (b) The dART frequency-independent signal component $\Theta$, which is a constant function of the presynaptic input $I$, increases by $\Delta$ during pairing. (c) Combined synaptic signal $T = S + (1-\alpha)\Theta$, where $0 < \alpha < 1$. At low presynaptic frequencies, pairing causes the signal to increase ($T^a = T^b + (1-\alpha)\Delta$), because of the increase in the frequency-independent signal component $\Theta$. At high presynaptic frequencies, pairing causes the signal to decrease ($T^a = T^b - \alpha\Delta$). (d) For presynaptic spike frequencies below the post-pairing saturation point of $S^a$, $T^a$ is greater than $T^b$. For frequencies above the pre-pairing saturation point of $S^b$, $T^a$ is less than $T^b$. The interval of intermediate frequencies contains the neutral point where $T^a = T^b$.

Parameters for the dART model were estimated by minimizing the chi-squared (Press, Teukolski, Vetterling, & Flannery, 1994) statistic: $\chi^2 = \sum_{i=1}^{N} \left( \frac{y_i - \hat{y}_i}{\sigma_i} \right)^2$, where $y_i$ and $\sigma_i$ are the mean value and standard deviation of the $i^{th}$ measurement point, respectively, while $\hat{y}_i$ is the model's prediction for that point. Four parameters were used: threshold before pairing ($\tau^b = 0.225$), threshold after pairing ($\tau^a = 0.39$), an input scale ($I = 33.28$ Hz), and the weighting coefficient ($\alpha = 0.6$), which determines the contribution of the frequency-dependent signal component $S$ relative to the frequency-independent component $\Theta$. The components of the dimensionless signal $T = S + (1-\alpha)\Theta$, for a system with a single node in the target field ($\nu = 1$), are $S = \left( I / \bar{I} \right) \wedge (1-\tau)$ and $\Theta = \tau$. The dART model provides a good fit of the experimental data ($\chi^2(3) = 1.085$, $p = 0.78$).
**Figure 4:** Transitional synaptic signal ratios. The dART model predicts that, if postsynaptic responses were measured at intermediate numbers of pairing intervals, the location of the neutral point, where pairing leaves the ratio $T^a/T^b$ unchanged, would move to the left on the graph. That is, the cross-over point would occur at lower frequencies $f$. 