Bibliography

Andrade, M. A., & Moràn, F. (1996). Structural study of the development of ocularity domains using a neural network model. *Biological Cybernetics*, *74*, 243–254.

Angelucci, A., Clasca, F., Bricolo, E., Cramer, K. S., & Sur, M. (1997). Experimentally induced retinal projections to the ferret auditory thalamus: development of clustered eye-specific patterns in a novel target. *Journal of Neuroscience*, *17*, 2040–2055.

Archer, S. M., Dubin, M. W., & Stark, L. A. (1982). Abnormal development of kitten retino-geniculate connectivity in the absence of action potentials. *Science*, *217*, 743–745.

Artola, A., Bröcher, S., & Singer, W. (1990). Different voltage-dependent thresholds for the induction of long-term depression and long-term potentiation in slices of the rat visual-cortex. *Nature*, *347*, 69–72.

Atick, J. J., & Redlich, A. N. (1992). What does the retina know about natural scenes? *Neural Computation*, *4*, 196–210.

Barrow, H. G. (1987). Learning receptive fields. In *IEEE 1st International Conference on Neural Networks*, IV, pp. 115–121.

Barrow, H. G., & Bray, A. J. (1992). A model of adaptive development of complex cortical cells. In Aleksander, I., & Taylor, J. (Eds.), *Artificial Neural Networks, 2: Proceedings of the International Conference on Artificial Neural Networks*. North-Holland.

Bauer, H.-U., Brockmann, D., & Geisel, T. (1997). Analysis of ocular dominance pattern formation in a high-dimensional self-organizing-map model. *Network: Computation in Neural Systems*, *8*, 17–33.

Berman, N. E. J., Naporn, A., & Payne, B. R. (1987). Shape and arrangement of 'on' and 'off' modules in cat dorsal lateral geniculate nucleus. In *Society for Neuroscience Abstracts*, Vol. 13, p. 202.

Berman, N. E. J., & Payne, B. R. (1989). Modular organization of on and off responses in the cat lateral geniculate nucleus. *Neuroscience*, *32*, 721–737.

Bienenstock, E. L., Cooper, L. N., & Munro, P. W. (1982). Theory for the development of neuron selectivity: orientation specificity and binocular interaction in visual cortex. *Journal of Neuroscience*, *2*, 32–48.

Blakemore, C., & Cooper, G. F. (1970). Development of the brain depends on the visual environment. *Nature*, *228*, 477–478.

Bliss, T. V., & Lømo, T. (1973). Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. *Journal of Physiology*, *232*, 331–356.

Bodnarenko, S. R., & Chalupa, L. M. (1993). Stratification of on and off ganglion cell dendrites depends on glutamate mediated afferent activity in the developing retina. *Nature*, *364*, 144–146.

Bodnarenko, S. R., Jeyarasasingam, G., & Chalupa, L. M. (1995). Development and regulation of dendritic stratification in retinal ganglion-cells by glutamate-mediated afferent activity. *Journal of Neuroscience*, *15*, 7037–7045.

Bowling, D. B. (1989a). Timing differences between the light responses of X cells recorded simultaneously in cat lateral geniculate nucleus. *Visual Neuroscience*, *2*, 383–389.

Bowling, D. B. (1989b). Evidence for sublaminar organization of the cells of origin of the geniculo-striate pathway in the cat: a novel method for cortical deposition of HRP. *Brain Research*, *502*, 180–188.

Bowling, D. B., & Caverhill, J. I. (1989). On/off organization in the cat lateral geniculate nucleus: sublaminae vs columns. *Journal of Comparative Neurology*, *283*, 161–168.

Bowling, D. B., & Michael, C. R. (1984). Terminal patterns of single, physiologically characterized optic tract fibres in the cat's lateral geniculate nucleus. *Journal of Neuroscience*, *4*, 198–216.

Bowling, D. B., & Wieniawa-Nakiewicz, E. (1986). The distribution of on- and off- centre X- and Y-like cells in the A layers of the cat's lateral geniculate nucleus. *Journal of Physiology*, *375*, 561–572.

Casagrande, V. A., & Brunso-Bechtold, J. K. (1985). Development of lamination in the lateral geniculate nucleus: critical factors. In Aslin, R. N. (Ed.), *Advances in Neural and Behavioral Development*, Vol. 1, pp. 33–69. Ablex.

Cleland, B. G., & Dubin, M. W. (1971). Simultaneous recording of input and output of lateral geniculate neurones. *Nature, New Biology*, *231*, 191–192.

Cleland, B. G., & Dubin, M. W. (1976). The intrinsic connectivity of the LGN of the cat. *Experimental Brain Research*, *Suppl. 1*, 493–496.

Cline, H. T., & Constantine-Paton, M. (1989). NMDA receptor antagonists disrupt the retinotectal topographic map. *Neuron*, *3*, 413–426.

Constantine-Paton, M., Cline, H. T., & Debski, E. (1990). Patterned activity, synaptic convergence, and the NMDA receptor in developing visual pathways. *Annual Review of Neuroscience*, *13*, 129–154.

Cottrell, M., & Fort, J. C. (1986). A stochastic model of retinotopy: a self-organizing process. *Biological Cybernetics*, *53*, 405–411.

Cowan, J. D., & Friedman, A. E. (1991). Studies of a model for the development and regeneration of eye-brain maps. In Lippmann, R. P., Moody, J. E., & Touretzky, D. S. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 3, pp. 3–10. Morgan Kaufmann, San Mateo.

Cramer, K. S., Angelucci, A., Hahm, J. O., Bogdanov, M. B., & Sur, M. (1996). A role for nitric oxide in the development of the ferret retinogeniculate projection. *Journal of Neuroscience*, *16*, 7995–8004.

Cramer, K. S., & Sur, M. (1997). Blockade of afferent impulse activity disrupts on/off sublamination in the ferret lateral geniculate nucleus. *Developmental Brain Research*, *98*, 287–290.

Da Silva Filho, A. C. R. (1992). Investigation of a generalised version of Amari's continuous model for neural networks. DPhil thesis, School of Cognitive and Computing Sciences, Sussex University, UK.

Dale, H. H. (1935). Pharmacology and nerve endings. *Proceedings of the Royal Society of Medicine*, *28*, 319–332.

Dan, Y., Atick, J. J., & Reid, R. C. (1996). Efficient coding of natural scenes in the lateral geniculate nucleus: experimental test of a computational theory. *Journal of Neuroscience*, *16*, 3351–3362.

Dayan, P. S., & Goodhill, G. J. (1992). Perturbing Hebbian rules. In Moody, J. E., Hanson, S. J., & Lippmann, R. P. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 4, pp. 19–26. Morgan Kaufmann, San Mateo.

Dowling, J. E. (1987). *The Retina: An approachable part of the brain*. Harvard University Press.

Dubin, M. W., Stark, A., & Archer, S. M. (1986). A role for action-potential activity in the development of neuronal connections in the kitten retinogeniculate pathway. *Journal of Neuroscience*, *6*, 1021–1036.

Durbin, R., & Mitchison, G. (1990). A dimension reduction framework for understanding cortical maps. *Nature*, *343*, 644–647.

Durbin, R., & Willshaw, D. (1987). An analogue approach to the travelling salesman problem using an elastic net method. *Nature*, *326*, 689–691.

Eglen, S. J. (1995). Modelling the development of the cat lateral geniculate nucleus with Hebbian learning. Tech. rep. CSRP 383, Cognitive and Computing Sciences, Sussex University.

Eglen, S. J. (1996). Modelling the prenatal development of the lateral geniculate nucleus. In Silva, F. L., Principe, J. C., & Almeida, L. B. (Eds.), *Frontiers in Artificial Intelligence and Applications*, Vol. 37, pp. 33–41. IOS Press, Amsterdam.

Elgeti, H., Elgeti, R., & Fleischhauer, K. (1976). Postnatal growth of the dorsal lateral geniculate nucleus of the cat. *Anatomy and Embryology*, *149*, 1–13.

Elliot, T., Howarth, C. I., & Shadbolt, N. R. (1996). Neural computation and statistical mechanics. *Proceedings of the Royal Society of London Series B*, *263*, 601–606.

Elliot, T., & Shadbolt, N. R. (1996). A mathematical model of activity-dependent, anatomical segregation induced by competition for neurotrophic support. *Biological Cybernetics*, *75*, 463–470.

Erwin, E., Obermayer, K., & Schulten, K. (1995). Models of orientation and ocular dominance columns in the visual-cortex — a critical comparison. *Neural Computation*, *7*, 425–468.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47.

Feller, M. B., Wellis, D. P., Stellwagen, D., Weblin, F. S., & Shatz, C. J. (1996). Requirement for cholinergic synaptic transmission in the propagation of spontaneous retinal waves. *Science*, *272*, 1182–1187.

Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical-cells. *Journal of the Optical Society of America A*, *4*, 2379–2394.

Földiák, P. (1991). Learning invariance from transformation sequences. *Neural Computation*, *3*, 194–200.

Frank, E. (1987). The influence of neuronal activity on patterns of synaptic connections. *Trends in Neuroscience*, *10*, 188–190.

Friedlander, M. J., Frégnac, Y., & Burke, J. P. (1993). Temporal covariance of postsynaptic membrane potential and synaptic input — role in synaptic efficiency in visual cortex. *Progress in Brain Research*, *95*, 207–223.

Galli, L., & Maffei, L. (1988). Spontaneous impulse activity of rat retinal ganglion cells in prenatal life. *Science*, *242*, 90–91.

Garraghty, P. E., Shatz, C. J., & Sur, M. (1988). Prenatal disruption of binocular interactions creates novel lamination in the cat's lateral geniculate nucleus. *Visual Neuroscience*, *1*, 93–102.

Gaze, R. M., & Sharma, S. C. (1970). Axial differences in the reinnervation of the goldfish optic tectum by regenerating optic nerve fibres. *Experimental Brain Research*, *10*, 171–181.

Goodhill, G. J. (1992). Correlations, competition and optimality: modelling the development of topography and ocular dominance. DPhil thesis, School of Cognitive and Computing Sciences, Sussex University, UK.

Goodhill, G. J. (1993). Topography and ocular dominance with positive correlations. In Hanson, S. J., Cowan, J. D., & Giles, C. L. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 5, pp. 985–992. Morgan Kaufmann, San Mateo.

Goodhill, G. J., & Barrow, H. G. (1994). The role of weight normalization in competitive learning. *Neural Computation*, *6*, 255–269.

Goodhill, G. J., & Löwel, S. (1995). Theory meets experiment — correlated neural activity helps determine ocular dominance column periodicity. *Trends in Neuroscience*, *18*, 437–439.

Goodhill, G. J., & Willshaw, D. J. (1990). Application of the elastic net algorithm to the formation of ocular dominance stripes. *Network: Computation in Neural Systems*, *4*, 41–59.

Goodhill, G. J., & Willshaw, D. J. (1994). Elastic net model of ocular dominance — overall stripe pattern and monocular deprivation. *Neural Computation*, *6*, 615–621.

Goodman, C. S., & Shatz, C. J. (1993). Developmental mechanisms that generate precise patterns of neuronal connectivity. *Cell*, *72*, 77–98.

Graybiel, A. M. (1975). Anatomical organisation of retinotectal afferents in the cat: an autoradiographic study. *Brain Research*, *96*, 1–23.

Greiner, J. V., & Weidman, T. A. (1980). Histogenesis of the cat retina. *Experimental Eye Research*, *30*, 439–453.

Guido, W., Lu, S. M., & Sherman, S. M. (1992). Relative contributions of burst and tonic responses to the receptive-field properties of lateral geniculate neurons in the cat. *Journal of Neurophysiology*, *68*, 2199–2211.

Guillery, R. W., Lamantia, A. S., Robson, J. A., & Huang, K. (1985). The influence of retinal afferents upon the development of layers in the dorsal lateral geniculate-nucleus of mustelids. *Journal of Neuroscience*, *5*, 1370–1379.

Hahm, J. O., Langda, R. B., & Sur, M. (1991). Disruption of retino geniculate afferent segregation by antagonists to NMDA receptors. *Nature*, *351*, 568–570.

Hancock, P. J. B., Smith, L. S., & Phillips, W. A. (1991). A biologically supported error-correcting learning rule. *Neural Computation*, *3*, 201–212.

Hankin, M., & Lund, R. (1991). How do retinal axons find their targets in the developing brain? *Trends in Neuroscience*, *14*, 224–228.

Häussler, A. F., & von der Malsburg, C. (1983). Development of retinotopic projections: an analytical treatment. *Journal of Theoretical Neurobiology*, *2*, 47–73.

Hayes, W. P., & Meyer, R. L. (1988a). Retinotopically inappropriate synapses of subnormal density formed by surgically misdirected optic fibers in goldfish tectum. *Developmental Brain Research*, *38*, 304–312.

Hayes, W. P., & Meyer, R. L. (1988b). Optic synapse number but not density is constrained during regeneration onto surgically halved tectum in goldfish — HRP-EM evidence that optic fibers compete for fixed numbers of postsynaptic sites on the tectum. *Journal of Comparative Neurology*, *274*, 539–559.

Hebb, D. O. (1949). *The organization of behaviour*. New York: Wiley.

Hirsch, H. V. B., & Spinelli, D. N. (1970). Visual experience modifies distribution of horizontally and vertically oriented receptive fields in cats. *Science*, *168*, 869–871.

Hodgkin, A. L., & Huxley, A. F. (1952). A quantitative description of membrane current and its application to conduction and excitation in nerve. *Journal of Physiology*, *117*, 500–544.

Hope, R. A., Hammond, B. J., & Gaze, R. M. (1976). The arrow model: retinotectal specificity and map formation in the goldfish visual system. *Proceedings of the Royal Society of London Series B*, *194*, 447–466.

Hubel, D. H., Levay, S., & Wiesel, T. N. (1975). Mode of termination of retinotectal fibres in macaque monkey: an autoradiographic study. *Brain Research*, *96*, 25–40.

Hubel, D. H., & Wiesel, T. N. (1961). Integrative action in the cat's lateral geniculate body. *Journal of Physiology*, *155*, 383–398.

Hubel, D. H., & Wiesel, T. N. (1963). Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. *Journal of Neurophysiology*, *26*, 994–1001.

Hubel, D. H., & Wiesel, T. N. (1972). Laminar and columnar distribution of geniculocortical fibres in macaque monkey,. *Journal of Comparative Neurology*, *146*, 421–450.

Hubel, D. H., & Wiesel, T. N. (1977). Functional architecture of the macaque monkey visual cortex. *Proceedings of the Royal Society of London Series B*, *198*, 1–59.

Hubel, D. H., Wiesel, T. N., & LeVay, S. (1977). Plasticity of ocular dominance columns in monkey striate cortex. *Philosophical Transactions of the Royal Society of London Series B*, *278*, 377–409.

Humphrey, A. L., & Weller, R. E. (1988). Functionally distinct groups of X-cells in the lateral geniculate nucleus of the cat. *Journal of Comparative Neurology*, *268*, 429–447.

Jeffery, G. (1989). Shifting retinal maps in the development of the lateral geniculate-nucleus. *Developmental Brain Research*, *46*, 187–196.

Johnson, J. K., & Casagrande, V. A. (1993). Prenatal development of axon outgrowth and connectivity in the ferret visual system. *Visual Neuroscience*, *10*, 117–130.

Jones, E. C. (1985). *The Thalamus*. Plenum Press: New York.

Kaas, J. H., Guillery, R. W., & Allman, J. M. (1972). Some principles of organization in the dorsal lateral geniculate nucleus. *Brain Behaviour and Evolution*, *6*, 253–299.

Kaas, J. H., Nelson, R. J., Sur, M., & Lin, C.-S. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science*, *204*, 521–523.

Kalil, R. E. (1980). A quantitative study of the effects of monocular enucleation and deprivation on cell growth in the lateral geniculate nucleus of the cat. *Journal of Comparative Neurology*, *189*, 438–524.

Kalil, R. E., Dubin, M. W., Scott, G., & Stark, L. A. (1986). Elimination of action potentials blocks the structural development of retinogeniculate synapses. *Nature*, *323*, 156–158.

Katz, L. C., & Shatz, C. J. (1996). Synaptic activity and the construction of cortical circuits. *Science*, *274*, 1133–1138.

Keesing, R., Stork, D. G., & Shatz, C. J. (1992). Retinogeniculate development: the role of competition and correlated retinal activity. In Moody, J. E., Hanson, S. J., & Lippmann, R. P. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 4, pp. 91–97. Morgan Kaufmann, San Mateo.

Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biological Cybernetics*, *43*, 59–69.

Kohonen, T. (1988). *Self-Organization and Associative Memory* (third edition). Springer-Verlag.

Lee, C. W., & Wong, R. O. L. (1996). Developmental patterns of on/off retinal ganglion cell activity lead to segregation of their afferents under a Hebbian synaptic rule. In *Society for Neuroscience Abstracts*, Vol. 22, p. 477.6.

Lee, D. Y., & Malpeli, J. G. (1994). Global form and singularity — modeling the blind spots role in lateral geniculate morphogenesis. *Science*, *263*, 1292–1294.

LeVay, S., & Ferster, D. (1979). Proportion of interneurons in the cat's lateral geniculate nucleus. *Brain Research*, *164*, 304–308.

LeVay, S., Hubel, D. H., & Wiesel, T. N. (1975). The pattern of ocular dominance columns in macaque visual cortex revealed by a reduced silver stain. *Journal of Comparative Neurology*, *159*, 559–576.

Leventhal, A. G., & Schall, J. D. (1983). Structural basis of orientation sensitivity of cat retinal ganglion-cells. *Journal of Comparative Neurology*, *220*, 465–475.

Levick, W. R., & Thibos, L. N. (1982). Analysis of orientation bias in cat retina. *Journal of Physiology*, *329*, 243–261.

Levine, M. W., Cleland, B. G., Mukherjee, P., & Kaplan, E. (1996). Tailoring of variability in the lateral geniculate nucleus of the cat. *Biological Cybernetics*, *75*, 219–227.

Linden, D. C., Guillery, R. W., & Cucchiaro, J. (1981). The dorsal lateral geniculate-nucleus of the normal ferret and its postnatal-development. *Journal of Comparative Neurology*, *203*, 189–211.

Linsker, R. (1986a). From basic network principles to neural architecture: emergence of spatial-opponent cells. *Proceedings of the National Academy Of Sciences of the U.S.A*, *83*, 7508–7512.

Linsker, R. (1986b). From basic network principles to neural architecture: emergence of orientation-selective cells. *Proceedings of the National Academy Of Sciences of the U.S.A*, *83*, 8390–8394.

Linsker, R. (1986c). From basic network principles to neural architecture: emergence of orientation columns. *Proceedings of the National Academy Of Sciences of the U.S.A*, *83*, 8779–8783.

Lippe, W. R. (1994). Rhythmic spontaneous activity in the developing avian auditory-system. *Journal of Neuroscience*, *14*, 1486–1495.

Löwel, S. (1994). Ocular dominance column development: strabismus changes the spacing of adjacent columns in cat visual cortex. *Journal of Neuroscience*, *14*, 7451–7468.

Löwel, S., & Singer, W. (1992). Selection of intrinsic horizontal connections in the visual cortex by correlated neural activity. *Science*, *255*, 209–211.

MacKay, D. J. C., & Miller, K. D. (1990a). Analysis of Linsker's simulations of Hebbian rules. *Neural Computation*, *2*, 173–187.

MacKay, D. J. C., & Miller, K. D. (1990b). Analysis of Linsker's application of Hebbian rules to linear networks. *Network: Computation in Neural Systems*, *1*, 257–297.

Maffei, L., & Galli, L. (1990). Correlation in the discharges of neighbouring rat retinal ganglion cells during prenatal life. *Proceedings of the National Academy Of Sciences of the U.S.A*, *87*, 2861–2864.

Markram, H., Lubke, J., Frotscher, M., & Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science*, *275*, 213–215.

Masland, R. H. (1996). Processing and encoding of visual information in the retina. *Current Opinion in Neurobiology*, *6*, 467–474.

Maslim, J., & Stone, J. (1988). Time course of stratification of the dendritic fields of ganglion cells in the retina of the cat. *Developmental Brain Research*, *44*, 87–93.

Mastronarde, D. N. (1983a). Correlated firing of cat retinal ganglion-cells. 1. Spontaneously active inputs to X-cell and Y-cell. *Journal of Neurophysiology*, *49*, 303–324.

Mastronarde, D. N. (1983b). Correlated firing of cat retinal ganglion-cells. 2. Responses of X-cell and Y-cell to single quantal events. *Journal of Neurophysiology*, *49*, 325–349.

Mastronarde, D. N. (1983c). Interactions between ganglion-cells in cat retina. *Journal of Neurophysiology*, *49*, 350–365.

Mastronarde, D. N. (1987a). 2 classes of single-input X-cells in cat lateral geniculate-nucleus. 1. Receptive-field properties and classification of cells. *Journal of Neurophysiology*, *57*, 357–380.

Mastronarde, D. N. (1987b). 2 classes of single-input X-cells in cat lateral geniculate-nucleus. 2. Retinal inputs and the generation of receptive-field properties. *Journal of Neurophysiology*, *57*, 381–413.

Mastronarde, D. N. (1989). Correlated firing of retinal ganglion cells. *Trends in Neuroscience*, *12*, 75–79.

Meister, M., Wong, R. O. L., Baylor, D. A., & Shatz, C. J. (1991). Synchronous bursts of action potentials in ganglion cells of the developing mammalian retina. *Science*, *252*, 939–943.

Métin, C., & Frost, D. O. (1989). Visual responses of neurons in somatosensory cortex of hamsters with experimentally induced retinal projections to somatosensory thalamus. *Proceedings of the National Academy Of Sciences of the U.S.A*, *86*, 357–361.

Meyer, R. L. (1979). Retinotectal projection in goldfish to an inappropriate region with a reversal in polarity. *Science*, *205*, 819–821.

Miller, K. D. (1994). A model for the development of simple cell receptive fields and the ordered arrangement of orientation columns through activity-dependent competition between on- and off-center inputs. *Journal of Neuroscience*, *14*, 409–441.

Miller, K. D. (1996). Synaptic economics: competition and cooperation in synaptic plasticity. *Neuron*, *17*, 371–374.

Miller, K. D., Keller, J. B., & Stryker, M. P. (1989). Ocular dominance column development — analysis and simulation. *Science*, *245*, 605–615.

Miller, K. D., & MacKay, D. J. C. (1992). The role of constraints in Hebbian learning. Tech. rep., CNS Memo 19, California Institute of Technology.

Miller, K. D., & Mackay, D. J. C. (1994). The role of constraints in Hebbian learning. *Neural Computation*, *6*, 100–126.

Montague, P. R., Gally, J. A., & Edelman, G. M. (1991). Spatial signalling in the development and function of neural connections. *Cerebral Cortex*, *1*, 199–220.

Montero, V. M. (1991). A quantitative study of synaptic contacts on interneurons and relay cells of the cat lateral geniculate-nucleus. *Experimental Brain Research*, *86*, 257–270.

Mooney, R., Madison, D. V., & Shatz, C. J. (1993). Enhancement of transmission at the developing retinogeniculate synapse. *Neuron*, *21*, 815–825.

Mooney, R., Penn, A. A., Gallego, R., & Shatz, C. J. (1996). Thalamic relay of spontaneous retinal activity prior to vision. *Neuron*, *17*, 863–874.

Mooney, R., Penn, A. A., & Shatz, C. J. (1995). Periodic synaptic currents in the neonatal LGN are generated by retinal activity. In *Society for Neuroscience Abstracts*, Vol. 21, p. 591.4.

Morgan, J., & Thompson, I. D. (1993). The segregation of on-center and off-center responses in the lateral geniculate-nucleus of normal and monocularly enucleated ferrets. *Visual Neuroscience*, *10*, 303–311.

Mumford, D. (1991). On the computational architecture of the neocortex. I. The role of the thalamo-cortical loop. *Biological Cybernetics*, *65*, 135–145.

Murphy, P. C., & Sillito, A. M. (1987). Corticofugal feedback influences the generation of length tuning in the visual pathway. *Nature*, *329*, 727–729.

Murphy, P. C., & Sillito, A. M. (1996). Functional-morphology of the feedback pathway from area-17 of the cat visual-cortex to the lateral geniculate-nucleus. *Journal of Neuroscience*, *16*, 1180–1192.

Nelson, M. E., & Bower, J. M. (1990). Brain maps and parallel computers. *Trends in Neuroscience*, *13*, 403–408.

Nelson, R., Famiglietti, E. V., & Kolb, H. (1978). Intracellular staining reveals different levels of stratification for on-centre and off-centre ganglion cells in the cat retina. *Journal of Neurophysiology*, *41*, 472–483.

Norden, J. J., & Constantine-Paton, M. (1994). Dynamics of retinotectal synaptogenesis in normal and 3-eyed frogs: evidence for the postsynaptic regulation of synapse number. *Journal of Comparative Neurology*, *348*, 461–479.

Obermayer, K., Blasdel, G. G., & Schulten, K. (1991). A neural network model for the formation and for the spatial structure of retinotopic maps, orientation- and ocular dominance columns. In Kohonen, T., Mäkisara, K., Simula, O., & Kangas, J. (Eds.), *Procedings of the Interntational Conference on Artificial Neural Networks* Helsinki.

Obermayer, K., Ritter, H., & Schulten, K. (1990). A principle for the formation of the spatial structure of cortical feature maps. *Proceedings of the National Academy Of Sciences of the U.S.A*, *87*, 8345–8349.

Obermayer, K., Ritter, H., & Schulten, K. (1991). Development and spatial structure of cortical feature maps: a model study. In Lippmann, R. P., Moody, J. E., & Touretzky, D. S. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 3, pp. 11–17. Morgan Kaufmann, San Mateo.

Oja, E. (1982). A simplified neuron model as a principal component analyzer. *Journal of Mathematical Biology*, *15*, 267–273.

Overton, K. J., & Arbib, M. A. (1982). The extended branch-arrow model of the formation of retino-tectal connections. *Biological Cybernetics*, *45*, 157–175.

Pallas, S. L., & Finlay, B. L. (1991). Compensation for population-size mismatches in the hamster retinotectal system: alterations in the organization of retinal projections. *Visual Neuroscience*, *6*, 271–281.

Penn, A. A., Gallego, R., Mooney, R., & Shatz, C. J. (1995). Spontaneous retinal inputs drive postsynaptic action potentials in the LGN. In *Society for Neuroscience Abstracts*, Vol. 21, p. 591.5.

Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, *47*, 329–342.

Prestige, M. C., & Willshaw, D. J. (1975). On a role for competition in the formation of patterned neural connexions. *Proceedings of the Royal Society of London Series B*, *190*, 77–98.

Reiter, H. O., & Stryker, M. P. (1988). Neural plasticity without postsynaptic action-potentials — less-active inputs become dominant when kitten visual cortical-cells are pharmacologically inhibited. *Proceedings of the National Academy Of Sciences of the U.S.A*, *85*, 3623–3627.

Rétaux, S., & Harris, W. A. (1996). Engrailed and retinotectal topography. *Trends in Neuroscience*, *19*, 542–546.

Ritter, H., & Schulten, K. (1988). Convergence properties of Kohonen's topology conserving maps: fluctuations, stability and dimension selection. *Biological Cybernetics*, *60*, 59–71.

Rochester, N., Holland, J. H., Haibt, L. H., & Duda, W. L. (1956). Tests on a cell assembly theory of the action of the brain using a large digital computer. *IRE Transactions on Information Theory*, *2*, 80–93.

Roe, A. W., Garraghty, P. E., Esguerra, M., & Sur, M. (1993). Experimentally-induced visual projections to the auditory thalamus in ferrets — evidence for a W cell pathway. *Journal of Comparative Neurology*, *334*, 263–280.

Sabel, B. A., & Schneider, G. E. (1988). The principle of conservation of total axonal arborizations — massive compensatory sprouting in the hamster subcortical visual-system after early tectal lesions. *Experimental Brain Research*, *73*, 505–518.

Sanderson, K. J. (1971a). The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. *Journal of Comparative Neurology*, *143*, 101–118.

Sanderson, K. J. (1971b). Visual field projection columns and magnification factors in the lateral geniculate nucleus of the cat. *Experimental Brain Research*, *13*, 159–177.

Saul, A. B., & Humphrey, A. L. (1990). Spatial and temporal response properties of lagged and nonlagged cells in cat lateral geniculate-nucleus. *Journal of Neurophysiology*, *64*, 206–224.

Schlaggar, B. L., & O'Leary, D. D. M. (1991). Potential of visual-cortex to develop an array of functional units unique to somatosensory cortex. *Science*, *252*, 1556–1560.

Schmidt, J. T., & Buzzard, M. (1993). Activity-driven sharpening of the retinotectal projection in goldfish — development under stroboscopic illumination prevents sharpening. *Journal of Neurobiology*, *24*, 384–399.

Schmidt, J. T., & Edwards, D. L. (1983). Activity sharpens the map during the regeneration of the retinotectal projection in goldfish. *Brain Research*, *209*, 29–39.

Sejnowski, T. J. (1977). Storing covariance with nonlinearly interacting neurons. *Journal of Mathematical Biology*, *4*, 303–321.

Sejnowski, T. J., Koch, C., & Churchland, P. S. (1988). Computational neuroscience. *Science*, *241*, 1299–1306.

Sernagor, E., & Grzywacz, N. M. (1996). Influence of spontaneous activity and visual experience on developing retinal receptive-fields. *Current Biology*, *6*, 1503–1508.

Shatz, C. J. (1977). A comparison of visual pathways in Boston and Midwestern Siamese cats. *Journal of Comparative Neurology*, *171*, 205–228.

Shatz, C. J. (1983). The prenatal development of the cats retinogeniculate pathway. *Journal of Neuroscience*, *3*, 482–499.

Shatz, C. J. (1994). Role for spontaneous neural activity in the patterning of connections between retina and LGN during visual system development. *International Journal of Developmental Neuroscience*, *12*, 531–546.

Shatz, C. J. (1996). Emergence of order in visual-system development. *Proceedings of the National Academy Of Sciences of the U.S.A*, *93*, 602–608.

Shatz, C. J., & Kirkwood, P. A. (1984). Prenatal development of functional connections in the cats retinogeniculate pathway. *Journal of Neuroscience*, *4*, 1378–1397.

Shatz, C. J., & Stryker, M. P. (1978). Ocular dominance in layer IV of the cat's visual cortex and the effects of monocular deprivation. *Journal of Physiology*, *281*, 267–283.

Shatz, C. J., & Stryker, M. P. (1988). Prenatal tetrodotoxin infusion blocks segregation of retinogeniculate afferents. *Science*, *242*, 87–89.

Sherman, S. M. (1985). Development of retinal projections to the cat's lateral geniculate nucleus. *Trends in Neuroscience*, *8*, 350–355.

Sherman, S. M., & Guillery, R. W. (1996). Functional-organization of thalamocortical relays. *Journal of Neurophysiology*, *76*, 1367–1395.

Sherman, S. M., & Koch, C. (1986). The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus. *Experimental Brain Research*, *63*, 1–20.

Sherman, S. M., & Koch, C. (1990). Thalamus. In Shepherd, G. M. (Ed.), *The synaptic organization of the brain* (3rd edition)., chap. 8, pp. 246–278. Oxford University Press, Oxford.

Shou, T. D., & Leventhal, A. G. (1989). Organized arrangement of orientation-sensitive relay cells in the cat's lateral geniculate nucleus. *Journal of Neuroscience*, *9*, 4287–4302.

Shou, T. D., Leventhal, A. G., Thompson, K. G., & Zhou, Y. F. (1995). Direction biases of X-type and Y-type retinal ganglion-cells in the cat. *Journal of Neurophysiology*, *73*, 1414–1421.

Sidman, R. L., & Wislocki, G. B. (1954). Histochemical observations on rods and cones in retinas of vertebrates. *Journal of Histochemistry and Cytochemistry*, *2*, 413–433.

Sillito, A. M., Jones, H. E., Gerstein, G. L., & West, D. C. (1994). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature*, *369*, 479–482.

Simon, D. K., Prusky, G. T., O'Leary, D. D. M., & Constantine-Paton, M. (1992). N-methyl-d-aspartate receptor antagonists disrupt the formation of a mammalian neural map. *Proceedings of the National Academy Of Sciences of the U.S.A*, *89*, 10593–10597.

Singer, W. (1977). Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiological Reviews*, *57*, 386–420.

Singer, W. (1994). A new job for the thalamus. *Nature*, *369*, 444–445.

Sirosh, J., & Miikkulainen, R. (1994). Cooperative self-organization of afferent and lateral connections in cortical maps. *Biological Cybernetics*, *71*, 65–78.

Sirosh, J., & Miikkulainen, R. (1995). Ocular dominance and patterned lateral connections in a self-organizing model of the primary visual cortex. In Tesauro, G., Touretzky, D. S., & Leen, T. K. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 7, pp. 109–116. The MIT Press, Cambridge.

Smetters, D. K., Hahm, J., & Sur, M. (1994). An n-methyl-d-aspartate receptor antagonist does not prevent eye-specific segregation in the ferret retinogeniculate pathway. *Brain Research*, *658*, 168–178.

Somers, D. C., Nelson, S. C., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortex simple cells. *Journal of Neuroscience*, *15*, 5448–5465.

Spear, P. D., Kim, C. B. Y., Ahmad, A., & Tom, B. W. (1996). Relationship between numbers of retinal ganglion-cells and lateral geniculate neurons in the rhesus-monkey. *Visual Neuroscience*, *13*, 199–203.

Sperry, R. W. (1963). Chemoaffinity in the orderly growth of nerve fibre patterns and connections. *Proceedings of the National Academy Of Sciences of the U.S.A*, *50*, 703–710.

Sretavan, D. W., & Shatz, C. J. (1986). Prenatal development of retinal ganglion-cell axons — segregation into eye-specific layers within the cats lateral geniculate-nucleus. *Journal of Neuroscience*, *6*, 234–251.

Sretavan, D. W., Shatz, C. J., & Stryker, M. P. (1988). Modification of retinal ganglion cell axon morphology by prenatal infusion of tetrodotoxin. *Nature*, *336*, 468–471.

Stone, J. (1978). The number and distribution of ganglion cells in the cat's retina. *Journal of Comparative Neurology*, *180*, 753–771.

Stone, J. (1983). *Parallel processing in the visual system: the classification of retinal ganglion cells and its impact on the neurobiology of vision*. Plenum Press, New York.

Stryker, M. P., & Harris, W. A. (1986). Binocular impulse blockade prevents the formation of ocular dominance columns in cat visual-cortex. *Journal of Neuroscience*, *6*, 2117–2133.

Stryker, M. P., & Zahs, K. R. (1983). On and off sublaminae in the lateral geniculate nucleus of the ferret. *Journal of Neuroscience*, *3*, 1943–1951.

Suarez, H., Koch, C., & Douglas, R. (1995). Modeling direction selectivity of simple cells in striate visual-cortex within the framework of the canonical microcircuit. *Journal of Neuroscience*, *15*, 6700–6719.

Sur, M. (1995). Visual activity and cortical development. In *Cerebral Cortex: Function and Development, (Lyon, France)*.

Sur, M., Esguerra, M., Garraghty, P. E., Kritzer, M. F., & Sherman, S. M. (1987). Morphology of physiologically identified retinogeniculate X- and Y- axons in the cat. *Journal of Neurophysiology*, *58*, 1–32.

Sur, M., Garraghty, P. E., & Roe, A. W. (1988). Experimentally induced visual projections into auditory thalamus and cortex. *Science*, *242*, 1437–1441.

Swindale, N. V. (1980). A model for the formation of ocular dominance stripes. *Proceedings of the Royal Society of London Series B*, *208*, 243–264.

Swindale, N. V. (1981). Rules for pattern formation in mammalian visual cortex. *Trends in Neuroscience*, *4*, 102–104.

Swindale, N. V. (1996). The development of topography in the visual cortex: a review of models. *Network: Computation in Neural Systems*, *7*, 161–247.

Thompson, K. G., Zhou, Y., & Leventhal, A. G. (1994). Direction–sensitive X and Y cells within the A laminae of the cat's LGNd. *Visual Neuroscience*, *11*, 927–938.

Thurlow, G. A., Bowling, D. B., & Cooper, R. M. (1993). ON and OFF activity gradients in the lateral geniculate nucleus of the cat: a combined ^{14}C 2-deoxyglucose and d,l-2-amino-4-phosphonobutyric acid study. *Visual Neuroscience*, *10*, 1027–1033.

Trevelyan, A., Thompson, I., & Willshaw, D. (1993). Waves of retinal activity: implications for the development of retinotopicity. In *Society for Neuroscience Abstracts*, Vol. 19, p. 52.

Tzonev, S., Schulten, K., & Malpeli, J. G. (1995). Morphogenesis of the lateral geniculate nucleus: how singularities affect global structure. In Tesauro, G., Touretzky, D. S., & Leen, T. K. (Eds.), *Advances in Neural Information Processing Systems*, Vol. 7, pp. 133–140. The MIT Press, Cambridge.

von der Malsburg, C. (1973). Self-organization of orientation sensitive cells in the striata cortex. *Kybernetik*, *14*, 85–100.

von der Malsburg, C. (1979). Development of ocularity domains and growth behaviour of axon terminals. *Biological Cybernetics*, *32*, 49–62.

von der Malsburg, C., & Singer, W. (1988). Principles of cortical network organization. In Rakic, P., & Singer, W. (Eds.), *Neurobiology of Neocortex*, pp. 69–99. John Wiley & Sons Ltd.

von der Malsburg, C., & Willshaw, D. J. (1976). A mechanism for producing continuous neural mappings: ocularity dominance stripes and ordered retino-tectal projections. *Experimental Brain Research*, *Supplement 1*, 463–469.

von der Malsburg, C., & Willshaw, D. J. (1977). How to label nerve cells so that they can interconnect in an ordered fashion. *Proceedings of the National Academy Of Sciences of the U.S.A*, *74*, 5176–5178.

Wallis, G., Rolls, E., & Földiák, P. (1993). Learning invariant responses to the natural transformations of objects. In *International Joint Conference on Neural Networks 2*, pp. 1087–1090.

Wassle, H., Boycott, B. B., & Illing, R. B. (1981a). Morphology and mosaic of on-beta and off-beta cells in the cat retina and some functional considerations. *Proceedings of the Royal Society of London Series B*, *212*, 177–195.

Wassle, H., Peichl, L., & Boycott, B. B. (1981b). Morphology and topography of on-alpha and off-alpha cells in the cat retina. *Proceedings of the Royal Society of London Series B*, *212*, 157–175.

Wehmeier, U., Dong, D., Koch, C., & Van Essen, D. (1989). Modeling the mammalian visual system. In Koch, C., & Segev, I. (Eds.), *Methods in Neuronal Modeling*, chap. 10. MIT Press.

Whitelaw, V. A., & Cowan, J. D. (1981). Specificity and plasticity of retinotectal connections: a computational model. *Journal of Neuroscience*, *1*, 1369–1387.

Wiesel, T. N., & Hubel, D. H. (1963a). Single cell responses in striate cortex of kittens deprived of vision in one eye. *Journal of Neurophysiology*, *26*, 1003–1017.

Wiesel, T. N., & Hubel, D. H. (1963b). Effects of visual deprivation on morphology and physiology of cells in the cats lateral geniculate body. *Journal of Neurophysiology*, *26*, 978–993.

Williams, R. W., Bastiani, M. J., Lia, B., & Chalupa, L. M. (1986). Growth cones, dying axons, and developmental fluctuations in the fiber population of the cat's optic nerve. *Journal of Comparative Neurology*, *246*, 32–69.

Willshaw, D. J., & Dayan, P. (1990). Optimal plasticity from matrix memories: what goes up must come down. *Neural Computation*, *2*, 85–93.

Willshaw, D. J., & von der Malsburg, C. (1976). How patterned neural connections can be set up by self-organization. *Proceedings of the Royal Society of London Series B*, *194*, 431–445.

Willshaw, D. J., & von der Malsburg, C. (1979). A marker induction mechanism for the establishment of ordered neural mappings: its application to the retinotectal problem. *Philosophical Transactions of the Royal Society of London Series B*, *287*, 203–243.

Wingate, R. J. T., & Thompson, I. D. (1995). The morphological development of mammalian retinal ganglion cells. *Progress in retinal and eye research*, *14*, 413–435.

Wong, R. O. L. (1993). The role of spatio-temporal firing patterns in neuronal development of sensory systems. *Current Opinion in Neurobiology*, *5*, 595–601.

Wong, R. O. L. (1995). Use, disuse, and growth of the brain. *Proceedings of the National Academy Of Sciences of the U.S.A*, *92*, 1797–1799.

Wong, R. O. L., Chernjavsky, A., Smith, S. J., & Shatz, C. J. (1995). Early functional neural networks in the developing retina. *Nature*, *374*, 716–718.

Wong, R. O. L., Herrmann, K., & Shatz, C. J. (1991). Remodeling of retinal ganglion-cell dendrites in the absence of action-potential activity. *Journal of Neurobiology*, *22*, 685–697.

Wong, R. O. L., & Hughes, A. (1987). Developing neuronal populations of the cat retinal ganglion cell layer. *Journal of Comparative Neurology*, *262*, 473–495.

Wong, R. O. L., Meister, M., & Shatz, C. J. (1993). Transient period of correlated bursting activity during development of the mammalian retina. *Neuron*, *11*, 923–938.

Wong, R. O. L., & Oakley, D. M. (1996). Changing patterns of spontaneous bursting activity of on and off retinal ganglion cells during development. *Neuron*, *16*, 1087–1095.

Xiong, M. J., Pallas, S. L., Lim, S., & Finlay, B. L. (1994). Regulation of retinal ganglion-cell axon arbor size by target availability — mechanisms of compression and expansion of the retinotectal projection. *Journal of Comparative Neurology*, *344*, 581–597.

Yuasa, J., Hirano, S., Yamagata, M., & Noda, M. (1996). Visual projection map specified by topographic expression of transcription factors in the retina. *Nature*, *382*, 632–635.

Yuste, R., Peinado, A., & Katz, L. C. (1992). Neuronal domains in developing neocortex. *Science*, *257*, 666–669.

Zahs, K. R., & Stryker, M. P. (1985). The projection of the visual-field onto the lateral geniculate-nucleus of the ferret. *Journal of Comparative Neurology*, *241*, 210–224.

Appendix A

Mathematical details

A.1 The derivation of $\frac{d\mathbf{w}}{dt} = \mathbf{Cw}$ from the covariance rule

Some models of visual system development assume that the covariance rule described by Sejnowski (1977) can be reduced to a rule of the form $\frac{d\mathbf{w}}{dt} = \mathbf{Cw}$ (Linsker, 1986a; Miller et al., 1989). In the descriptions of these models, the details of this derivation are omitted. The derivation is non-trivial, and so is included here since no other full derivation has been published in the literature to the author's knowledge.

Consider a set of n presynaptic units $x_k, k = 1 \ldots n$, connected by weights w_k to one postsynaptic unit. The activation of the postsynaptic unit, y, is:

$$y = \sum_k w_k x_k \tag{A.1}$$

The covariance rule (Sejnowski, 1977) for updating weights upon presentation of one input vector is:

$$\begin{aligned} \Delta w_i &= \alpha(y - y_0)(x_i - x_0) \qquad (\alpha,\ x_0,\ y_0 \text{ are constants}) && \text{(A.2)} \\ \Delta w_i &= \alpha y x_i - \alpha y_0 x_i - \alpha y x_0 + \alpha y_0 x_0 \end{aligned}$$

This rule can be averaged over a set of inputs, assuming that the weights do not change during presentation of the inputs:

$$\begin{aligned} \langle \Delta w_i \rangle &= \alpha \langle y x_i \rangle - \alpha y_0 \langle x_i \rangle - \alpha x_0 \langle y \rangle + \alpha y_0 x_0 && \text{(A.3)} \\ \langle \Delta w_i \rangle &= \alpha \langle \sum_k w_k x_k x_i \rangle - \alpha y_0 \langle x_i \rangle - \alpha x_0 \langle \sum_k w_k x_k \rangle + \alpha y_0 x_0 && \text{(Substituting for } y \text{ from A.1)} \\ &= \alpha \sum_k w_k \langle x_i x_k \rangle - \alpha y_0 \langle x_i \rangle - \alpha x_0 \sum_k w_k \langle x_k \rangle + \alpha y_0 x_0 \end{aligned}$$

Assuming that the average value of each input is the same:

$$\langle x_i \rangle = \bar{x}, \quad \forall i \tag{A.4}$$

$$\langle \Delta w_i \rangle = \alpha \sum_k w_k \langle x_i x_k \rangle - \alpha y_0 \bar{x} - \alpha x_0 \bar{x} \sum_k w_k + \alpha y_0 x_0 \tag{A.5}$$

The covariance matrix of the inputs, **C**, is defined as:

$$\begin{aligned}
\mathbf{C}_{ij} &= \langle (x_i - \bar{x}_i)(x_j - \bar{x}_j) \rangle \\
&= \langle x_i x_j \rangle - \langle x_i \bar{x}_j \rangle - \langle \bar{x}_i x_j \rangle + \langle \bar{x}_i \bar{x}_j \rangle \\
&= \langle x_i x_j \rangle - \bar{x}_j \langle x_i \rangle - \bar{x}_i \langle x_j \rangle + \bar{x}_i \bar{x}_j \\
&= \langle x_i x_j \rangle - \bar{x}_i \bar{x}_j - \bar{x}_i \bar{x}_j + \bar{x}_i \bar{x}_j \\
\mathbf{C}_{ij} &= \langle x_i x_j \rangle - \bar{x}^2 && \text{(using A.4)} \\
\langle x_i x_j \rangle &= \mathbf{C}_{ij} + \bar{x}^2
\end{aligned}$$

This value of $\langle x_i x_j \rangle$ can be substituted into equation A.5:

$$\begin{aligned}
\langle \Delta w_i \rangle &= \alpha \sum_k w_k (\mathbf{C}_{ik} + \bar{x}^2) - \alpha y_0 \bar{x} - \alpha x_0 \bar{x} \sum_k w_k + \alpha y_0 x_0 \\
&= \alpha \sum_k w_k \mathbf{C}_{ik} + \alpha \sum_k w_k \bar{x}^2 - \alpha y_0 \bar{x} - \alpha x_0 \bar{x} \sum_k w_k + \alpha y_0 x_0 \\
&= \alpha \sum_k w_k \mathbf{C}_{ik} + \sum_k w_k (\bar{x}^2 \alpha - \alpha x_0 \bar{x}) - \alpha y_0 \bar{x} + \alpha y_0 x_0 \\
&= \alpha \sum_k w_k \mathbf{C}_{ik} + \bar{x} \alpha \sum_k w_k (\bar{x} - x_0) - \alpha y_0 (\bar{x} - x_0)
\end{aligned}$$

Assuming that the average input activity $\bar{x}$ is equal to x_0, $\langle \Delta w_i \rangle$ reduces to:

$$\begin{aligned}
\langle \Delta w_i \rangle &= \alpha \sum_k w_k \mathbf{C}_{ik} \\
\text{or } \frac{d\mathbf{w}}{dt} &= \mathbf{C}\mathbf{w}, \mathbf{w} = (w_1, w_2, \ldots w_n)^T
\end{aligned}$$

Hence, given the two assumptions that weight changes occur on a slower timescale than presentation of inputs and that the average activation of all input units is x_0, the covariance rule reduces to $\frac{d\mathbf{w}}{dt} = \mathbf{C}\mathbf{w}$. This form of the covariance rule is much simpler because it relies only upon presynaptic, and not postsynaptic, activity levels.

A.2 Why eigenvectors dominate development in correlational-based modification rules

Modification rules of the form $\frac{d\mathbf{w}}{dt} = \mathbf{C}\mathbf{w}$ are often analysed by eigenvector analysis. Let us assume that the eigenvectors of **C** are $\mathbf{e}_a$ with eigenvalues λ_a. If C is real and symmetric, there are n real eigenvectors. Writing **w** in terms of the eigenvectors of **C**:

$$\mathbf{w} = \sum_a \mathbf{e}_a w_a \quad \text{where } w_a = \mathbf{e}_a \cdot \mathbf{w} \tag{A.6}$$

$$\frac{d\mathbf{w}}{dt} = \mathbf{C}\mathbf{w} = \mathbf{C}\sum_a \mathbf{e}_a w_a \tag{A.7}$$

$$= \mathbf{C}\mathbf{e}_1 w_1 + \mathbf{C}\mathbf{e}_2 w_2 + \cdots + \mathbf{C}\mathbf{e}_n w_n \tag{A.8}$$

$$\frac{d\mathbf{w}}{dt} = \lambda_1 w_1 \mathbf{e}_1 + \lambda_2 w_2 \mathbf{e}_2 + \cdots + \lambda_n w_n \mathbf{e}_n \tag{A.9}$$

Therefore the rate of growth of the weight vector in the direction of each eigenvector is determined by its eigenvalue. Any component of the weight vector in the direction of an eigenvector with negative eigenvalue is quickly removed. Components of the weight vector in the direction of an eigenvector with positive eigenvalue grows exponentially, with the eigenvector with highest eigenvalue quickly dominating development. Assuming that the maximum eigenvector dominates weight development before any constraint limits are met (such as normalisation), the weight vector will develop to become similar to the maximum eigenvector.

A.3 Implementation of subtractive normalisation

The task of subtractive normalisation is to normalise the set of weights $w_i, i = 1 \ldots n$, so that $\sum_{i=1}^{n} w_i = t$, where t is the target value. If the sum is less than the target before normalisation, it is a simple case of adding $(t - \sum_{i=1}^{n} w_i)/n$ to each weight (assuming there is no upper limit on individual weights). However, if the sum is bigger than the target, the following iterative procedure must be used to prevent weights from taking negative values:

1. Initialise $\Delta = \sum_{i=1}^{n} w_i - t$, $N = n$.
2. Set $\delta = \Delta/N$ and then $\Delta = 0$.
3. For each weight i:
   (a) Set the new value of w_i:
   $$w_i = \begin{cases} w_i - \delta & \text{if } w_i > 0 \\ 0 & \text{otherwise} \end{cases}$$
   (b) If $w_i < 0$, then set $\Delta = \Delta - w_i$, $w_i = 0$, $N = N - 1$.
4. Go back to step 2 unless $\Delta = 0$.