letters to nature

18. Gilinsky, N. L. in *Analytical Paleobiology* (eds Gilinsky, N. L. & Signor, P. W.) 157–174 (The Paleontological Society, Knoxville, Tennessee, 1991).
19. Cleveland, W. S. & McGill, R. The many faces of a scatterplot. *J. Am. Stat. Assoc.* **79**, 807–822 (1984).

....

Simple rules yield complex food webs

Richard J. Williams & Neo D. Martinez

Romberg Tiburon Center, Department of Biology, San Francisco State University, PO Box 855, Tiburon, California 94920, USA

....

Several of the most ambitious theories in ecology[1-14] describe food webs that document the structure of strong and weak trophic links[9] that is responsible for ecological dynamics among diverse assemblages of species[4,11-13]. Early mechanism-based theory asserted that food webs have little omnivory and several properties that are independent of species richness[1-4,6]. This theory was overturned by empirical studies that found food webs to be much more complex[5,7-9,14-18], but these studies did not provide mechanistic explanations for the complexity[9]. Here we show that a remarkably simple model fills this scientific void by successfully predicting key structural properties of the most complex and comprehensive food webs in the primary literature. These properties include the fractions of species at top, intermediate and basal trophic levels, the means and variabilities of generality, vulnerability and food-chain length, and the degrees of cannibalism, omnivory, looping and trophic similarity. Using only two empirical parameters, species number and connectance, our 'niche model' extends the existing 'cascade model'[3,19] and improves its fit ten-fold by constraining species to consume a contiguous sequence of prey in a one-dimensional trophic niche[20].

We compare the abilities of two earlier models, the random and cascade models[3,19], and our new niche model to predict a dozen properties for each of seven food webs. The parameters of all models are set to synthesize webs with the empirically observed species number and connectance level. We compare model predictions with the largest and highest-quality empirical food webs that include autotrophs and were originally documented to study food web structure comprehensively (Table 1). Three are from freshwater habitats: Skipwith Pond, Little Rock Lake and Bridge Brook Lake;

two are from habitats at freshwater–marine interfaces: Chesapeake Bay and Ythan Estuary; and two are from terrestrial habitats: Coachella Valley and the island of St Martin.

Throughout this work, 'species' refers to trophic species, which are functional groups of taxa that share the same predators and prey in a food web[3]. 'Trophic species' is a widely accepted[3,4,8,14,17,18] and sometimes criticized convention[5,14] within structural food-web studies that reduces methodological biases in the data[3,4,8]. A matrix with S rows and columns represents a food web with S species. Element a_{ij} is 1 if species j consumes species i and 0 if not. There are S^2 possible and L actual links. Directed connectance[17] (C) equals L/S^2.

In the random model[3,19], any link among S species occurs with the same probability (P) equal to C of the empirical web. This creates webs as free as possible from biological structuring while maintaining the observed S and C. The cascade model[3,19] assigns each species a random value drawn uniformly from the interval [0,1] and each species has probability $P = 2CS/(S - 1)$ of consuming only species with values less than its own. This pecking order helps to explain species richness among trophic levels[3] but underestimates interspecific trophic similarity[19] and overestimates food-chain length and number in larger webs[3,18]. The niche model (Fig. 1) similarly assigns each species a randomly drawn 'niche value'. The species are then constrained to consume all prey species within one range of values whose randomly chosen centre is less than the consumer's niche value. The single range adds a previously discussed[20] community-level contiguity of niche space to the cascade model by causing species with similar niche values to share consumers frequently within the community. The placement of the niche partially relaxes the cascade hierarchy by allowing up to half a consumer's range to include species with niche values higher than the consumer's value. All three models incorporate substantial stochastic variability along with dependence on S and C.

Twelve properties of each empirical and model web are measured (see Methods):
(i–iii) Species types[1-8,14-18,21]: the fractions of top (T, species with no predators), intermediate (I, species with both predators and prey) and basal (B, species with no prey) species.
(iv, v) The standard deviations (s.d.) of generality[14] ($GenSD$) and vulnerability[14] ($VulSD$) quantify the respective variabilities of species' normalized prey (G_i) and predator (V_i) counts:

$$G_i = \frac{1}{L/S} \sum_{j=1}^{s} a_{ji} \qquad V_i = \frac{1}{L/S} \sum_{j=1}^{s} a_{ij}$$

Normalizing with L/S makes s.d. comparable across different webs by forcing mean G_i and V_i to equal 1.
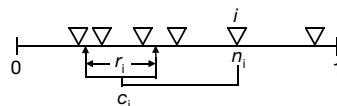

Figure 1 Diagram of the niche model. Each of S species (for example, $S = 6$, each shown as an inverted triangle) is assigned a 'niche value' parameter (n_i) drawn uniformly from the interval [0,1]. Species i consumes all species falling in a range (r_i) that is placed by uniformly drawing the centre of the range (c_i) from [$r_i/2$, n_i]. This permits looping and cannibalism by allowing up to half of r_i to include values $\geq n_i$. The size of r_i is assigned by using a beta function to randomly draw values from [0,1] whose expected value is $2C$ and then multiplying that value by n_i [expected E(n_i) = 0.5] to obtain the desired C. A beta distribution with $\alpha = 1$ has the form $f(x|1, \beta) = \beta(1-x)^{\beta-1}$, $0 < x < 1$, 0 otherwise, and E(X) = 1/(1+β). In this case, $x = 1-(1-y)^{1/\beta}$ is a random variable from the beta distribution if y is a uniform random variable and β is chosen to obtain the desired expected value. We chose this form because of its simplicity and ease of calculation. The fundamental generality of species i is measured by r_i. The number of species falling within r_i measures realized generality. Occasionally, model-generated webs contain completely disconnected or trophically identical species. Such species are eliminated and replaced until the web is free of such species. The species with the smallest n_i has $r_i = 0$ so that every web has at least one basal species.

Table 1 Basic properties of empirical food webs

Name	Taxa	**S**	**L/S**	**C(L/S²)**
Skipwith Pond	35	25	7.9	0.32
Little Rock Lake	181	92	10.8	0.12
Bridge Brook Lake	75	25	4.3	0.17
Chesapeake Bay	33	31	2.2	0.072
Ythan Estuary	92	78	4.8	0.061
Coachella Valley	30	29	9.0	0.31
St Martin Island	44	42	4.9	0.12

'Taxa' refers to the original names for groups of organisms found in the primary reference. **S** refers to trophic species[3]. The seven food webs address (1) primarily invertebrates in Skipwith Pond[15]; (2) pelagic and benthic species in Little Rock Lake[17], the largest food web in the primary literature; (3) Bridge Brook Lake, the largest among a recent set of 50 Adirondak lake pelagic food webs[6,7]; (4) the pelagic portion of Chesapeake Bay emphasizing larger fishes[30]; (5) mostly birds and fishes among invertebrates and primary producers in the Ythan Estuary[16]; (6) a wide range of highly aggregated taxa in the Coachella desert[5]; and (7) trophic interactions emphasizing *Anolis* lizards on the Caribbean island of St Martin[18].

(vi) Trophic similarity of a pair of species (s_{ij}) is the number of predators and prey shared in common divided by the pair's total number of predators and prey[17,19]. We average all species' largest similarity index to calculate mean maximum similarity (*MxSim*) of a web:

$$MxSim = \frac{1}{S} \sum_{i=1}^{s} \max_{i \neq j} s_{ij}.$$

(vii–ix) A food chain is a linked path from a species to a basal species[17]. The mean (*ChnLg*) and s.d. (*ChnSD*) of food chain lengths and the log of the number of food chains (*ChnNo*) are measured. Computational considerations require that chains with loops be ignored[17].

(x, xi) The fraction of species that are cannibals (*Cannib*) and the fraction of species involved in longer 'loops' (*Loop*), which are food chains that include the same species twice[5,17].

(xii) Omnivory[5] is the fraction of species that consume two or more species and have food chains of different lengths (*Omniv*).

Raw error is the difference between empirical properties and a model's mean predicted by Monte Carlo simulations (see Methods). We normalize raw errors by dividing them by the s.d. of the property's simulated distribution. As expected, an average of 95.8% (s.d. = 1.5, n = 202) of synthetic webs have properties

within 2 model s.d. of the model's mean, which makes normalized errors between −2 and 2 a good fit because they are within the model's expected range.

Figure 2 shows the overall performance of the three models. Generally, the niche model estimates the central tendency of the empirical data remarkably well. The average normalized error is 0.22, although the s.d. of 1.8 (expected value 1) illustrates greater variability in the empirical data than in the niche model[21] despite three distinct stochastic model components. The cascade model is over an order of magnitude worse, with an average normalized error of −3.0 and s.d. of 14.1. The random model's average of 27.1 and s.d. of 202 indicates an even worse fit. The niche model performs similarly across the different webs (Fig. 3) and consistently predicts individual properties across the group of webs more accurately than the other models (Fig. 4).

The random model's large errors show that simply matching an empirical web's *S* and *C* does little to account for empirical food-web properties except *Cannib*, which is surprisingly close to our null expectation. The cascade model improves over the random model for all properties except *Cannib* and closely estimates **T**, **I** and **B**, as suggested earlier[3] but previously untested against all seven webs. It
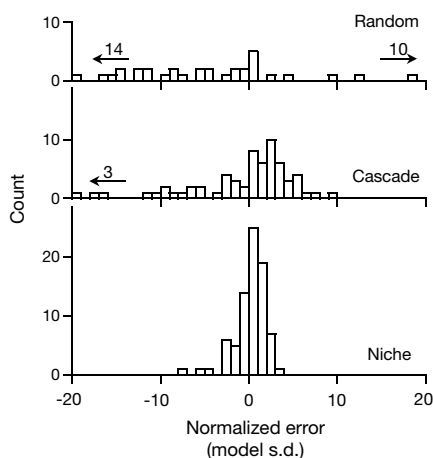

Figure 2 Distribution of normalized errors between empirical data and model means for all properties of the random, cascade and niche models. Arrows show the number of errors beyond the *x*-axis. Of the 56 random-model means (8 properties of 7 webs), 16% are within 2 model s.d. of the empirical data. Of the 66 cascade-model means (10 properties of 6 webs and 6 properties of one web), 27% are within this range. In contrast, 79% of 80 niche-model means (12 properties of 6 webs and 8 properties of one web) are within 2 model s.d. of the empirical data. Although attention to normalized-error magnitudes tends to reward models for increased variability, this tendency is kept in check by normalized-error s.d. < 1 that indicates excessive variability.
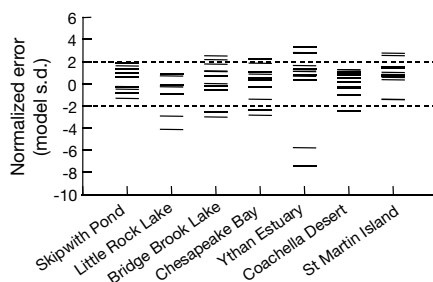

Figure 3 The niche model's normalized errors for each property of each food web. Errors are < 2 model s.d. for all properties of the Skipwith Pond web and most properties of the other webs.
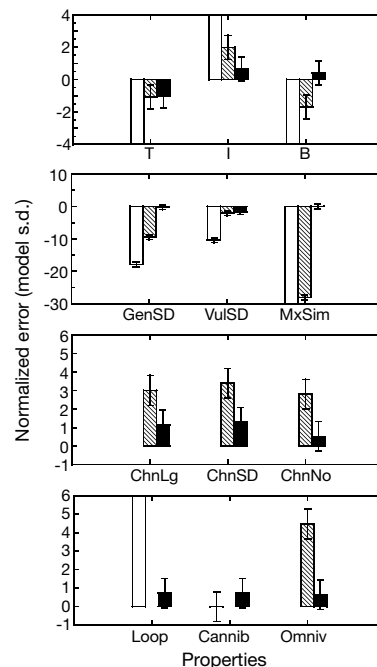

Figure 4 Mean normalized error of each property for each model averaged across the seven food webs (Table 1). The three models are indicated by open bars (random model), hatched bars (cascade model) and filled bars (niche model). Properties are described in the text. Ideally, the across-web sample average should not significantly differ from the model average of zero. Significant positive and negative average errors indicate that on average the model over- and underestimates empirical properties, respectively. Error bars show 95% confidence limits on the value of the mean assuming the empirical data are drawn from the model distribution and therefore have known population mean 0 and s.d. 1. The expected average of zero falls within the 95% confidence limits for only one property of the random model (*Cannib*), no properties of the cascade model, and eight properties of the niche model. Normalized errors do not directly correspond to raw errors because niche-model s.d. is twice as large (mean, 2.0; s.d., 0.84; n = 66) as cascade-model s.d. However, even in absolute terms, the magnitudes of the niche model's raw errors (Table 2) are roughly one-fifth (median 0.19, n = 77) of the raw errors of the random model and about one-quarter (median 0.27, n = 80) of the raw errors of the cascade model. In addition, the niche model has smaller average raw errors than the cascade model for all properties except *T* and smaller s.d. of those averages for 9 of 12 properties (see Supplementary Information). These findings show that the much greater accuracy and precision of the niche model's predictive abilities are robust to the distinction between normalized and raw errors.

also closely estimates *VulSD* but has quite large errors for other properties. The niche model improves over the cascade model for all 12 properties including *Cannib* and *Loop*, which invariably equal zero in cascade webs. This improvement is most dramatic for *MxSim*, which determines how quickly species are initially lumped in aggregation studies[17,19] and is poorly predicted by the cascade model[19].

The niche model's most significant errors may indicate problems with the data. For example, the model's underestimation of empirical variability may well be due to methodological inconsistencies among studies[21]. Also, the niche model's small but consistent overestimation of *ChnLg* and *ChnSD* (Fig. 4, Table 2) could be reduced by overcoming the well known bias against including parasites in food webs[2,22,23]. Underestimating *T* in the Ythan Estuary web by 5.8 model s.d. (Table 2) appears to result from the web's bias towards many 'top' bird species whose consumers were excluded[22]. Consequently, *I* and *B* are overestimated by 3.4 and 2.8 model s.d., respectively. The other 18 empirical observations of *T*, *I* and *B* are within 1.9 model s.d. except for two at −2.3 and −2.5. Bias towards top species with zero vulnerability inflates *VulSD* and explains the niche model's underestimation of the Ythan web's *VulSD* by 7.4 model s.d.

By definition, constraining all consumers to eat one contiguous interval within a fixed sequence of species causes the niche model to generate 'interval' webs[20]. However, larger empirical webs are rarely interval[3]. This discrepancy may be due to the delicacy of the intervality property. Among niche model webs with the same *S* and *C* as the seven empirical webs, intervality is broken by losing any one of almost half (mean, 41%) of the links in the webs. This suggests that we should devise a measure of the degree of intervality rather than considering intervality solely as a yes or no condition. We hypothesize that this degree is very high in empirical food webs.

A classic formulation of niche space[24] is of an '*n*-dimensional hyperspace' with *n* corresponding to innumerable ecological or environmental characteristics. An often-considered space that inspired our model is a species' feeding niche that restricts feeding to resources whose characteristics fall within a contiguous region of niche space[20,24–26]. Our results show that, with respect to food-web structure, community niche space is usefully collapsible to one dimension[20]. Whereas niche theory often infers repulsion of overlapping niches owing to interspecies competition[24,26], our model lacks such repulsion. Adding it or other modifications might improve the model's fit. The success for a model as simple as ours is very unexpected given the wide variety of aquatic and terrestrial food webs examined and the recently recognized complexity of their structure[5,7–10,14–19,21,25]. The niche model merits further testing against webs from other habitats that avoid biases such as those in the Ythan web.

As it stands, the niche dimension is an empirically successful model component that facilitates a relaxed hierarchy of trophic interactions among species ordered in one dimension. Future exploration may determine the dimension's meaning and measur-

ability in the field. Such work should focus on the relationship between the mechanics of the niche model and one or more physical, evolutionary, behavioural or other mechanisms responsible for species' trophic activities. Mechanisms related to body size should be explored[27,28], as should algorithms that order species in empirical food webs in their 'most interval' sequence. If applying such algorithms yields strongly phylogenetic orders, evolutionary mechanisms as opposed to more conventionally invoked ecological dynamics would be suggested[8,9,14]. Ordering algorithms would also help test the niche model's predictions, including: (1) empirical webs are close to interval; (2) species with similar niche values tend to share more predators than prey because close proximity on the niche dimension greatly increases the probability of being eaten by the same consumers while still allowing substantial differences in diet; and (3) species' niche values positively correlate with generality because species' niche ranges are products of these values (Fig. 1).

The niche model provides a benchmark for evaluating food webs as well as a structural framework to extend studies of link-strength distributions to systems larger than those previously examined[11–13]. Link strength may be highest and lowest, respectively, for prey species near the centre and ends of a species' niche range. Although our model lacks this and many other biological mechanisms, its empirical success indicates that exploring more of the model's predictions is warranted. For example, the general effects of losing functionally distinct species on ecological systems with different levels of *S* and *C* could be predicted by simulating species losses and observing how many other species lose all their resource or consumer species. Such observations could predict extirpations due to starvation and population increases due to predation release. Effects due to species' functional traits such as omnivory could be distinguished from effects more generally due to the number of species[29] by simulating all possible combinations of fixed numbers of species lost. Such analyses could greatly advance scientific understanding of the potentially catastrophic consequences of species loss for the complex ecological systems on which all organisms depend. □

Methods

Monte Carlo simulations generated 1,000 webs with the same *S* and within 3% of the same *C* as an empirical web. Three per cent represents a compromise between closely matching the *C* of the empirical web and inefficiently rejecting too many model webs to find one with the empirical *C*. Several properties of some webs could not be normalized or computed. The cascade model prohibits looping and cannibalism resulting in model s.d. = 0 and raw errors that cannot be normalized. When normalized errors are discussed, these properties of the cascade model are excluded. In many random webs, *B* = 0 eliminates meaningful food-chain and omnivory properties. High *ChnLg* and *Loop* in random webs with *B* >0 make their computation impracticable. Little Rock Lake has too many chains to compute *Omniv* or food-chain properties in a reasonable length of time for any of the models[17].

1. May, R. M. How many species are there on earth? *Science* **241**, 1441–1449 (1988).
2. Lawton, J. H. in *Ecological Concepts* (ed. Cherrett, J. M.) 43–78 (Blackwell Scientific, Oxford, 1989).
3. Cohen, J. E., Briand, F. & Newman, C. M. *Community Food Webs: Data and Theory* (Biomathematics Vol. 20) (Springer, Berlin, 1990).

Table 2 Comparison of empirically observed properties with niche-model means

Property	Skipwith Pond	Little Rock Lake	Bridge Brook Lake	Chesapeake Bay	Ythan Estuary	Coachella Desert	St Martin Island
T	0.040 (0.030)	0.011 (0.043)	0 (0.081)	0.32* (0.14)	0.37† (0.073)	0 (0.029)	0.17 (0.078)
I	0.92 (0.88)	0.86 (0.85)	0.68 (0.75)	0.52 (0.59)	0.54† (0.74)	0.90 (0.88)	0.69 (0.75)
B	0.040 (0.095)	0.13 (0.11)	0.32* (0.17)	0.16 (0.27)	0.090* (0.19)	0.10 (0.089)	0.14 (0.17)
GenSD	0.92 (0.81)	1.42† (1.08)	1.09 (1.02)	0.78* (1.13)	1.14 (1.18)	0.73 (0.82)	1.02 (1.09)
VulSD	0.54 (0.51)	0.61 (0.58)	0.61 (0.61)	1.12* (0.72)	1.41† (0.65)	0.60 (0.51)	0.78 (0.62)
MxSim	0.76 (0.75)	0.75* (0.69)	0.74* (0.62)	0.50 (0.49)	0.52* (0.59)	0.72 (0.76)	0.54* (0.62)
ChnLg	6.22 (7.30)		4.04 (5.75)	3.99 (4.23)	5.91 (7.37)	6.69 (7.92)	5.20 (6.73)
ChnSD	1.43 (1.56)		0.93* (1.48)	1.20 (1.34)	1.46 (1.87)	1.45 (1.63)	1.30 (1.67)
ChnNo	3.71 (4.09)		2.85 (3.10)	2.37 (2.31)	4.03 (4.36)	4.31 (4.60)	3.52 (3.86)
Loop	0.40 (0.69)	0.33 (0.47)	0.32 (0.27)	0 (0.030)	0 (0.098)	0.62 (0.73)	0 (0.21)
Cannib	0.32 (0.46)	0.14 (0.14)	0.12 (0.21)	0.032 (0.082)	0.038 (0.069)	0.66* (0.45)	0* (0.13)
Omniv	0.60 (0.75)		0.40* (0.60)	0.52 (0.41)	0.54 (0.60)	0.76 (0.77)	0.60 (0.62)

Niche-model means are in parentheses. See text for property descriptions. See Supplementary Information for complete results for all three models.
* Normalized errors between 2 and 3 model s.d.
† Normalized errors >3 model s.c.

4. Pimm, S. L., Lawton, J. H. & Cohen, J. E. Food web patterns and their consequences. *Nature* **350**, 669–674 (1991).

5. Polis, G. A. Complex desert food webs: an empirical critique of food web theory. *Am. Nat.* **138**, 123–155 (1991).

6. Havens, K. Scale and structure in natural food webs. *Science* **257**, 1107–1109 (1992).

7. Martinez, N. D. Effects of scale on food web structure. *Science* **260**, 242–243 (1993).

8. Martinez, N. D. Scale-dependent constraints on food-web structure. *Am. Nat.* **144**, 935–953 (1994).

9. Lawton, J. H. Webbing and WIWACS. *Oikos* **72**, 305–306 (1995).

10. Polis, G. A. & Winemiller, K. (Eds) *Food Webs: Integration of Patterns and Dynamics* (Chapman and Hall, New York, 1996).

11. deRuiter, P. C., Neutel, A-M & Moore, J. C. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260 (1995).

12. McCann, K., Hastings, A. & Huxel, G. R. Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798 (1998).

13. Berlow, E. L. Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334 (1999).

14. Schoener, T. W. Food webs from the small to the large. *Ecology* **70**, 1559–1589 (1989).

15. Warren, P. H. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* **55**, 299–311 (1989).

16. Hall, S. J. & Raffaelli, D. Food-web patterns: lessons from a species-rich web. *J. Anim. Ecol.* **60**, 823–842 (1991).

17. Martinez, N. D. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monog.* **61**, 367–392 (1991).

18. Goldwasser, L. & Roughgarden, J. Construction of a large Caribbean food web. *Ecology* **74**, 1216–1233 (1993).

19. Solow, A. R. & Beet, A. R. On lumping species in food webs. *Ecology* **79**, 2013–2018 (1998).

20. Cohen, J. E. *Food Webs and Niche Space* (Princeton Univ. Press, Princeton, 1978).

21. Murtaugh, P. A. & Kollath, J. P. Variation of trophic fractions and connectance in food webs. *Ecology* **78**, 1382–1287 (1997).

22. Huxman, M., Raffaelli, D. & Pike, A. Parasites and food web patterns. *J. Anim. Ecol.* **64**, 168–176 (1995).

23. Marcogliese, D. J. & Cone, D. K. Food webs: A plea for parasites. *Trends Ecol. Evol.* **12**, 320–325 (1997).

24. Hutchinson, G. E. Concluding remarks. Population studies: Animal ecology and demography. *Cold Spring Harbor Symp. Quant. Biol.* **22**, 415–427 (1957).

25. Warren, P. H. in *Aspects of the Genesis and Maintenance of Biological Diversity* (eds Hochberg, M. E., Clobert, J. & Barbault, R.) 142–161 (Oxford Univ. Press, New York, 1996).

26. Begon, M., Harper, J. L. & Townsend, C. R. *Ecology: Individuals, Populations, and Communities* 3rd edn (Blackwell Science, Oxford, 1996).

27. Warren, P. H. & Lawton, J. H. Invertebrate predator–prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* **74**, 231–235 (1987).

28. Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldana, J. Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* **62**, 67–78 (1993).

29. Symstad, A. J., Tilman, D., Willson, J. & Knops, J. M. H. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* **81**, 389–397 (1998).

30. Baird D. & Ulanowicz, R. E. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* **59**, 329–364 (1989).

....

Inhibitory threshold for critical-period activation in primary visual cortex

Michela Fagiolini & Takao K. Hensch

Laboratory for Neuronal Circuit Development, Brain Science Institute RIKEN, 2-1 Hirosawa, Wako-shi, Saitama 351-0198, Japan

....

Neuronal circuits across several systems display remarkable plasticity to sensory input during postnatal development[1–10]. Experience-dependent refinements are often restricted to well-defined critical periods in early life, but how these are established remains mostly unknown. A representative example is the loss of responsiveness in neocortex to an eye deprived of vision[2–6]. Here we show that the potential for plasticity is retained throughout life until an inhibitory threshold is attained. In mice of all ages lacking an isoform of GABA (γ-aminobutyric acid) synthetic enzyme (GAD65), as well as in immature wild-type animals before the onset of their natural critical period, benzodiazepines selectively reduced a prolonged discharge phenotype to unmask plasticity. Enhancing GABA-mediated transmission early in life rendered mutant animals insensitive to monocular deprivation as adults, similar to normal wild-type mice. Short-term presynaptic dynamics reflected a synaptic reorganization in GAD65 knockout mice after chronic diazepam treatment. A threshold level of inhibition within the visual cortex may thus trigger, once in life, an experience-dependent critical period for circuit consolidation, which may otherwise lie dormant.

The term 'critical period' refers to a cascade of functional and anatomical events in the brain, which ultimately consolidate synaptic connections into their final wiring patterns. Once activated within visual cortex, this machinery bestows a transient sensitivity to brief monocular deprivation, which is very low just after eye opening, peaks around four weeks, and rapidly declines over the next days (rats[4]; mice[5], Fig. 1b) or weeks (cat[2]; monkey[3]; human[6]). The critical period, however, is not a simple age-dependent maturational process, but is rather a series of events itself controlled in a
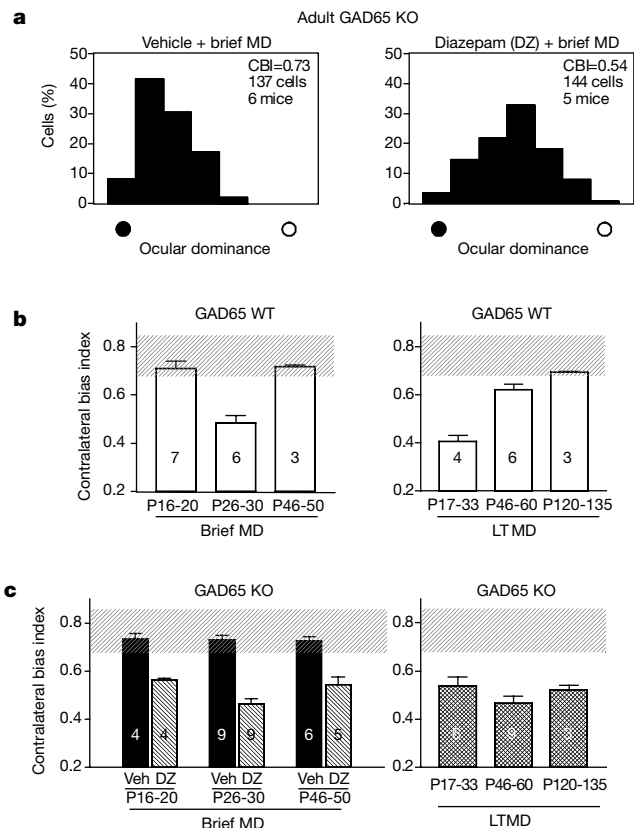

Figure 1 GAD65 knockout (KO) mice can express experience-dependent plasticity throughout life. **a**, Adult knockout mice exhibit ocular dominance shifts (diazepam versus vehicle, $P < 0.0001$, χ^2 test). **b**, Left, wild-type (WT) mice display a critical period. Brief monocular deprivation (MD) induces a significant CBI reduction only at ~P26. CBI indicates distribution bias in favour of contralateral eye (P26–30 versus non-deprived, CBI = 0.77 ± 0.02, 6 mice, $P < 0.0001$, t-test). Right, LTMD is strongly effective only early in life. Little or no effect is detected after P45 or P120 (P17–33 versus non-deprived, $P < 0.0001$, t-test). **c**, Left, brief monocular deprivation with diazepam (DZ) infusion induces plasticity of similar strength across ages in knockout mice ($P < 0.001$ within each group, t-test). Right, LTMD is similarly effective throughout life (each group versus non-deprived, CBI = 0.77 ± 0.03, 5 mice, $P < 0.0001$, t-test). Shaded region, range of non-deprived mice. The number of animals is indicated per group.